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Temporal dynamics and central species in a plant-hummingbird interaction network in an inter-Andean valley in the southern Peruvian Andes

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Temporal dynamics and central species in a plant-hummingbird interaction network in an inter-Andean valley in the southern Peruvian Andes

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Running head: Plant-hummingbird interactions in Sogay

Abstract

Plant-hummingbird interactions are key components of Neotropical ecosystems, yet they remain poorly documented in arid inter-Andean valleys of southern Peru, where floral resources are strongly seasonal. We evaluated the structure, temporal dynamics, and central species of a plant-hummingbird interaction network in the Sogay valley, Arequipa. From March to August 2025, feeding, perching, and competitive interactions were recorded through direct observation surveys. The feeding network comprised 10 plant species, four hummingbird species, and 21 observed links. It showed moderately high connectance (0.525), intermediate specialization (H2' = 0.550), moderate modularity (Q = 0.386), and presence-absence-based nestedness (NODF = 65.23). Visits were concentrated on *Tecoma fulva* (47.5%), *Ligaria cuneifolia* (25.1%), and *Nicotiana glauca* (10.3%), whereas *Rhodopis vesper* was the most central hummingbird species. Activity peaked in May and June, which also showed the highest temporal similarity. Nectar concentration was not associated with visitation frequency (ρ = 0.018; p = 0.969), and floral length showed only a non-significant positive trend. These results suggest a temporally dynamic network structured by core floral resources and by the complementary use of plants as perches and sites of agonistic interaction. Overall, this study highlights the ecological importance of floral and structural resources in sustaining hummingbird assemblages in arid Andean landscapes.

Key words: arid valleys, floral resources, mutualistic networks, nectar, ornithophily, Trochilidae

Introduction

Plant-animal interactions are fundamental to the maintenance of biodiversity and ecosystem functioning. Among these interactions, pollination is a key ecological process because it directly influences plant reproduction, population persistence, and the organization of biological communities (Bascompte and Jordano 2007). Approximately 87.5% of angiosperms are estimated to depend, at least partially, on animal-mediated pollination, highlighting the importance of these interactions for the conservation of plant diversity (Ollerton et al. 2011). In this context, the loss of ecological interactions may represent an early form of functional ecosystem degradation, even before the local extinction of the species involved (Valiente-Banuet et al. 2015).

Hummingbird-plant relationships are among the most representative mutualistic systems in the Neotropics. Hummingbirds, family Trochilidae, exhibit morphological, physiological, and behavioral adaptations that allow them to exploit floral nectar efficiently, including hovering flight, elongated bills, extensible tongues, and high energetic demands (Cotton 1998; Sonne et al. 2016). In turn, many plants visited by these birds show traits associated with the ornithophily syndrome, such as tubular flowers, conspicuous colors, low scent production, and nectar secretion, all of which favor the attraction of nectar-feeding birds and pollen transfer (Faegri and van der Pijl 1979; Dalsgaard et al. 2009). Although plant-hummingbird interactions are often considered a classic example of coevolution, recent syntheses indicate that the ecological and evolutionary outcomes of this mutualism are heterogeneous and may depend on plant traits, hummingbird morphology, foraging behavior, environmental context, and the degree of specialization of the interacting

species (Barreto et al. 2024). Therefore, local interaction datasets remain essential for understanding how these relationships are structured in poorly studied environments.

However, hummingbird-plant interactions do not always reflect strict specialization. Several studies have shown that hummingbirds can use both ornithophilous flowers and flowers lacking classic bird-pollination traits, behaving as generalist floral visitors in certain ecological contexts (Dalsgaard et al. 2009; Rodrigues and Araujo 2011; Morales-Contreras et al. 2020). This plasticity may be associated with their high energetic requirements, temporal variation in flowering, and local resource availability. Non-ornithophilous flowers may also constitute important resources for hummingbirds in seasonal Neotropical environments or in areas with limited floral availability (Maruyama et al. 2013).

The ecological network approach allows these interactions to be analyzed from a community-level perspective by simultaneously considering multiple plant and hummingbird species. In bipartite plant-pollinator networks, species are represented as nodes and interactions as links, which can be weighted according to their frequency or intensity (Bascompte and Jordano 2007; Dormann et al. 2008). This approach makes it possible to estimate metrics such as connectance, specialization, nestedness, modularity, and centrality, which are useful for identifying core species and understanding community organization. In hummingbird-plant networks, these metrics have been used to evaluate the degree of specialization, identify important floral resources, and compare spatial or temporal changes in interaction structure (Martínez-García and Ortiz-Pulido 2014; Infante et al. 2020). This is especially relevant in arid or seasonally dry environments, which are characterized by sparse vegetation and high environmental heterogeneity, such as the western slopes of the southern Peruvian Andes (Weberbauer 1945; Arroyo et al. 1983; SENAMHI 2021). In these systems, floral resources may be highly seasonal or spatially concentrated, potentially leading to changes in visitation frequency, local movements, and variation in floral resource use by hummingbirds (Ortiz-Pulido and Vargas-Licona 2008; Fonseca et al. 2015).

In Peru, knowledge of pollination and floral-visitor interactions remains spatially uneven. A recent national synthesis compiled 162 bibliographic sources and 2,537 pollination and floral-visitor interactions, corresponding to 970 plant species or morphospecies and 671 animal species or morphospecies, but also highlighted important geographic gaps in interaction data across the country (Bernabé Paniagua et al. 2024). In southern Peru, hummingbirds are part of the characteristic avifauna of arid environments, shrublands, agricultural areas, and riparian sectors of the western Andean slopes. However, available information has focused mainly on records of occurrence and distribution (Villegas et al. 2025), whereas functional interactions between hummingbirds and plants remain poorly known. This knowledge gap is relevant because the conservation of nectar-feeding birds also depends on identifying the floral resources and vegetation structures that support their feeding, movement, and behavior.

In this context, the present study aimed to evaluate the temporal use of floral resources by hummingbirds in an inter-Andean valley of southern Peru using an interaction network approach. Specifically, we sought to identify the plant and hummingbird species involved in feeding events, characterize the quantitative structure of the plant-hummingbird network, identify central species, evaluate monthly variation in interactions, and explore the relationship between visitation frequency and selected floral traits.

Methods

Study site

The study was conducted in the inter-Andean valley of Sogay-Quequeña, Yarabamba District (16°33.817'S; 71°27.069'W), province and department of Arequipa, on the western slope of the southern Peruvian Andes. The evaluated area is located at approximately 2500-3000 m a.s.l. and is part of an arid to semi-arid landscape characteristic of the western Andean foothills. This area shows marked climatic seasonality, with rainfall mainly concentrated between December and March, and naturally sparse vegetation shaped by aridity and local water availability (Weberbauer 1945; SENAMHI 2021). The landscape of the study area consists of a mosaic of agricultural areas, riparian vegetation, shrubland, rocky slopes, and sectors with

floral resources associated with streams, irrigation canals, and crop fields. These elements generate localized vegetation patches with greater floral availability and quality, particularly during the post-rainy season, and they can function as activity hubs for nectar-feeding birds.

The evaluated area comprised the section between the exit of the Quequeña annex and the entrance to the Sogay annex, including sectors near the road leading to the Sogay waterfalls. This local gradient includes agricultural terraces, crop edges, riparian vegetation associated with the riverbed and irrigation canals, shrubland on slopes, and rocky sectors with native and naturalized plants. The area was selected based on the presence of active floral resources during the evaluation period, accessibility for repeated surveys, and previous observations of high hummingbird activity. This criterion is consistent with plant-hummingbird interaction studies that prioritize sites with active flowering and the presence of nectar-feeding birds to maximize the recording of floral visits (Ortiz-Pulido and Díaz 2001; Martínez-García and Ortiz-Pulido 2014). For analytical purposes, the Sogay-Quequeña valley (Fig. 1) was considered a single study unit because of the geographic proximity between both sectors, the continuity of the evaluated landscape, and the ecological similarity of their environments.

