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The flowerpiercers interactions with a community of high Andean plants

Jairo Andrés Cuta-Pineda[1,2]*, Luis Alejandro Arias-Sosa[1]* and Roxibell C. Pelayo[3]

Abstract

Background: Flowerpiercers (*Diglossa*) are traditionally considered as "parasites" of the pollination processes, as they can access the nectar without entering in contact with the reproductive structures of the plants. Nevertheless, the effect of flowerpiercers seems to vary according to their behavior and the flower's traits. So, in this work, we aimed to explore the floral characteristics that may determine the susceptibility to robbing and pollen transport by flowerpiercers. Also, we identified the potential types of interactions and studied interaction network properties.

Methods: We collected the information of 16 ornithophilic plants regarding their floral traits and robbing frequency. Also, we captured 4 species of flowerpiercers and evaluated pollen transport (frequency and loads). We tested the correlation between floral traits, robbing frequency, and pollen transportation. Later, we used these variables in a cluster and principal component analyses to identify the potential types of interactions. Finally, we analyzed and compared the structure of the plants-flowerpiercers interaction network.

Results: Nectar production significantly influenced both nectar robbing and pollen transportation. While the corolla length was only correlated to the robbing susceptibility. Also, we found that particular flowerpiercers species transported higher loads of some plant pollen, which can be related to the differences in behavior and morphometric traits. We proposed the classification of five different types of plant-flowerpiercer interactions, that showed different potential mutualist or antagonist relations based on the affectation of nectar robbing and the service of pollen transportation. The interaction networks consisted of 49 links, with 2.4 links per species, and presented indicators of a medium to high resilience, stability, and resistance (nestedness, connectance, and robustness). Also, the network presented medium to low specialization and substantial niche overlap.

Conclusions: The ecological role of the flowerpiercers goes beyond its classic assignation as "parasites" as they can actively transport pollen of several Andean plants, affecting its evolutionary history and the stability of the systems.

Keywords: *Diglossa*, Flower traits, Nectar robbing, Nectivorous birds, Pollen transport, Pollination

Background

The process of pollination is a crucial step in plant reproduction that influences its genetic variability, and therefore its adaptation capacity and diversification; likewise, the nectar and other rewards are an essential resource for the animal communities (Kearns et al. 1998; Rojas-Nossa

2005; Johnson 2010). Thus, it is one of the most critical animals–plant mutualistic interactions, especially in the tropics, where about 94% of the angiosperms are animal-pollinated (Ollerton et al. 2011). Nevertheless, these resources also attract nectar robbers, that extract the resource without making contact with the reproductive structures (anthers and stigma) avoiding pollination (Irwin et al. 2010). The nectar robbing can negatively affect the plant's reproductive success, restricting the visit of legitimate pollinators and reducing the production of fruits and seeds (Roubik 1982; Irwin and Brody

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1998). However, in some cases, nectar robbers can engage mutualist interaction acting as effective pollinators depending on the robbers' behavior and flower/inflorescence characteristics (Graves 1982; Navarro 2000).

Although insects are the primary pollinators, birds play an essential role, with about 65 flowering plant families presenting ornithophily syndrome (Cronk and Ojeda 2008). Likewise, the majority of research regarding nectar robbing is focused on insects (especially in bumblebees), while this phenomenon in birds has been little studied (Irwin et al. 2010). In the Andes, the main nectarivorous birds correspond to hummingbirds (Trochilidae) and flowerpiercers (*Diglossa*), being the hummingbirds more specialized in legitimate pollination. While flowerpiercers mainly access the resource by nectar robbing (Stiles 1981; Schondube and del Rio 2003; Fleming and Muchhala 2008). The flowerpiercers present a peak with an enlarged curved hook that allows them to perforate the corolla of tubular flowers and rob the nectar, being the more specialized nectar-feeding passerines (Schondube and del Rio 2003, 2004).

Although the flowerpiercers specialized in nectar robbing, a previous study showed that they could legitimately access the nectar in 24–50% of the visits, and they transported a high amount of pollen, even more than some hummingbirds (Rojas-Nossa 2007). Likewise, there are other reports of plants with short and open corollas that seem to be regularly and consistently pollinated by flowerpiercers (Stiles et al. 1992; Villareal 2014). Thus, this group of birds appears to be exciting models of study that presented both mutualistic and antagonist animal-plant interactions, and its ecological role needs to be further study.

Nectar robbing has been associated with specific plant and animal characteristics, mainly morphological features. Previous research found that flowers with long corollas and larger nectar glands were more susceptible to nectar robbing (Castro et al. 2009; Navarro and Medel 2009; Rojas-Nossa 2013). A relation that has been proposed as a negative selective pressure that balances the selection of longer corollas (Castro et al. 2009; Navarro and Medel 2009). Likewise, the morphology of flowerpiercers could influence the type of interaction, as species with larger beaks tend to make more legitimate visits (Rojas-Nossa 2007).

Currently, network analysis is one of the most popular tools to study the animal-plant interactions and their potential ecological implications (Memmott 2009). A strategy that has been widely used in the research of pollination service across different landscapes (Campbell et al. 2011; Ballantyne et al. 2015; Hu et al. 2019; Willcox et al. 2019). However, the role of nectar robbers on the ecological networks has been little studied (Maruyama

et al. 2015). Further, the interactions of nectar robbers are usually removed from the networks, which can lead to important changes in the network properties (Gonzalez and Loiselle 2016).

We evaluated the different characteristics associated with nectar robbing and pollen transport by a community of flowerpiercers in an Andean forest. We aimed to study how flower traits influenced the incidence of nectar robbing or the transportation of pollen. Also, we proposed the classification of five potential types of interactions that improved the understanding of the ecological roles that these groups of birds could play. Finally, we analyzed the structure of the network of plants/flowerpiercers.

Methods

Study area

We developed the research in the Natural Park "El Sinaí" in the municipality of Pachavita (Boyacá state) in a fragment of a Hight Andean Rainforest, between 2500 and 2700 m asl. In the zone, there was a unimodal rain period, with a rainy season from May to August and a dry period from December to March (IDEAM 2016).

To obtain representative data, we implemented four field data collection of eight days each. We made two of them during the rainy season in July 2015 and August 2016, and two during the dry season in February and March 2016.

Evaluation of the floral traits and nectar robbing

We set three linear transects of 200 m long and 5 m wide on each side, placed them in locations with a high number of flowering plants to established the species that could be used as a resource for the flowerpiercers (Chapman et al. 1994). In each transect, we marked all plants with characteristics of the ornithophilic syndrome; in the case of epiphytes, we marked the tree or shrub (Parada-Quintero et al. 2012). We collected two or three specimens per species for subsequent identification in the laboratory.

To estimate the nectar robbing frequency of the plant species, we counted the number of flowers of each species. In the case of species with more than 200 flowers, we quantified the total flowers on one branch, and we extrapolated the total number according to the number of branches per individual (Parada-Quintero et al. 2012). Simultaneously, we counted the number of flowers with nectar robbing according to the distinctive marks left by the flowerpiercers and established the nectar robbing frequency calculated as $\frac{\text{Number of flowers with robbing marks of each species}}{\text{Total number of flowers of each species}}$ (Rojas-Nossa 2007).

We measured the effective corolla length, corolla diameter, nectar production (nectar volume), and sugar

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concentration as potential variables that affect the rates of nectar robbing and pollen transportation (Rojas-Nossa 2007). We bagged the flowers for 24 h to evaluate the nectar volume and sugar concentration. We measured the level of sugars in the nectar by using a refractometer (Brix 0–32, Aichose). We calculated the volume of nectar using microcapillaries of different sizes (5, 10, and 15 μL) depending on the flower dimensions.

Also, we took the qualitative characteristics of the flowers: color, presence of protective structures, and plant growth habits. The last variable was classified in one of the five forms of growth: tree, shrub, climber or vines, terrestrial, and epiphytic.

We collected pollen samples from mature anthers of the plants to establish a reference catalog. In the laboratory, we characterized the morphology of the pollen and took reference photographs with a scanning electron microscope and optical microscope.

Evaluation of the morphological traits and pollen transportation in the flowerpiercers

To study the flowerpiercers morphology and capacity to transport pollen, we placed nine mist nets of 12×3 m. The nets were active from 5:30–11:00 to 14:00–17:30 h during four and a half days (in each of the four field data collection trips) to a total of 1458 h/net. We weighed each captured individual and measured the total culmen, exposed culmen, beak width, and height. We marked the captured individuals to avoid pseudoreplication.

Also, we sampled each captured bird individually to identify whether they were transporting pollen. We used glycerin jelly stained with fuchsine to collect pollen samples presented in the body, throat, and head of the birds (Roitman et al. 1997; Traveset et al. 2015). Later, we placed the cubes on microscope slides and melted them with a controlled heat source to obtain a layer of colored pollen grains (Traveset et al. 2015). These slides were evaluated by microscopy to identify the pollen using the previously established reference catalog, and we quantified the pollen loads. Using these data, we estimate two variables:

1) The pollen frequency: measured as $\frac{\text{the number of samples positive for pollen presence}}{\text{total number of samples}}$. This variable was measured for each flowerpiercer and plant species.
2) Pollen loads: The number of pollen grains of each plant species presented in the flowerpiercer sampled.

We chose to evaluate pollen transportation instead of flower visitation because it is a more informative indicator of probable pollination and the functional role of the animals in pollination networks (Popic et al. 2013).

Statistical analysis

We used the R 3.3.6 free software and R-Commander package with a $p < 0.05$ as a significant threshold. First, we studied the relation between the floral traits and the susceptibility of the plants to nectar robbing and pollen transportation. We evaluated the normality of the data by the Kolmogorov Smirnov test to determine the appropriate data treatment. As the variables were normally distributed, we used parametric tests of Pearson correlation to evaluate if the effective corolla length, corolla diameter, nectar volume, and sugar concentration were correlated to the response variables: robbing frequency, pollen frequency, and pollen loads. For the qualitative flower traits (color, presence of protective structures, and plant growth habit), we used the ANOVA test to evaluate if there were differences in the three response variables.

Later, we assessed if the flowerpiercer species presented different capacities in the transportation of pollen and its morphometric traits. To achieve this, we used the ANOVA test to study if there were significant differences in the weigh and beak length across flowerpiercers species. We used the Kruskal Wallis test to analyze differences in pollen loads because this variable across species was non-normally distributed.

To better understand the flowerpiercer-plant interaction, we implemented a cluster analysis using the three response variables, and the floral traits found significantly correlated in the univariate analysis. To make these variables comparable, we transformed them by *z*-score methodology $\left(\frac{x - \text{mean}}{\text{Standard deviation}} \right)$.

Finally, we implemented a multivariate principal component analysis (PCA) with the same variables as the cluster analysis. The first two axis of PCA were used in scatter plot to see potential aggrupation. Analyzing the cluster and PCA plotting results, we proposed five different types of interactions associated with flowerpiercers visits. We based this classification on the possible reciprocal effect of the interaction (mutualistic or antagonist) and the way the flowerpiercer access the nectar (legitimate visit or nectar robbing).

Network analysis

We used R software and bipartite package to get the interaction networks of the plant-flowerpiercers. The network analysis was implemented only with the mutualistic interactions (pollen transportation). We did not include data of antagonism interaction (robbing frequency) because we could not take this information for each flowerpiercer species using our methodological approach. We generated two quantitative pollen-transport networks (Dormann et al. 2008, 2009) using the pollen frequency and pollen loads as estimators of interaction strength

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(Tur et al. 2014). The evaluation of pollen loads has been described as a good indicator of animal foraging patterns and probable pollination in bipartite network analysis (Popic et al. 2013; Tur et al. 2014). We implemented a flowerpiercer-plant interaction rarefaction analysis using the CHAO 1, Jackknife 1, ACE, and Bootstrap index in the free software Estimate 9.1.

We measured the network properties: (1) Number of links, number of plants-flowerpiercers interactions; (2) Links per species, this metric indicates the mean number of interactions that each plant or flowerpiercer species had. It is related to the complexity of the system and resilience to species loss (Montoya et al. 2006; Gresty et al. 2018); (3) Connectance, it is the number of possible links in the network (Gresty et al. 2018). In range to 0–1, with values close to 0 related to poor connectance and close to 1 with higher connectance. Higher levels are related to better stability and resilience to perturbance of the systems (Baumgartner 2020); (4) Specialization (*H*2), it ranges from 0–1, being 0 a perfect generalist network and 1 a perfect specialist one. It reflects the degree of specialization at the community and network level. It is an adequate metric for quantitative data, and elevate values indicate a higher selectivity of the species in the network (Willcox et al. 2019); (5) Nestedness by weighted NODF, it ranges from 0 to 100, being 100 a perfectly neatened network. The NODF methodology is more appropriate for quantitative data and less susceptible to type I errors (Almeida-Neto et al. 2008). Nestedness is related to the diversity, stability, and resilience of the ecosystems (Saavedra et al. 2016; Cantor et al. 2017; Valverde et al. 2018; Baumgartner 2020); (6) Niche overlap, it is a metric that can reflect the potential coexistence or competition for resources in the system (Kuhnen et al. 2017). It ranges between 0 (no overlap, all species use a different resource) and 1 (complete overlap, all species use the same resources).

For each of the network metrics, we compare if the observed value was significantly different from those expected by random interactions using null models ($N = 1000$) (Dormann et al. 2008). To generate the null models we used the Patefield algorithm that maintain the network marginal totals obtained in the observed original network. Also to assess the stability of the network we calculated the robustness index. This index assess if the network is robust or fragile to the loss of species by calculating the area below the extinction curve ($N = 1000$) (Memmott et al. 2004; Burgos et al. 2007). It ranges from 0 to 1, being higher values associated with robust systems where the extinction curve has a small decrease. In other words, removal of several pollinator species has a mild effect on the survival of plant species (or vice-versa). While lower values are related to fragile systems where

the removal of any pollinator leads to the extinction of several plant species (or vice-versa).