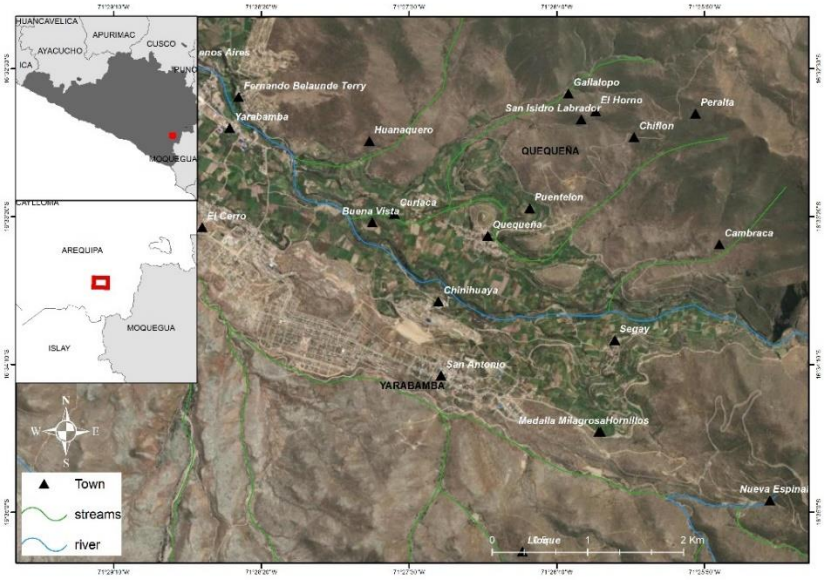

Figure 1. Location of the study area in the Sogay-Quequeña valley, Arequipa, southern Peru. The map shows the evaluated valley sector, nearby towns, streams and the main river corridor associated with the observation area.

Evaluation period and observation schedule

Field evaluations were conducted between March and August 2025, during the period following the main rainy season in the region. This period was selected because it coincides with greater availability of floral resources in the study area and a higher probability of recording interactions between hummingbirds and plants. It also corresponds to a period of overlap in the distributions of several hummingbird species. During this period, four monthly evaluations were carried out, maintaining the same survey routes during each visit to reduce variation associated with sampling effort. Surveys were conducted between 06:00 and 11:00 h, a time interval during which hummingbirds usually show greater foraging activity and movement among floral resources (León-Camargo and Rangel-Churio 2015). During each evaluation, the previously delimited sectors were surveyed slowly, prioritizing areas with flowering plants and visible hummingbird activity. Observations were conducted while maintaining sufficient distance to avoid altering the natural behavior of the birds.

Recording of plant-hummingbird interactions

Records were obtained through direct observation using 10 × 42 binoculars and photographic support with a Nikon Coolpix P1000 camera. Surveys were conducted along transects of variable length and width, adapted to the terrain topography and the spatial distribution of floral resources. This strategy was necessary because of the heterogeneity of the study area. The use of terrain-adapted survey routes is appropriate for fauna studies in heterogeneous environments, where visibility, accessibility, and resource distribution may vary spatially (MINAM 2015).

For each event, we recorded the hummingbird species, plant species used, time, type of interaction, foraging strategy, approximate event duration, effective feeding time, interaction height, and behavioral observations. Feeding interactions were defined as any event in which a hummingbird inserted its bill into a flower or accessed the floral resource to consume nectar. This definition is consistent with previous studies of hummingbird-plant networks, in which an interaction is established when a hummingbird visits a flower and inserts its bill into the corolla or directly uses the floral resource (Martínez-García and Ortiz-Pulido 2014). Perching events, defined as the use of a plant as physical support, were also recorded, as were competition or agonistic interaction events, including chases, displacements, resource defense, patrolling, and territorial behaviors.

Foraging strategy was classified as hover feeding, perched feeding, or a mixed strategy. Complementary observations allowed us to record behaviors such as vocalizations, defense of floral resources, intra- and interspecific displacements, repeated flight routes, and possible nectar-robbing events. This classification made it possible to distinguish interactions directly associated with nectar consumption from other behavioral or structural uses of plants. Only feeding events were included in the main network analysis, whereas perching and competition events were analyzed complementarily.

Identification of floral resources and plant traits

Plant species used by hummingbirds were recorded through photographs. The specimens were taxonomically identified with specialized support, considering family, genus, and species. For each floral resource, we recorded attributes associated with hummingbird use, including floral color, growth habit, ornithophilous or non-ornithophilous condition, and floral morphometric measurements.

Morphometric characterization was performed using ten representative flowers per species, selected from different individual plants whenever possible. We considered floral length measurements related to nectar accessibility: FL, TL1, and TL2. Total floral length (FL) corresponded to the complete length of the flower; TL1 corresponded to the distance from the base of the corolla to the beginning of the floral tube opening; and TL2 corresponded to the distance from the base of the corolla, at the insertion point, to the most distal end of the petals or lobes when fully extended. In addition, nectar was evaluated in the plant species recorded as floral resources used by hummingbirds. Measurements were taken between 07:00 and 09:00 h. For each plant species, recently opened flowers were selected to obtain representative samples of the nectar available during the period of greatest plant-hummingbird interaction.

Nectar was extracted directly from the base of the corolla using 5 µL capillary tubes, a procedure commonly used to characterize floral resources in pollination and floral visitor ecology studies (Kearns and Inouye 1993; Dafni et al. 2005). Because nectar volume per flower was very low in several species, nectar from multiple flowers of the same species was pooled until a sufficient volume was obtained for measurement. Sugar concentration was estimated using a portable 0-30 °Brix refractometer, with five replicates recorded for each floral resource evaluated. °Brix values were used as an approximation of the relative sugar concentration of nectar, a relevant variable for assessing the potential quality of floral resources used by nectar-feeding birds (Nicolson and Fleming 2003; Dafni et al. 2005).

Plants were classified as ornithophilous or non-ornithophilous based on the presence of traits commonly associated with bird pollination, such as tubular flowers, conspicuous colors, low scent production, and nectar presence, following general criteria in pollination ecology (Faegri and van der Pijl 1979; Dalsgaard et al. 2009). Nevertheless, all plants visited by hummingbirds were included regardless of their floral

classification, because hummingbirds may also use floral resources that do not exhibit typical ornithophilous traits (Maruyama et al. 2013; Morales-Contreras et al. 2020). Plant material was recorded and measured only when birds were not using the plant, in order to minimize disturbance to natural behavior.

Data analysis

To characterize interaction structure, we constructed a quantitative plant-hummingbird matrix. Rows represented plant species, columns represented hummingbird species, and each cell corresponded to the number of feeding events recorded for each plant-hummingbird pair. This quantitative approach allowed us to incorporate interaction intensity rather than only presence or absence, which is appropriate for the analysis of plant-animal mutualistic networks and hummingbird-plant networks (Bascompte and Jordano 2007; Blüthgen et al. 2006; Dormann et al. 2008; Martínez-García and Ortiz-Pulido 2014).