Also, we evaluated the importance of each plant and flowerpiercer by measure the normalized degree that refers to the number of interactions of plant's species with pollinator taxa or vice versa. The normalized degree is the degree divided by the possible interactions, and it ranges between 0 and 1 (Stewart et al. 2018; Adedoja et al. 2019). It means that a plant with a value of 1 interacts with all pollinators, while a plant with a value close to 0 interacts with few pollinators. Species with a higher normalized degree are more relevant to maintain the network robustness and have a more generalist behavior (Stewart et al. 2018).

Results

Flowerpiercers and ornithophilic plants richness

We captured 123 individuals of 4 flowerpiercers species: 60 of White-sided Flowerpiercer (*Diglossa albilatera*), 34 of Masked Flowerpiercer (*D. cyanea*), 27 of Bluish Flowerpiercer (*D. caerulescens*), and 2 of Black Flowerpiercer (*D. humeralis*).

We found 16 species of ornithophilic plants in bloom. The most representative family was Ericaceae with seven species (*Cavendishia bracteata, Disterigma alaternoides, Gaultheria anastomosans, Gaultheria erecta, Macleania rupestris, Psamisia* sp., and *Sphyrospermum* sp.), followed by Campanulaceae with two species (*Siphocampylus scandens* and *Siphocampylus* sp.), Gentianaceae with two species (*Macrocarpaea* sp. and *Symbolanthus* sp.) and Rubiaceae with two species (*Palicourea angustifolia* and *Palicourea aschersonianoides*). The other families only presented one species: Alstroemeriaceae (*Bomarea* sp.), Gesneriaceae (*Columnea strigosa*), and Melastomataceae (*Axinaea scutigera*).

The most abundant species was *Disterigma alaternoides* (26.69%), followed by *Symbolanthus* sp. (18.44%), *Gaultheria erecta* (13.1%), and *Columnea strigosa* (9.46%). The relative abundance of *A. scutigera* could not be adequately measured as most of the individuals were in areas of difficult access. The characteristic of the plant studied is presented in Table 1.

Flowers characteristics associated with nectar robbing and pollen transportation by flowerpiercers

The nectar robbing rate varied from 0 to 100% among the different species of plants. The effective corolla length and nectar volume were moderate to strong positive correlated to nectar robbing ($r = 0.56$, $p < 0.05$ and $r = 0.79$, $p < 0.001$, respectively). Thus, the morphological mismatch and nectar production seems to influence the preference for nectar robbing.

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Table 1 Traits of the ornithophilic plants evaluated

Ornithophilic plants	Effective corolla length (mm)	Nectar volume (µL)	Sugar concentration (%)	Corolla diameter (mm)	Relative abundance (%)	Nectar robbing frequency (%)	Pollen load (number of grains)	Pollen frequency (%)
Axinaea scutigera	12.5 (± 1.5)	–	–	13.4 (± 0.9)	–	0	13344	56.1
Bomarea sp.	24.2 (± 0.7)	5.1 (± 3.9)	17.01 (± 3.3)	10.57 (± 2.6)	0.99	0	39	19.51
Cavendishia bracteata	17.68 (± 1.4)	5.42 (± 4.3)	18.79 (± 2.0)	2.81 (± 0.3)	2.72	35.47	640	15.45
Siphocampylus scandens	35.28 (± 5.1)	30.54 (± 77.9)	14. 82 (± 2.6)	4.9 (± 1.0)	3.22	52.25	700	62.6
Siphocampylus sp.	32.77 (± 2.8)	71.80 (± 75.2)	16.68 (± 0.9)	6.17 (± 0.7)	1.49	100	1265	45.53
Columnea strigosa	31.22 (± 5.2)	8.17 (± 8.8)	8.83 (± 4.0)	13.26 (± 1.9)	9.65	0	112	4.07
Disterigma alaternoides	6.20 (± 0.4)	0.18 (± 0.0)	11.15 (± 4.0)	2.60 (± 0.7)	27.23	0	619	33.33
Gaultheria anastomosans	6.25 (± 0.6)	0.4 (± 0.3)	20.46 (± 8.0)	2.07 (± 0.4)	5.45	0	17	4.88
Gaultheria erecta	7.42 (± 0.5)	0.68 (± 0.5)	14.60 (± 1.7)	1.54 (± 0.4)	13.37	9.95	35	13.01
Macleania rupestris	16.85 (± 1.3)	15.22 (± 19.2)	16.60 (± 3.9)	3.35 (± 0.8)	2.72	14.29	456	17.89
Macrocarpaea sp.	52.23 (± 1.9)	39.40 (± 22.5)	11.07 (± 0.1)	14.10 (± 0.8)	1.73	80	159	1.63
Palicourea angustifolia	8.74 (± 1.1)	2.71 (± 4.3)	23.12 (± 8.4)	3.96 (± 0.8)	0.74	32.96	16	8.94
Palicourea aschersonianoides	18.19 (± 2.7)	9.68 (± 9.8)	24.25 (± 23.7)	3.61 (± 0.6)	6.44	61.03	44	11.38
Psamisia sp.	21.8 (± 0)	23.86 (± 0.3)	23.4 (± 0.2)	4.1 (± 0.4)	0.99	42.22	45	16.26
Sphyrospermum sp.	9.23 (± 1.5)	1.50 (± 2.6)	15.08 (± 6.5)	1.48 (± 0.3)	4.7	44.55	100	19.51
Symbolanthus sp.	57.65 (± 7.5)	11.57 (± 7.1)	18.94 (± 6.8)	8.65 (± 1.8)	18.56	51.33	9	5.69

Regarding pollen transportation, only the nectar volume was significantly correlated to the pollen frequency ($r = 0.6$, $p < 0.001$) and marginally significant correlated to pollen loads ($r = 0.45$, $p = 0.08$). Thus, nectar production is the leading floral trait that attracts flowerpiercers in nectar robbing and legitimate visits.

The other quantitative variables were not significantly correlated to response variables ($p > 0.05$). Likewise, none of the qualitative variables presented significant differences ($p > 0.05$) in nectar robbing frequency, pollen frequency, or pollen loads. So, these variables were not taking into account in the multivariate analysis.

Differences in flowerpiercers morphology and pollen loads

All morphological traits varied significantly among flowerpiercers species ($p < 0.05$). *D. albilatera* was smaller and with a shorter beak, while *D. cyanea* and *D. caerulescens* were bigger and with longer beaks. As we only captured two individuals of *D. humeralis*, we did not include them in the analysis.

The pollen loads of the 4 plants presented differences across the flowerpiercer species. *D. caerulescens* and *D. cyanea* transported the majority of pollen of *Axinaea scutigera* ($p < 0.001$). For *Cavendishia bracteata* and *Columnea strigosa* pollen loads were higher in *D. caerulescens* ($p < 0.05$), while *D. albilatera* transported the higher pollen loads of *Gaultheria erecta* ($p < 0.05$).

Identification of the plant-flowerpiercer types of interactions

Considering our univariate analysis, we used the nectar robbing frequency, pollen frequency, pollen load, corolla length, and nectar volume variables in cluster analysis. The result of this test identified five major groups of plant-flowerpiercer interactions (Fig. 1).