At the network level, we calculated plant and hummingbird richness, the number of observed links, the number of possible links, connectance, interaction evenness, nestedness, the NODF index, weighted NODF, and complementary specialization H2'. Connectance was estimated as the proportion of observed links relative to the total number of possible links. The H2' index was used as a network-level measure of specialization because it incorporates the relative frequency of interactions and allows the degree of specialization in quantitative networks to be assessed. Values range from 0, when the network is more generalized, to 1, when the network is more specialized (Blüthgen et al. 2006). These metrics were calculated using the bipartite package in R, which is designed for the analysis of bipartite ecological networks (Dormann et al. 2008).

Network modularity was estimated using the QuanBiMo algorithm, implemented in the computeModules function of the bipartite package (Dormann and Strauss 2014). This procedure detects modules or subsets of species that interact more frequently with each other than with the rest of the network, while incorporating interaction weights in quantitative bipartite matrices (Dormann and Strauss 2014). Modularity was interpreted as evidence of internal organization within the network.

At the species level, we calculated degree, species strength, betweenness, closeness, and species-level specialization d' for plants and hummingbirds. Degree was interpreted as the number of species with which each node interacted, whereas species strength represented the weighted importance of a species within the network, considering the intensity of its interactions. Betweenness was used to identify species that connect different sectors of the network, and closeness was used to evaluate the relative proximity of each species to all other nodes. To summarize the relative structural importance of each species, degree, weighted strength, betweenness, and closeness were standardized and combined into a composite centrality index, calculated separately for plants and hummingbirds. This index was used to identify central species, defined as those with the greatest relative contribution to network connectivity and interaction intensity (Bascompte and Jordano 2007; Dormann et al. 2008; Csárdi and Nepusz 2006).

The dependence of each interaction was calculated in two directions: the dependence of each plant on each hummingbird and the dependence of each hummingbird on each plant. Plant-to-hummingbird dependence was estimated as the proportion of visits to a plant performed by a given hummingbird species, whereas hummingbird-to-plant dependence was calculated as the proportion of visits by a hummingbird directed to a given plant. Based on these values, interaction asymmetry was calculated to identify relationships that were more balanced or more dependent in a single direction.

Sampling sufficiency was evaluated using interaction rarefaction and extrapolation. For this analysis, each plant-hummingbird combination was treated as an interaction richness unit, and the frequency of each interaction corresponded to the number of observed feeding records. A general rarefaction/extrapolation curve was estimated for the accumulated network, and monthly curves were generated to evaluate sampling completeness in each period. Sample coverage, understood as the estimated proportion of the interaction community represented by sampling, was also calculated. These analyses were performed using the iNEXT package (Hsieh et al. 2016).

To evaluate temporal variation in the network, feeding records were grouped by month and monthly plant-hummingbird matrices were constructed. For each monthly matrix, we calculated the number of records, plant richness, hummingbird richness, number of unique interactions, connectance, the H2' index, and nestedness. This procedure allowed us to describe temporal changes in network complexity, connectivity, and specialization. Monthly centrality metrics were also calculated to evaluate whether central species remained constant or changed throughout the evaluation period.

Monthly networks were compared using dissimilarity matrices calculated from the interaction frequency of each plant-hummingbird pair. The Bray-Curtis index was used to evaluate quantitative differences in the composition and intensity of interactions among months (Bray and Curtis 1957). The resulting dissimilarity matrix was transformed into temporal similarity values as 1-Bray-Curtis dissimilarity, allowing direct comparison of the resemblance among monthly networks. These analyses were performed using the vegan package (Oksanen et al. 2025).

Finally, feeding records were integrated with the available floral traits, including ornithophilous condition, growth habit, floral morphometric variables, and nectar concentration. The association between visitation frequency, nectar concentration, and floral length was evaluated through exploratory correlations and count models. All analyses were performed in RStudio (R Core Team 2024).

Results

Evaluation effort and types of interactions recorded

During the evaluation period, 349 plant-hummingbird interaction records were obtained. In total, four hummingbird species and 19 plant species were recorded as being used in different interaction contexts. Of all records, 63.9% corresponded to feeding events and 36.1% to perching events. The feeding network included 21 observed plant-hummingbird links. Interaction richness estimators suggested that additional rare links may not have been detected, with expected values of 51.55 interactions according to Chao, 28.64 according to Jackknife 1, 35.04 according to Jackknife 2, and 24.22 according to Bootstrap. Relative to the Chao estimator, the observed links represented an approximate completeness of 40.7%, indicating that the accumulated network may include rare interactions not recorded during the study period. However, monthly sample coverage was high on average (94.48%; range: 77.41-100%), with the lowest value recorded in July (77.41%) and complete coverage estimated for August (100%). Thus, although additional rare interactions may occur in the system, the sampling adequately represented the dominant interactions during most months, particularly during the periods of greatest activity.

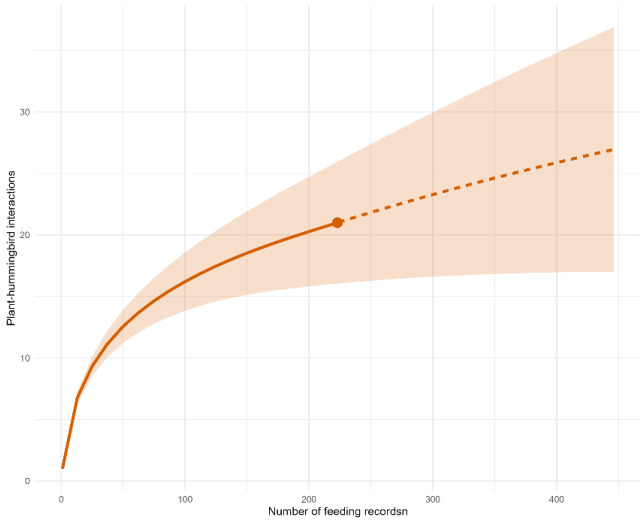

Figure 2. Rarefaction and extrapolation curve of plant-hummingbird interactions recorded in Sogay.

General structure of the floral resource-hummingbird network

The feeding network consisted of 10 plant species and four hummingbird species, with 21 observed links out of 40 possible links, corresponding to a connectance of 0.525 (Fig. 3). The complementary specialization index was H2' = 0.550, indicating a network with intermediate specialization. This suggests that the network was neither completely generalized nor highly specialized. Several hummingbird species shared floral resources, although interaction intensity was concentrated in certain plant-hummingbird pairs. Interaction evenness was 0.612, indicating that interaction frequencies were not distributed completely homogeneously among plant-hummingbird pairs. In addition, the network showed moderate modularity (Q = 0.386), suggesting some degree of internal organization into subsets of species that interacted more intensely with each other. Nestedness (NODF = 65.23) was more evident when considering the presence or absence of interactions than when incorporating visitation intensity.

Hummingbird generality was 2.54, whereas plant vulnerability was 2.19, where in average, each hummingbird used slightly more than two floral resources when weighted by frequency, while each plant was visited by slightly more than two hummingbird species. Overall, these results shows a network with moderately high connectivity, intermediate specialization, and a structure organized around a subset of central species.