We named the first cluster "Mutualistic legitimate visits". It consisted of plants with absent or very low nectar
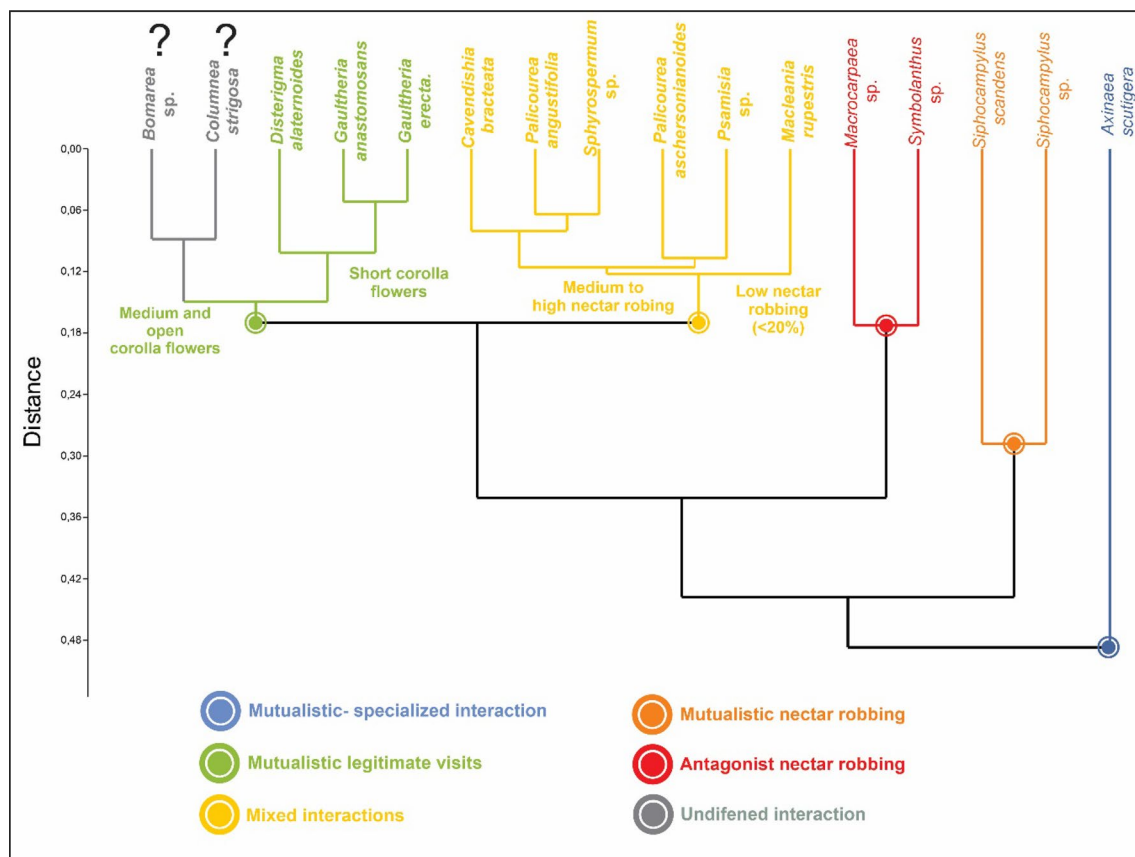
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Fig. 1 Flowerpiercer-plant interaction cluster analysis. We use the nectar robbing frequency and pollen transportation (frequency and loads) with the flower traits of corolla length and nectar volume to group ornithophilic plant species according to its potential interaction with the flowerpiercers

robbing (< 10%). Inside this cluster was a subdivision of plants with short corollas that are likely to get legitimate visits. In this case, the flowerpiercer took the flower by its natural opening using its maxilla and introduced its lower jaw and tongue to get the nectar entering in contact with the reproductive structures (Fig. 2).

The other subdivision corresponded to flowers with longer and open corollas. In the case of *Bomarea* sp*.,* the flowerpiercers can access the nectar by introducing their head entering in contact with the reproductive structures. Still, the pollen loads were too low, making it difficult to define the type of interaction accurately. In the case of *Columnea strigosa*, we considered that its classification is uncertain as it presented a too long corolla (> 30 mm), which makes it difficult to the legitimate visits. Also, it showed low pollen frequency (< 5%), which could adhere to the flowerpiercers incidentally or secondarily.

The second cluster was named "Mixed interactions". In this case, the plants are likely to receive both legitimate visits and nectar robbing. The flowers within this interaction presented small to medium corollas that are accessible to legitimate visits. It is difficult to say if the interaction is negative or positive and probably depends on the frequency of each type of visit and the specific characteristic of each plant species. For example, *Macleania rupestris* presented a lower incidence of nectar robbing (14.2%), while *Palicourea aschersonianoides* was profoundly affected by this phenomenon (61%), so, the final effect on plant fitness may differ.

The third cluster was named "Antagonist nectar robbing" as the plant presented a high affectation of nectar robbing, corollas too long to be legitime visit, and low pollen transportation. These plants represented the classic view of parasitic plant-flowerpiercer interaction, in which the flowers lost the reward resources (nectar) and got exposed to potential damage risk without the compensative pollination role.

The fourth cluster was named "Mutualistic nectar robbing" as the flowers were profoundly affected by nectar robbing and presented long corollas that did not allow legitimate visits. But the pollen frequency and loads were
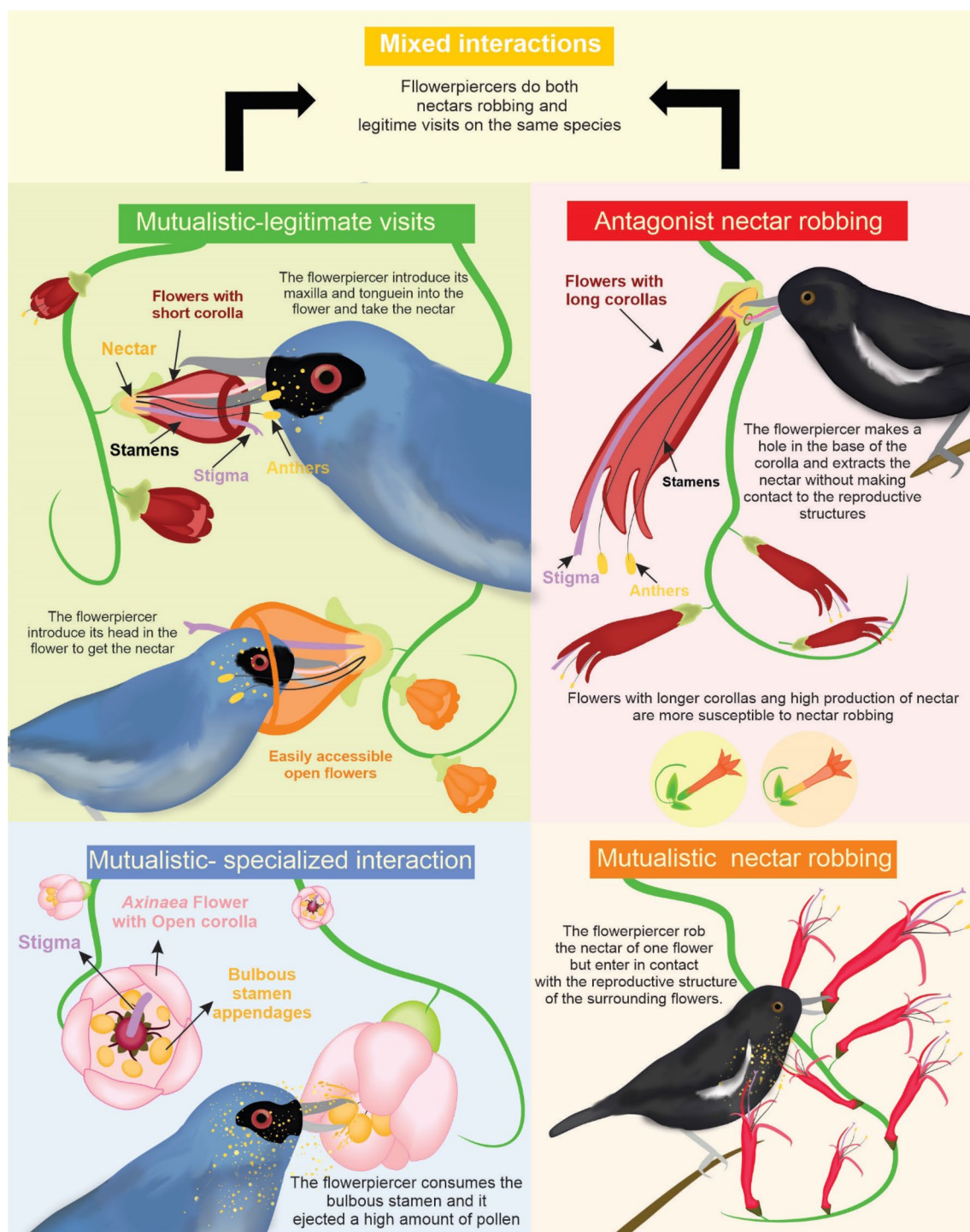
Fig. 2 Illustrative model of the flowerpiercers-flower types of interactions. We show how the *Diglossas* interact and manipulate the flowers based on its characteristics and how this can lead to nectar robbing or pollen transportation

notoriously high. In this case, although it is evident that flowerpiercers accessed the resource only and frequently by nectar robbing, they served as important pollen vectors and potential pollinators. Further, the pollen frequency and loads of this group were higher than in flowers with legitimate visits. This interaction seems to be

influenced by the spatial arrangement of the *Siphocampylus* inflorescences. Because its flowers are directed upward and grouped in a way that its reproductive structures can enter in contact with the flowerpiercers while robbing the nectar of the neighbor flower.

The last cluster corresponds to a single species (*Axinaea scutigera*). We named it "Specialized mutualistic interaction." This plant presented no nectar robbing, a high pollen frequency, and far superior pollen loads (more than ten times higher than the other species). *A. scutigera* did not use nectar as a reward, but bulbous stamen appendages similar to fruits. Thus, this plant uses a strategy independent of the corolla length and nectar production that leads to very effective pollen transportation and potential pollination by the flowerpiercers.

In the PCA analysis, the two first axis explained 81% of the variance. The PCA1 was positively loaded with nectar volume (0.52), corolla length (0.54), and nectar robbing frequency (0.59), while it loaded negative to pollen frequency (−0.27) and load (−0.08). The PCA2 was positively loaded with nectar volume (0.31), corolla length (0.073) and nectar robbing frequency (0.03), pollen fre-
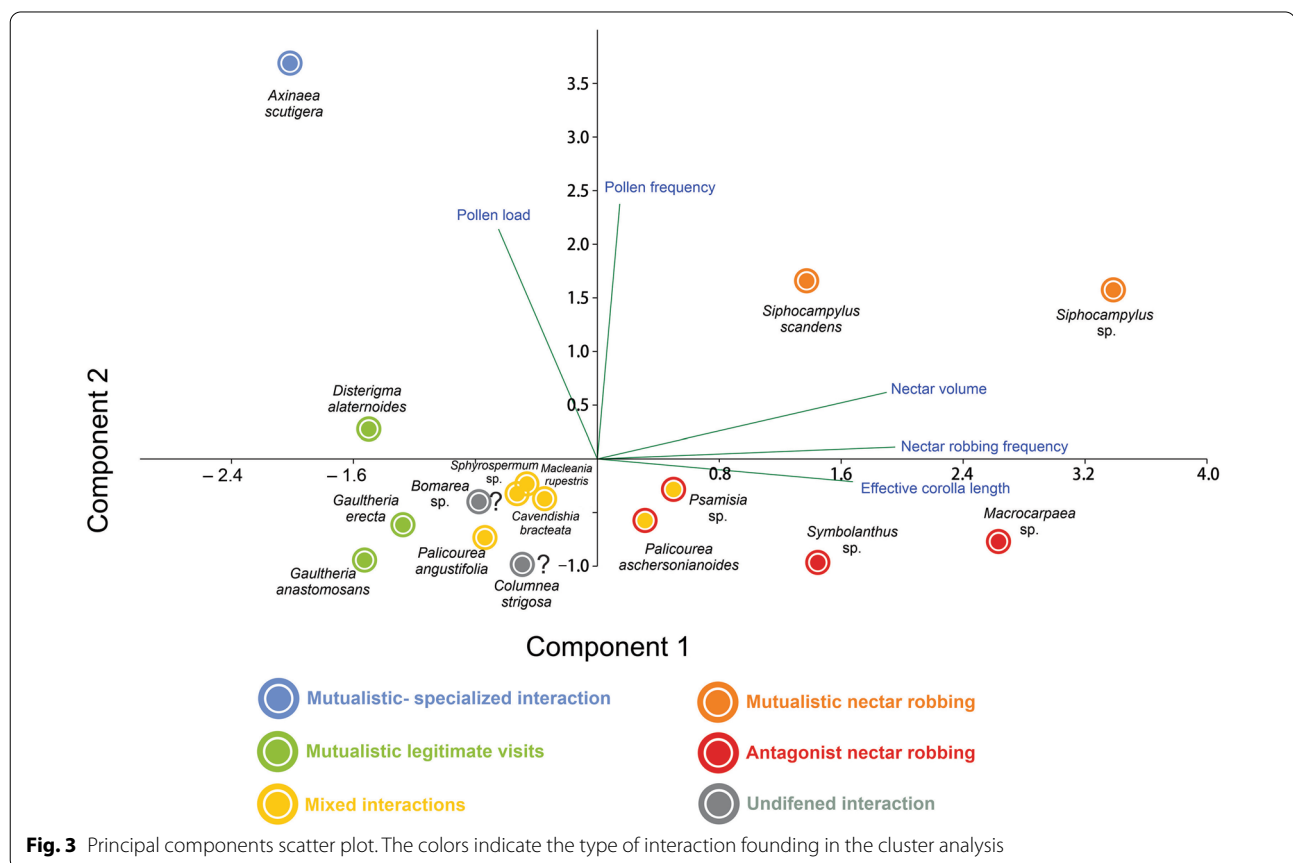
the affectation of nectar robbing and the flower traits, while PCA2 indicates the potential pollen transportation.