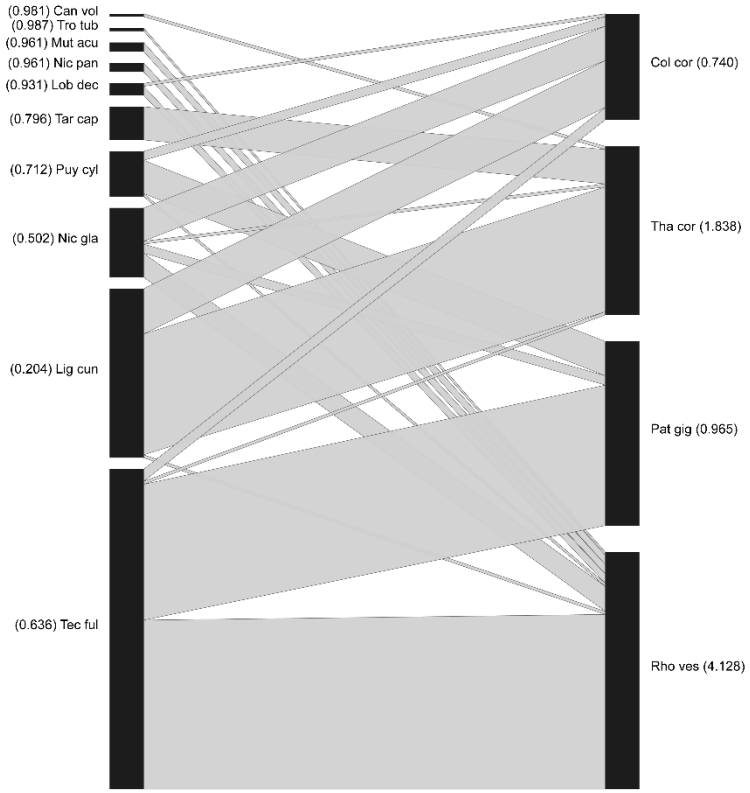

Figure 3. Accumulated bipartite network representing interactions between plant species (left) and hummingbird species (right) recorded in the Sogay valley, southern Peru. Box width represents the degree of each species, defined as the number of interaction links. Line thickness indicates the frequency of visits recorded between each hummingbird species and floral resource. Asymmetry values are shown in parentheses.

Use of floral resources by hummingbirds

The use of floral resources was strongly concentrated in a few plant species. *Tecoma fulva* was the most frequently used resource, with 106 visits, representing 47.5% of all feeding records. It was followed by

Ligaria cuneifolia, with 56 visits (25.1%), and *Nicotiana glauca*, with 23 visits (10.3%). Together, these three species accounted for 185 visits, equivalent to 83.0% of all feeding records.

Other floral resources showed lower frequencies of use, including *Puya cylindrica* with 15 visits (6.7%), *Tarasa capitata* with 11 visits (4.9%), *Lobelia decurrens* with four visits (1.8%), *Mutisia acuminata* and *Nicotiana paniculata* with three visits each (1.3% each), and *Cantua volcanica* and *Tropaeolum tuberosum* with one visit each (0.4% each). At the hummingbird level, *Rhodopis vesper* accumulated the highest number of visits, with 76 records (34.1%), followed by *Patagona gigas* with 59 records (26.5%), *Thaumastura cora* with 54 records (24.2%), and *Colibri coruscans* with 34 records (15.2%)(Fig. 4). The most frequent interactions were *Tecoma fulva-Rhodopis vesper*, with 56 visits (25.1% of the total), *Tecoma fulva-Patagona gigas*, with 45 visits (20.2%), and *Ligaria cuneifolia-Thaumastura cora*, with 40 visits (17.9%). These three interactions accounted for 141 records, equivalent to 63.2% of all feeding visits, evidencing a strong dominance of a few plant-hummingbird pairs within the network.

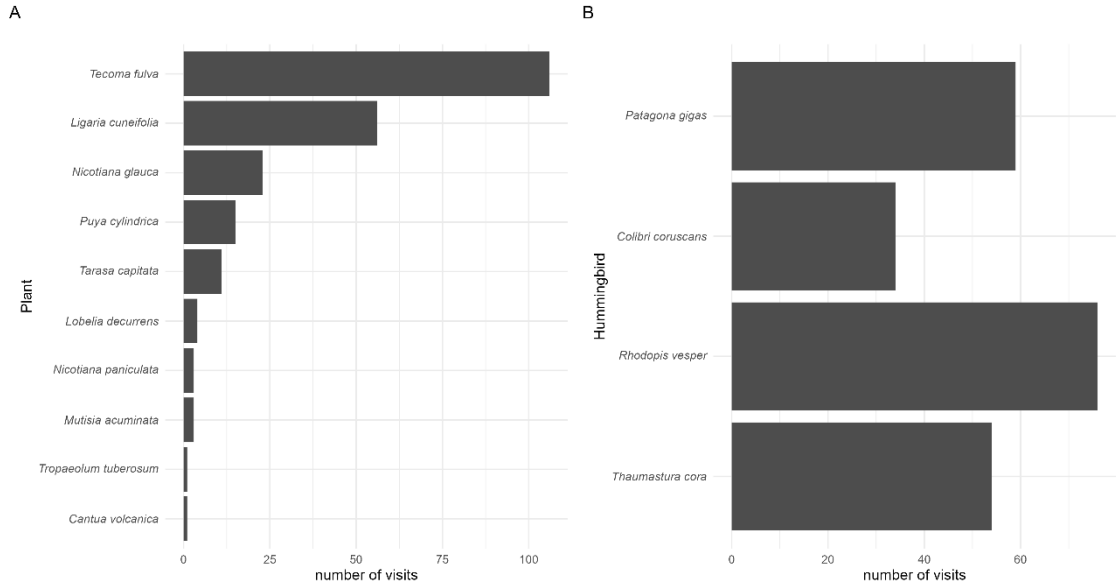

Figure 4. Frequency of floral visits by plant species and hummingbird species in Sogay. A) Number of visits recorded for each plant species used as floral resource. B) Number of visits recorded for each hummingbird species. Bars represent total feeding records during the study period.

Interaction dependence and asymmetry

Dominant interactions showed different patterns of dependence between plants and hummingbirds. In the *Tecoma fulva-Rhodopis vesper* interaction, visits represented 52.8% of all visits received by *T. fulva* and 73.7% of all visits performed by *R. vesper*, with an asymmetry value of -0.209. In the *Tecoma fulva-Patagona gigas* interaction, plant dependence on the hummingbird was 0.425, whereas hummingbird dependence on the plant was 0.763, with an asymmetry value of -0.338. This indicates that *T. fulva* was a particularly important resource for *P. gigas* and *R. vesper*, although the plant was visited by more than one hummingbird species.

In contrast, the *Ligaria cuneifolia-Thaumastura cora* interaction showed relatively balanced dependence, with plant dependence on the hummingbird of 0.714 and hummingbird dependence on the plant of 0.741, as well as an asymmetry value close to zero (-0.026). This pattern suggests a strong and relatively reciprocal association between both species within the recorded network.

Some less frequent interactions showed high plant dependence on a single visitor. For example, *Tarasa capitata-Thaumastura cora* showed plant-hummingbird dependence of 1.000, indicating that all visits recorded for this plant were performed by *T. cora*. Similarly, *Nicotiana paniculata*, *Mutisia acuminata*, *Cantua*

volcanica, and *Tropaeolum tuberosum* showed complete dependence on a single recorded hummingbird species, although visitation frequencies were low.