The scatter plot (Fig. 3) was consistent with our cluster analysis and give us some details about the types of interactions. We observed that *Palicourea aschersonianoides* and *Psamisia* sp. seems to be more related to the "Antagonist nectar robbing" interaction than the other species of the "Mixed interactions" cluster. Because these species presented a high frequency of nectar robbing (61% and 41%) and low indicator of pollen transport, thus, they seem to be more exploited by nectar robbing than legitimate visits. Nevertheless, more observational studies are required.
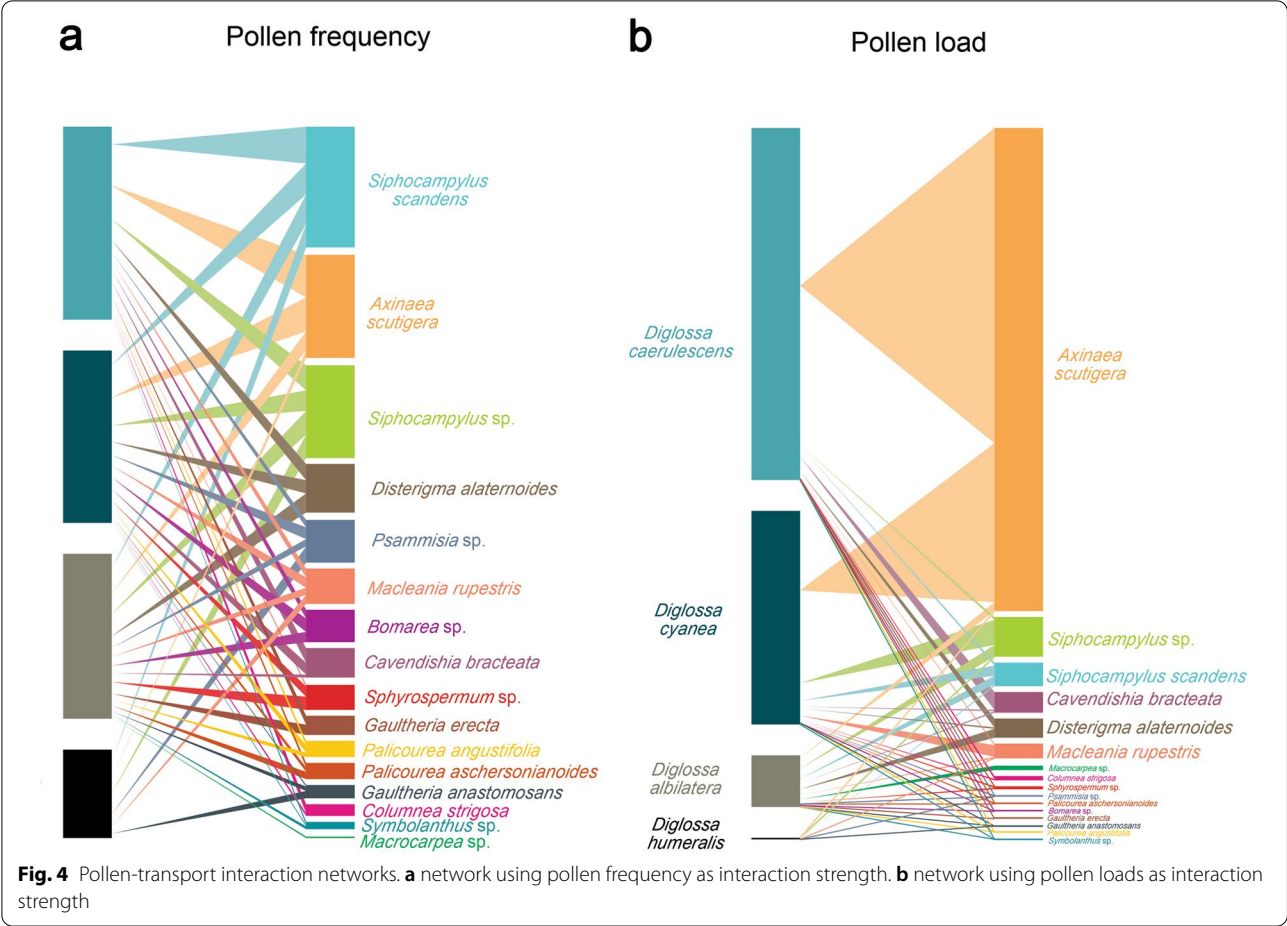
Also, the plot showed that the more effective strategy regarding pollen transportation was the specialized rewards used by *Axinaea scutigera*, followed by the *Siphocampylus* inflorescence characteristics that allow pollen attachment during nectar robbing and the legitimate visits in *Disterigma alaternoides*.

Network analysis

The networks generated consisted of 49 different flower-

Fig. 3 Principal components scatter plot. The colors indicate the type of interaction founding in the cluster analysis

quency (0.6) and load (0.73). So PCA1 is associated with

piercer-plant interactions (Fig. 4), 2.4 links per species,

Fig. 4 Pollen-transport interaction networks. **a** network using pollen frequency as interaction strength. **b** network using pollen loads as interaction strength

and a high connectance. The observed value of connectance was significantly higher than expected using null models ($p < 0.001$), while the links per species were significantly lower than the null models ($p < 0.001$). The flowerpiercer-plant interaction rarefaction analysis showed a good sampling efficiency of 82–92% based on the CHAO 1 (59, 96), Jackknife 1 (59, 66), ACE (54, 88), and Bootstrap (53, 69) index.

The network created using pollen frequency presented low specialization and medium nestedness, medium–high plant niche overlap, and high bird niche overlap (Table 2). The network generated using pollen loads exhibited medium–low specialization, medium nestedness, medium plant niche overlaps, and medium–low birds niche overlap (Table 2). Thus, the estimator of interaction strength seems to affect the network properties. The use of pollen loads indicated higher specialization and there for a lower niche overlap than the one using pollen frequency (Table 2). For both networks, the observed values, nestedness, and specialization were significantly higher than the expected using null models ($p < 0.001$); while niche overlap was significantly lower

than the null models ($p < 0.001$). Finally, both networks

Table 2 Properties of the flowerpiercer-plant pollen transportation network

Network property	Pollen frequency	Pollen loads
Number of links	49	49
Links per species	2.4	2.4
Connectance	0.75	0.75
Specialization	0.1	0.4
Nestedness	49.4	43.2
Plant niche overlap	0.7	0.6
Bird niche overlap	0.8	0.4
Plant robustness	0.95	0.94
Bird robustness	0.85	0.85

showed high robustness for both plants and birds, indicating that these networks are stable and resistant to species removal.