Table 1. Dependence and asymmetry of plant-hummingbird interactions in Sogay

Plant (P)	Hummingbird (H)	Visits	Dependence P - H	Dependence H - P	Asimetry
Cantua volcanica	*Thaumastura cora*	1	1.000	0.019	0.981
Ligaria cuneifolia	*Thaumastura cora*	40	0.714	0.741	-0.026
Nicotiana glauca	*Thaumastura cora*	1	0.043	0.019	0.025
Tarasa capitata	*Thaumastura cora*	11	1.000	0.204	0.796
Tecoma fulva	*Thaumastura cora*	1	0.009	0.019	-0.009
Ligaria cuneifolia	*Colibri coruscans*	15	0.268	0.441	-0.173
Lobelia decurrens	*Colibri coruscans*	1	0.250	0.029	0.221
Nicotiana glauca	*Colibri coruscans*	11	0.478	0.324	0.155
Puya cylindrica	*Colibri coruscans*	3	0.200	0.088	0.112
Tecoma fulva	*Colibri coruscans*	4	0.038	0.118	-0.080
Ligaria cuneifolia	*Rhodopis vesper*	1	0.018	0.013	0.005
Lobelia decurrens	*Rhodopis vesper*	3	0.750	0.039	0.711
Mutisia acuminata	*Rhodopis vesper*	3	1.000	0.039	0.961
Nicotiana glauca	*Rhodopis vesper*	8	0.348	0.105	0.243
Nicotiana paniculata	*Rhodopis vesper*	3	1.000	0.039	0.961
Puya cylindrica	*Rhodopis vesper*	1	0.067	0.013	0.054
Tecoma fulva	*Rhodopis vesper*	56	0.528	0.737	-0.209
Tropaeolum tuberosum	*Rhodopis vesper*	1	1.000	0.013	0.987
Nicotiana glauca	*Patagona gigas*	3	0.130	0.051	0.080
Puya cylindrica	*Patagona gigas*	11	0.733	0.186	0.547
Tecoma fulva	*Patagona gigas*	45	0.425	0.763	-0.338

Central species in the network

The centrality analysis identified *Rhodopis vesper* as the most central hummingbird species in the network. This species had the highest degree among hummingbirds (degree = 8), the highest weighted strength (strength = 76), the highest betweenness (betweenness = 0.705), and the highest closeness (closeness = 2.694). Its composite centrality index was 1.184, higher than that of the other hummingbird species. This indicates that *R. vesper* was not only a frequent species but also an articulating node in the network, connecting with a greater number of plants and contributing to the overall connectivity of the system.

Among plants, *Tecoma fulva* was the most central species, with degree = 4, strength = 106, betweenness = 0.218, closeness = 2.616, eigenvector = 1.000, and a composite centrality index of 1.748. It was followed by *Nicotiana glauca*, with a centrality index of 0.926, and *Ligaria cuneifolia*, with an index of 0.748. These

results indicate that *T. fulva* was the main floral resource structuring the network, whereas *N. glauca* and *L. cuneifolia* functioned as secondary resources of importance.

In addition, *Tecoma fulva* showed the highest species strength among plants (species strength = 1.636) and high connectivity (degree = 4), whereas *Rhodopis vesper* showed the highest species strength among hummingbirds (species strength = 4.711) and the highest number of connections (degree = 8). These results further support the identification of both species as central nodes in the Sogay plant-hummingbird network.

Temporal variation in the feeding network

Network structure varied throughout the evaluation period. The number of feeding records increased from 17 records in March to peak values in May and June, with 68 and 82 records, respectively. Subsequently, records decreased to 17 in July and seven in August.

The number of unique interactions also showed temporal variation. Four interactions were recorded in March, increasing to 10 in April, 12 in May, and 11 in June. This value then decreased to six interactions in July and three in August. Therefore, the network reached its greatest complexity between May and June, when the highest number of records and unique interactions was concentrated.

Network metrics also varied among months. Connectance was high in March (0.667) and August (0.750), although these values were influenced by the smaller size of the monthly networks. During the months of greatest activity, connectance was 0.600 in May and 0.550 in June, indicating that during the main activity period, an important proportion of observed interactions relative to possible interactions was maintained. April and July showed lower connectance values, with 0.357 and 0.375, respectively.

The H2' index varied among months, with values of 1.000 in March, 0.625 in April, 0.518 in May, 0.630 in June, 0.720 in July, and 0.520 in August. During the months of greatest activity, May and June showed intermediate H2' values, indicating a network in which several species shared floral resources but dominant interactions were still present. Nestedness also varied temporally. May showed the highest weighted NODF value (44.79), followed by June (32.29), whereas April and July showed lower values (18.52 and 8.33, respectively). This indicates that during May and June, the network showed a more consistent structure of shared resources and dominant species.

Temporal comparison of monthly networks and central species.

The comparison among monthly networks showed that May and June were the most similar, with a similarity value of 0.733. This indicates that both months shared a relatively similar composition and intensity of interactions, forming the main temporal core of network activity.

Other moderate similarities were observed between April and July (0.571), March and April (0.408), and April and June (0.404). In contrast, August was the most differentiated month, showing no similarity with March or April and very low similarity with May (0.107), June (0.090), and July (0.083). This pattern shows a marked change in the composition and intensity of interactions toward the end of the evaluation period.

In terms of interaction presence/absence, Jaccard similarity was also highest between May and June (0.643), confirming that these months shared an important set of interactions and not only similar frequencies. Jaccard similarity between June and July was 0.417, whereas August showed low similarity with all other months.

For the case of the identity of central species varied among months. In March, the most central hummingbird was *Thaumastura cora*, with a composite centrality index of 0.707, whereas the most central plant was *Ligaria cuneifolia*, with an index of 0.785. In April, the central hummingbird changed to *Rhodopis vesper* (index = 1.329), and the central plant was *Tecoma fulva* (index = 1.390). In May, the hummingbird with the highest centrality was *Colibri coruscans* (index = 0.767), whereas *Tecoma fulva* remained the most central plant (index = 1.086). In June, *Rhodopis vesper* again became the most central hummingbird (index = 0.819), and *Tecoma fulva* reached its highest monthly centrality (index = 1.462). In July, *R. vesper* and *T.*

fulva continued to be central species, with indices of 0.891 and 1.172, respectively. Finally, in August, the network was dominated by *Rhodopis vesper* and *Nicotiana glauca*, both with a centrality index of 0.707 (Fig. 5).

These results show that *Tecoma fulva* was the central floral resource during most of the evaluation period, especially between April and July, whereas *Rhodopis vesper* was the most consistently central hummingbird species in the total network and across several months.

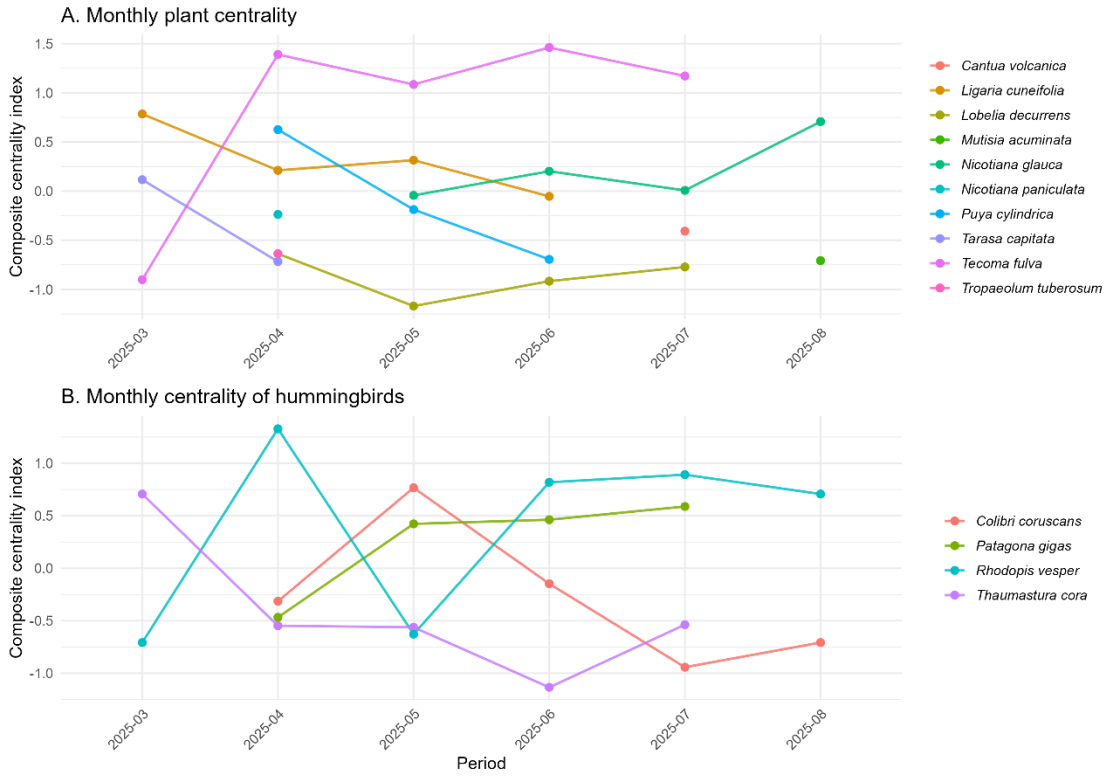

Figure 5. Temporal variation in plant and hummingbird centrality within the plant-hummingbird interaction network of Sogay. A) Monthly composite centrality index for plant species. B) Monthly composite centrality index for hummingbird species. The index summarizes the relative structural importance of each species within the monthly interaction networks.

Association between floral traits and visitation frequency

Most floral resources used in feeding events corresponded to plants classified as ornithophilous. Of the 10 plant species included in the feeding network, eight were classified as ornithophilous and two as non-ornithophilous. Ornithophilous plants concentrated most visits. These plants had a mean of 26.4 visits, although with high variability due to the strong influence of *Tecoma fulva*. Non-ornithophilous plants had a mean of 6.0 visits, based on only two species.

The relationship between mean floral length LT1 and visitation frequency was positive but not significant (Spearman $\rho = 0.504$, $p = 0.166$, $n = 9$). This indicates an exploratory trend toward a higher number of visits in plants with longer flowers, although the association was influenced by particular species, especially *Tecoma fulva*, which had a mean floral length of 6.24 cm and concentrated 106 visits. In contrast, *Ligaria cuneifolia* had a shorter floral length (1.97 cm) but accumulated 56 visits, indicating that floral length alone does not fully explain use intensity. Similarly, other floral morphological measurements showed no significant associations with visitation frequency. Total floral length FL showed a weak and non-significant positive correlation with visits (Spearman $\rho = 0.285$, $p = 0.458$), as did LT2 (Spearman $\rho = 0.285$, $p = 0.458$).

Nectar concentration varied among the evaluated floral resources, with higher mean values in *Nicotiana paniculata*, *Nicotiana glauca*, *Puya cylindrica*, and *Tecoma fulva*. However, mean nectar concentration was

not significantly associated with floral visitation frequency (Spearman ρ = 0.018; p = 0.969; n = 7). In particular, *Tecoma fulva* was the most visited resource, although it did not have the highest nectar concentration, whereas *N. paniculata* showed high °Brix values but a low visitation frequency.

The exploratory models indicated that floral visitation frequency was not clearly explained by nectar concentration or floral length LT1. In the quasi-Poisson models, the null model showed the best relative fit (QAIC = 7.30), followed by LT1 (ΔQAIC = 1.04), °Brix (ΔQAIC = 1.11), and °Brix + LT1 (ΔQAIC = 2.35). Similarly, in the negative binomial models, the null model had the lowest AIC (AIC = 65.5), followed by °Brix (ΔAIC = 1.95) and °Brix + LT1 (ΔAIC = 2.85). None of the predictors was significant: in the combined negative binomial model, °Brix showed a non-significant negative effect (estimate = 0.560; p = 0.211), whereas LT1 showed a non-significant positive effect (estimate = 1.49; p = 0.384). These results were consistent with the Spearman correlations, where °Brix was not associated with visits (ρ = 0.018; p = 0.969; n = 7), LT1 showed a non-significant positive trend (ρ = 0.504; p = 0.166; n = 9), and °Brix was not related to LT1 (ρ = 0.214; p = 0.645; n = 7). Overall, these results indicate that floral resource use intensity was not determined by a single floral variable.

Feeding strategies, perch use, and associated behavior

During floral visits, hover feeding was the predominant strategy, followed by mixed events involving both hover feeding and perched feeding. Exclusively perched feeding was less frequent and was observed mainly on resources that provided nearby support structures during visits. Hover feeding was common in all four hummingbird species, especially during visits to *Tecoma fulva*, *Ligaria cuneifolia*, *Nicotiana glauca*, and *Puya cylindrica*, whereas mixed events were recorded mainly on *L. cuneifolia*, *Tarasa capitata*, *T. fulva*, and *P. cylindrica*.

Interaction height, measured from ground level to the point of use of the floral resource or vegetation structure, varied according to plant species and growth habit. Visits to herbs, bromeliads, and low-growing plants generally occurred between 0.5 and 2 m, whereas interactions with shrubs and trees were more frequently recorded between 3 and 11 m. Perching events reached greater heights, especially on *Schinus molle*, where some records occurred up to approximately 15 m. Effective feeding time was generally brief, with visits lasting only a few seconds per event; most records with direct measurement showed feeding times between 1 and 2 s, although some events lasted between 2 and 7 s, especially on *T. fulva*, *N. glauca*, *Lobelia decurrens*, and *Mutisia acuminata*.

A total of 126 perching events were recorded. The plants most frequently used as support were *S. molle*, with 55 records, equivalent to 43.7% of all perching events, and *T. fulva*, with 45 records, equivalent to 35.7%. Together, these two species accounted for 100 records, or 79.4% of all perching events. Other plants used as perches showed lower frequencies, including *Baccharis latifolia* and *N. glauca*, with four records each, as well as *Corryocactus* sp., *L. cuneifolia*, *P. cylindrica*, and *Viguiera* sp., with three records each.

On *S. molle*, individuals were observed perched at different heights and repeatedly using branches as resting or vigilance points. On *T. fulva*, perching events frequently occurred near flowers used for feeding, evidencing its dual function as both a floral resource and a support structure.

A total of 21 intra- and interspecific competition events associated with floral resources were recorded, involving the four hummingbird species and four plant species. The highest frequency of competitive events was associated with *T. fulva*, with 11 events, equivalent to 52.4%, followed by *L. cuneifolia*, with seven events, equivalent to 33.3%. At the hummingbird level, the greatest participation in competitive events was recorded for *Patagona gigas*, with 11 events, equivalent to 28.2%, and *Thaumastura cora*, with 10 events, equivalent to 25.6%. *Rhodopis vesper* recorded eight events, equivalent to 20.5%, whereas *Colibri coruscans* showed six events, equivalent to 15.4%. Competitive events for floral resources involving another floral visitor were also recorded, as in the case of *Conirostrum cinereum* (Fig. 6).

Observed behaviors included chases, displacement of individuals from flowers or perches, defense of floral resources, and repeated permanence at the same feeding points. In several cases, agonistic events occurred on plants that also concentrated high visitation frequencies, such as *T. fulva* and *L. cuneifolia*. Finally, observations associated with reproductive activity were recorded, including the presence of nests, juveniles, and transport of plant material, mainly in *R. vesper* and *T. cora*. These behaviors were observed in association with plants used as perches or nearby support structures, such as *T. fulva*, *S. molle*, *Ophyosporum peruvianus*, and *Viguiera* sp.