We calculated the normalized degree, which was the same for both networks as it measures the interaction

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regarding the strength (Table 3). We found that the most central plant species were *Axinaea scutigera*, *Macleania rupestris*, *Psamisia* sp., *Siphocampylus scandens*, and *Siphocampylus* sp. that interacted with four flowerpiercers species (Normalized degree = 1). In the case of flowerpiercers, the most important was *D. albilareta*, as it interacted with most of the plant species (Normalized degree = 0.94). *D. cyanea* and *D. caerulescens* also interacted with the majority of plants in the network (Normalized degree = 0.83), while *D. humeralis* interacted with few species (Normalized degree = 0.38).

Discussion

Our results showed that flowerpiercers ecological interactions are more diverse than their traditional assigned role as "parasites" of pollination processes. We observed that they could act as pollen vectors of multiple plants. Popic et al. (2013) indicated that the evaluation of pollen transportation is a better indicator of potential effective pollination than analysis of observed visits. Thus, our study evidenced that flowerpiercers may act as a potential pollinator of several Andean plants. Although, more studies on pollen deposition on a conspecific stigma are necessary.

The richness of ornithophilic plants found in our study was similar to the reported in other high Andean forests with a notorious representation of the Ericaceae family and abundance of *Disterigma alaternoides* and *Macleania rupestris* (Parada-Quintero et al. 2012). The flowerpiercers richness was similar to a previous report in another high Andean forest; however, the abundance of the species differed because we found higher dominance of *D. albilatera* and low presence of *D. Humeralis* (Rojas-Nossa 2007). This similarity suggests that our results could be extrapolated in other Andean systems, helping to understand the role of these birds in the ecological dynamics of these environments.

Similar to our results, previous studies reported that the corolla length and nectar production were the main traits associated with the susceptibility of flowers to nectar robbing (Lara and Ornelas 2001; Castro et al. 2009; Navarro and Medel 2009; Rojas-Nossa 2013; Rojas-Nossa et al. 2016a). The plants with long flowers and abundant nectar are more susceptible to be robbed by insects and birds (Rojas-Nossa et al. 2016a). Because the morphological mismatch promotes the access of the nectar by robbing and nectarivorous birds are more attracted to flowers with high energetic rewards (Rojas-Nossa 2013).

Table 3 Normalized degree of the flowerpiercers and plants

Flowerpiercer species	Normalized degree (flowerpiercers)
Diglossa albilatera	0.94
Diglossa caerulescens	0.83
Diglossa cyanea	0.83
Diglossa humeralis	0.38
Plant species	**Normalized degree (plants)**
Axinaea scutigera	1
Macleania rupestris	1
Psamisia sp.	1
Siphocampylus scandens	1
Siphocampylus sp.	1
Bomarea sp.	0.75
Cavendishia Bracteata	0.75
Disterigma alaternoides	0.75
Gaultheria anastomosans	0.75
Palicourea angustifolia	0.75
Palicourea aschersonianoides	0.75
Sphyrospermum sp.	0.75
Symbolanthus sp.	0.75
Columnea ct strigosa	0.5
Gaultheria erecta	0.5
Macrocarpea sp.	0.25

However, we found that nectar volume is also correlated to pollen transportation. Thus, this feature influences both robbing rates and pollen dissemination by flowerpiercers.

The elucidation of this complex plant-flowerpiercer interaction is essential to understand the pollination networks, as they can represent about 9% to 27% of nectarivorous interactions in Andean systems (Gonzalez and Loiselle 2016; Pelayo et al. 2019). We found that plant-flowerpiercer interaction is complex, and the line between mutualist and antagonist behavior can be blurry. The best example was the interactions with *Siphocampylus* plants that, at first glance, seemed to be clearly illegitimate and parasitic due to the length of their flowers and their high levels of robbing. However, after we examined the pollen loads, we realized that the flowerpiercers highly transported the pollen of these plants, acting as potential pollinators.

As a contribution to a better interpretation, we proposed five potential types of relationships based on morphological traits, degree of robbing, and pollen transportation.

Antagonist nectar robbing

In our study, we showed that some Andean plants were profoundly affected by nectar robbing and did not seem to receive a direct pollination service in return (low pollen transportation). They represented the classic view of the "parasitic" role of the flowerpiercers.

Nevertheless, the final effect of nectar robbing on plant fitness is still uncertain. Several authors reported a negative impact on the reproductive fitness associated with a reduction in fruit production and visit of legitimate pollinators (Navarro 2001; Castro et al. 2009; Navarro and Medel 2009; Maruyama et al. 2015; Hazlehurst and Karubian 2018). However, other studies stated a neutral effect over the reproductive success and pollinator's visits (Richardson 2004; Cuevas and Rosas-Guerrero 2016; Rojas-Nossa et al. 2016b; Ye et al. 2017). Because of the capacity of some plants to replace the loss of nectar and that some pollinator cannot differentiate robbed and unrobbed flowers (Richardson 2004; Cuevas and Rosas-Guerrero 2016; Ye et al. 2017). Further, there is a report of a positive effect of nectar robbing in fruit production of *Tecomella undulata* (Bignoniaceae) (Singh et al. 2014). Also, a study in three different sympatric *Corydalis* species visited by the same bumblebee robber found that each one responded differently. The authors described negative, positive, and neutral effects in the three species associated with its mating systems (Zhang et al. 2009).

Regarding flowerpiercers, a study in the Venezuela Andes found that the robbing of nectar has a neutral impact on *Castilleja* and *Tacsonia* fitness (del

Carmen Pelayo Escalona 2017). Also, there is a report of an indirect positive effect on *Passiflora mixta*, as robbing reduced the resource offered to legitimate hummingbird visitors, promoting an increase in pollen flow (Pelayo et al. 2011). Also, research in *Oreocallis grandiflora* found that flowerpiercers decreases the visitation rates by hummingbirds, but it was neutral regarding seed production (Hazlehurst and Karubian 2016). As we see, even when we classify the interaction as an antagonist, the final effect on reproductive fitness can be detrimental, neutral, or positive, and further studies with a more in-depth evaluation of the species response are required.

Mutualistic legitimate visits

We found that some plants seem to be visited only or mainly by legitimate visits. The morphometry of these species was consistent with the reported in other legitimate visited species like *Brachyotum* and *Vaccinium meridionale* (Stiles et al. 1992; del Carmen Pelayo Escalona 2017). These flowers presented short corollas that allowed the flowerpiercer to access the nectar by inserting its lower jaw and tongue.

The more effective plant within this interaction was *Disterigma alaternoides*, whose pollen was frequently transported by the flowerpiercers (33%). The high abundance of *D. alaternoides* may explain the success of this interaction, as it would be a valuable resource. Previous work found that *D. albilatera* effectively transported the pollen of *D. stereophyllum* to the stigma; nevertheless, the efficiency was lower compared to hummingbirds (Navarro et al. 2008). Other plants grouped in this category were the *Gaultheria* species, which is similar to a previous study that reported that flowerpiercers act as pollinators of *G. myrsinoides* (del Carmen Pelayo Escalona 2017).