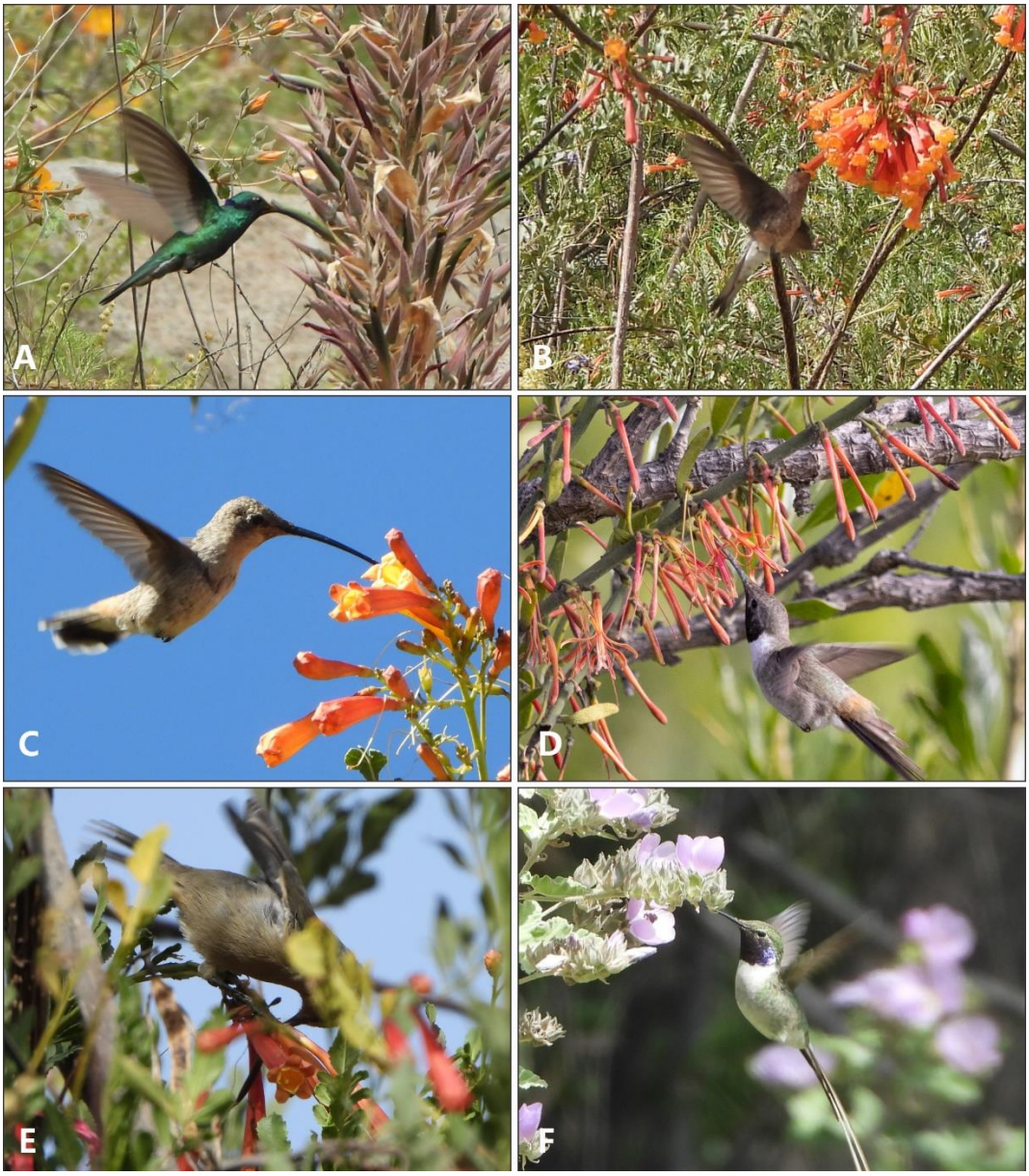

Figure 6. Use of floral resources by hummingbirds recorded in Sogay, Arequipa, Perú. (A) *Colibri coruscans-Puya cylindrica.* (B) *Patagona gigas-Tecoma fulva*. (C) *Rhodopis vesper-Tecoma fulva*. (D) *Rhodopis vesper-Ligaria cuneifolia*. (E) *Conirostrum cinereum* stealing nectar from *Tecoma fulva* (F) *Thaumastura cora-Tarasa capitata.*

Discussion

General network structure and concentrated use of floral resources

The plant-hummingbird network recorded in Sogay showed an intermediate level of specialization, relatively high connectance, and a marked concentration of visits on a few plant species. This indicates that the

network was neither completely generalized nor highly specialized, but rather showed an intermediate degree of resource partitioning. This result is consistent with the use of quantitative interaction matrices, in which H2' allows specialization to be evaluated by considering the relative frequency of interactions and not only the presence or absence of links (Blüthgen et al. 2006).

The connectance found in this study indicates that more than half of the possible interactions among the species present in the network were recorded, suggesting a relatively high level of floral resource sharing. However, the distribution of visits was not homogeneous, as *Tecoma fulva*, *Ligaria cuneifolia*, and *Nicotiana glauca* accounted for 83.0% of feeding records. This pattern is consistent with the typical structure of many mutualistic networks, in which several species interact in a generalized way, but most interaction flow is concentrated in a reduced subset of more connected or abundant species. Mutualistic networks are often heterogeneous, with weak and asymmetric interactions and a core of species that contribute disproportionately to the overall connectivity of the system (Bascompte and Jordano 2007).

In this study, the dominance of *T. fulva* as a floral resource suggests that this species played a structuring role within the observed network. In addition to concentrating the highest number of visits, it interacted with several hummingbird species and showed high centrality, reinforcing its importance within the system. Studies of plant-hummingbird networks have shown that certain plant species, particularly trees or shrubs with specialized flowers, can function as key resources supporting interactions with hummingbirds, even in modified environments or landscapes with heterogeneous floral availability (Maruyama et al. 2019).

Central species, dependence, and interaction asymmetry

The centrality analysis identified *Rhodopis vesper* as the most central hummingbird species in the network and *Tecoma fulva* as the plant species with the greatest structural importance. *Rhodopis vesper* showed the highest degree, weighted strength, betweenness, closeness, and composite centrality index among hummingbirds, indicating that this species was not only frequent but also relevant for connecting different floral resources within the network. In ecological networks, species with high centrality may contribute to maintaining the structural cohesion of the system because they connect different subsets of species and concentrate an important portion of interaction flow (Bascompte and Jordano 2007).

The importance of *R. vesper* was also reflected in its dominant interaction with *T. fulva*. However, this relationship was not strictly reciprocal. The dependence of *R. vesper* on *T. fulva* was high, whereas *T. fulva* was used by more than one hummingbird species. This pattern of asymmetric dependence is common in plant-animal networks, where an animal species may depend strongly on one resource, while the plant maintains interactions with several visitors. In hummingbird-plant networks, dependence and asymmetry make it possible to identify dominant interactions and species that may contribute differentially to network maintenance (Martínez-García and Ortiz-Pulido 2014).

The *Ligaria cuneifolia-Thaumastura cora* interaction showed a different pattern, with relatively balanced dependence between both species. This suggests a strong and relatively reciprocal association within the observed network. This relationship may be influenced by the temporal availability of *L. cuneifolia*, floral accessibility, or the morphological and behavioral compatibility of *T. cora* with this resource. In contrast, plant species with few records, such as *Cantua volcanica*, *Tropaeolum tuberosum*, *Mutisia acuminata*, and *Nicotiana paniculata*, showed high dependence on a single recorded visitor. Nevertheless, these may represent exploratory use of floral resources by hummingbirds or rare interactions within the network.