In the case of *Bomarea* sp., the legitimate visit role is less clear as this species presented longer corolla, and there are reports in the genus of both nectar robbing and legitimate visits allowed by its broad and accessible corolla (Stiles et al. 1992; del Carmen Pelayo Escalona 2017). Rojas-Nossa (2007) also reported the absence of robbing marks in *Bomarea* species, but like in our work, the pollen transportation indicator was low. The author suggested that flowerpiercers can steal the nectar of *Bomarea* by introducing the bill between the petals of the corolla without leaving marks. So, assigned this species to a specific type of interaction is conflictive.

Mutualistic nectar robbing

Two species of *Siphocampylus* exhibited a particular relation with the flowerpiercers. They presented high indicatives of pollen transportation, although they were exclusively visited by nectar robbing strategy. There is

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another reported case of this type of interaction in *Tristerix mistletoe*. This ornithophilic plant was broadly robbed by *D. brunneiventris* and *D. humeralis*, but unexpectedly the individuals more affected were adequately pollinated and set more fruits (Graves 1982). The researcher realized that this species presented a cluster of long tubular upturned flowers arranged in a way that when the flowerpiercers try to rob the nectar of the centrally located flowers, they enter in contact with the stamens and pistils of the neighbor flowers (Graves 1982). This floral organization is very similar to *Siphocampylus* plants that set a cluster of long upward flowers that makes accessible the contact of the reproductive structures with approaching visitors.

A previous study found that flowerpiercers highly robbed *S. columnae*, but the pollen frequency was low (Rojas-Nossa 2007). This result may be because *S. columnae* inflorescences consisted of few flowers horizontally or downward oriented that makes difficult the contact of flowerpiercers with the reproductive structures. Thus, not all *Siphocampylus* species can use flowerpiercers as pollen vectors, and floral spatial arrangement is fundamental to the mutualistic interaction to occurs.

Nectar robbing bumblebees can also engage in this type of robbing-pollination relationship. Studies in *Anthyllis vulneraria* and *Primula secundiflora* found that bumblebees highly rob these plants, but effectible pollinate them (Navarro 2000; Zhu et al. 2010). Even robbed plants of *A. vulneraria* presented higher rates of fructification than unrobbed ones. A phenomenon that occurs because the body of the bumblebees enters in contact with the reproductive structure of the flowers while robbing, acting as legitimate pollinators (Navarro 2000; Zhu et al. 2010).

Mixed interactions
We found that some plants like *Macleania rupestris* and *Cavendishia bracteata* seems to be visited both by nectar robbing and legitimate visits. Previous reports indicated that these species are robbed and visited legitimately by flowerpiercers, acting as potential pollinators (Rojas-Nossa 2007). Further, *M. rupestris* seems to be more frequently visited legitimately (Rojas-Nossa 2007). Information consistent with the low nectar robbing frequency (< 15%) and the relative high pollen loads found in our study. Nevertheless, other species like *Psamisia* sp., *Palicourea aschersonianoides*, and *P. angustifolia* are more affected by nectar robbing and presented little pollen transportation.

Mutualistic- specialized interaction
The pollen transport of *A. scutigera* was far superior to the other species, making flowerpiercers more efficient vectors. The *Axinaea* genus has a unique ornithophilic pollination system consisting of the production of bulbous stamen appendages as body rewards connected to an air pressure system that ejects a high amount of pollen when the birds consume them (Dellinger et al. 2014). Our results showed that *D. caerulescens* and *D. cyanea* transported more pollen of *A. scutigera*. These differences probably occur because the *Axinaea* pollination strategy is based on attracting frugivorous passerines, and these two flowerpiercers have a more frugivorous behavior than *D. albilatera* and *D. humeralis*. (Dellinger et al. 2014; Aguilar and Tinoco 2017).

Network analysis
Prior work in Andean bird's pollination network also reported four flowerpiercers species interacted with Andean plants. The researcher used field observations and reported 20 flowerpiercer-plant interactions, but they cataloged all as nectar robbing relations and were later removed from the network (Gonzalez and Loiselle 2016). Likewise, another study of a different animal-plant interaction network that included one flowerpiercer (*D. gloriosa*) reported 9 interactions based on field observations (Pelayo et al. 2019). In our case, using pollen transport evaluation, we found 49 flowerpiercers-plant interactions.

Our research showed that flowerpiercer may have a role in bird-plant interaction networks and that the misinterpretation of flowerpiercer interactions can lead to unprecise results in ecological studies. Previous research found that the removal of flowerpiercers interaction led to a loss of links, a decrease of connectance, nestedness, and evenness of the pollination network (Gonzalez and Loiselle 2016).

We found high and medium levels of connectance and nestedness in the network, but those were higher than expected in random null models. These properties are related to diversity, resilience, stability, and resistance of the system (Saavedra et al. 2016; Cantor et al. 2017; Valverde et al. 2018; Baumgartner 2020). Likewise, the robustness of the network was high for both levels (plants and birds), which indicates a high tolerance and stability in scenarios of species extinctions (Memmott et al. 2004). Thus, flowerpiercer may have an important role in the conservation of Andean natural systems, promoting the stability of the pollination networks. The properties of specialization (*H*2) and niche overlap varied according to the strength measurements used. A previous study also found differences at the network and species level using distinct interaction strength measurements (Novella-Fernandez et al. 2019). The specialization (*H*2) was low to medium, and it indicates that the species are little to middle selective (Willcox et al. 2019). This leads to a medium to high niche overlaps that show an important

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competition between the species in the network (Kuhnen et al. 2017).

Conclusions

As we observed, the interactions of flowerpiercers are complex, and they need to be considered more than robbers and competitors of pollinators like hummingbirds. These birds serve as pollen vectors and potential pollinators of several Andean plants, and some of them have developed specific strategies that allow effective pollen transportation by flowerpiercers. Thus, flowerpiercers could influence the reproductive success of ornithophilic plants and need to be considered in the analysis of animal-plant ecological networks. Nevertheless, we are based mainly on nectar robbing frequencies and pollen transportation. So, further studies, including variables like fruit/seed production, hummingbirds' visits, and the effectiveness of pollen transportation to the stigma, are required to better evaluate the final effect on the plant's reproductive fitness.

Authors' contributions
JAC-P and LAA-S contributed to the analysis and interpretation of data. JAC-P collected the data and made the laboratory analysis. LAA-S wrote the manuscript. RCP revised and approved the submitted version. All authors read and approved the final manuscript.

Availability of data and materials
Most of the data underlying this article are available in the article. Specifically, the data used in the correlations between the floral traits and identification of the type of interaction is found in Table 1. The data of individual pollen loads will be shared on a reasonable request to the corresponding author.

Declarations

Ethics approval and consent to participate
The research was approved by the ethic committee of the "Universidad Pedagógica y Tecnológica de Colombia" under project "Patrones de forrajeo de una comunidad de aves nectarívoras para el aprovechamiento del recurso florístico en un área de boque altoandino del parque natural municipal el Sinaí, Pachavita, Boyacá, SGI-1753".

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Research Group "Grupo Ecología de Organismos (GEO-UPTC)", Tunja, Colombia. [2]Maestría en Ciencia Biológicas, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia. [3]Instituto de Ciencias Ambientales y Ecológicas (ICAE), Universidad de Los Andes, Mérida, Venezuela.

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