Temporal dynamics of the plant-hummingbird network

The structure of the plant–hummingbird network showed marked temporal variation during the evaluation period. May and June concentrated the highest number of feeding records, the greatest richness of unique interactions, and the highest temporal similarity. These months can therefore be interpreted as the temporal core of network activity, probably reflecting a period in which several dominant floral resources were simultaneously available. In contrast, August showed a simplified network, with fewer records, fewer

interactions, and low similarity relative to previous months, suggesting temporal turnover in the composition and intensity of interactions.

This pattern is consistent with previous studies showing that plant–hummingbird networks are not static, but may vary substantially among months or seasons in response to changes in floral phenology, nectar availability, and visitor activity (Fonseca et al. 2015; Infante et al. 2020). Temporal variation in nectar availability can influence hummingbird movements, foraging areas, and consequently the distribution of plant–hummingbird interactions across time (Fonseca et al. 2015). In Sogay, the high similarity between May and June suggests that a relatively stable set of dominant interactions was maintained during this period, probably supported by resources such as *Tecoma fulva*, *Ligaria cuneifolia*, *Nicotiana glauca*, and *Puya cylindrica*. However, because floral availability was not systematically quantified, these temporal changes should be interpreted as variation in observed resource use rather than as direct evidence of changes in floral abundance.

In Sogay, the high similarity between May and June suggests that a relatively stable set of dominant interactions was maintained during this period, probably supported by resources such as *Tecoma fulva*, *Ligaria cuneifolia*, *Nicotiana glauca*, and *Puya cylindrica*. In plant-hummingbird networks, the temporal persistence of some floral resources may contribute to maintaining network connectivity and favoring the local persistence of nectar-feeding birds, especially when other resources are more ephemeral or less available (Fonseca et al. 2015; Maruyama et al. 2019). The reduction in interaction records toward July and August is also consistent with the seasonality of arid inter-Andean environments. In systems with marked climatic variation, hummingbirds may modify their spatial use patterns and move locally in response to changes in flower and nectar availability (Ortiz-Pulido and Vargas-Licona 2008). Therefore, the low similarity of August relative to previous months does not necessarily imply the absence of resources in the landscape, but rather a possible redistribution of interactions toward other resources, sectors, or patches that were not represented with the same intensity during sampling.

Although the general rarefaction analysis suggested that rare undetected interactions may exist, monthly coverage indicated that dominant interactions were adequately represented in most months. This difference should not be interpreted as a contradiction. On the one hand, the total richness of network links may continue to increase with greater sampling effort; on the other hand, monthly coverage allows evaluation of whether the most frequent interactions were reasonably captured. In this sense, sample coverage-based methods are useful because they compare communities or assemblages based on the proportion of diversity represented by sampling, rather than only on the number of individuals or records (Chao and Jost 2012; Hsieh et al. 2016). Thus, although the analysis indicates that the complete network may contain additional rare links, the results obtained are suitable for interpreting the dominant interactions that structured the network during the study period. In addition, no other hummingbird species have been reported for the area, except for *Metallura phoebe*, which occasionally descends altitudinally to this valley. In the case of floral resource availability, additional species may occur outside the spatial range of the sampling, including species with non-ornithophilous traits.

Feeding strategies, perch use, and competition

The results show that plant use by hummingbirds in Sogay was not limited to nectar consumption. This behavioral component broadens the interpretation of the network because it allows plants to be understood not only as floral resources, but also as habitat elements used for resting, vigilance, defense, or remaining near feeding areas. In hummingbirds, perch use may represent an important component of the activity budget because these birds alternate feeding periods with resting, vigilance, and defense of floral resources (Calviño-Cancela 2006; Gutiérrez-Zamora 2008).

In-flight feeding was the predominant strategy during floral visits, which is consistent with the morphological and physiological adaptations of hummingbirds for exploiting flowers through hovering flight and direct access to nectar (Cotton 1998; Sonne et al. 2016). However, mixed events and some perched feeding

events were also recorded, mainly on plants that provided nearby support structures. This behavioral variation suggests that foraging mode may depend on the hummingbird species, plant architecture, flower position, nectar accessibility, and availability of nearby perches. Studies of plant-hummingbird networks have shown that interactions do not depend only on morphological matching between flower and bill, but also on spatial and temporal overlap, plant architecture, and local encounter opportunities between visitors and floral resources (Maruyama et al. 2014; Rodríguez-Flores et al. 2019).

The role of *Schinus molle* as the main perch plant is especially relevant because this species was not one of the main floral feeding resources, but accounted for 43.7% of perching events. This shows that some plant species may have functional importance that is not detected when only floral visits are analyzed. In contrast, *Tecoma fulva* fulfilled a dual function: it was the most visited floral resource and the second most frequently used perch plant. This dual role may increase its ecological importance within the valley by providing both nectar and support structures near feeding sites. According to the literature, the availability of perches close to floral resources may favor vigilance, resting, and territorial defense, especially when resources are spatially concentrated or energetically profitable (Jacobi and Antonini 2008; Rousseu et al. 2014).

Competition events were mainly associated with *T. fulva*, *L. cuneifolia*, and *S. molle*, suggesting that the most frequently used floral resources or support structures also functioned as sites of agonistic interaction. Observations of chases, displacements, and resource defense are consistent with hummingbird ecology, in which territorial defense may intensify when resources are spatially concentrated, temporally limited, or energetically valuable (Jacobi and Antonini 2008; Rousseu et al. 2014), as documented for hummingbirds in territories associated with *T. fulva* in arid environments of northern Chile (Clark et al. 2013). Likewise, the nectar-robbing event observed in *T. cora* on *T. fulva* is relevant, because nectar robbing can modify the mutualistic function of a floral visit by allowing access to the resource without effective contact with the reproductive structures of the flower (Irwin et al. 2010). This behavior has previously been recorded in *T. cora* feeding on *T. fulva* through perforations made by *Conirostrum cinereum* (Clark et al. 2013).

Floral traits, nectar, and resource use

Most visits in Sogay were concentrated on plants classified as ornithophilous, particularly *Tecoma fulva*, *Ligaria cuneifolia*, and *Nicotiana glauca*. However, the exploratory analyses did not show statistically significant differences in visitation frequency between ornithophilous and non-ornithophilous plants, nor a significant association between floral length and number of visits. These results suggest that the floral traits measured in this study may contribute to hummingbird resource use, but they did not explain by themselves the observed structure of visits. In plant–hummingbird networks, interaction frequency may depend on multiple factors acting simultaneously, including floral morphology, temporal overlap, flower abundance, nectar rewards, accessibility, plant architecture, and spatial overlap between plants and birds (Dalsgaard et al. 2009; Maruyama et al. 2014; Rodríguez-Flores et al. 2019).

Although nectar is a fundamental energetic resource for nectar-feeding birds, its effect on visitation may depend not only on sugar concentration, but also on nectar volume, renewal rate, floral accessibility, flower abundance, and the temporal and spatial distribution of the resource. In nectar-feeding birds, more dilute nectar solutions may be compensated for by higher consumption rates, although this involves physiological constraints associated with water and energy balance (Nicolson and Fleming 2003). In Sogay, nectar concentration was not associated with visitation frequency, and the exploratory models indicated that °Brix and floral length LT1 did not improve the explanation of the number of visits relative to the null model. This suggests that nectar concentration alone was not a strong predictor of the intensity of floral resource use.

This pattern is consistent with recent evidence showing that nectar traits may be less predictive of plant–hummingbird interaction frequency than morphological matching between hummingbird bills and floral corollas. Maglianesi et al. (2024) found that interaction frequency increased when bill and corolla lengths were similar, whereas nectar traits were unrelated to interaction frequency, suggesting that nectar may play

a secondary or context-dependent role within plant–hummingbird networks. In the present study, *T. fulva* was the most visited floral resource, despite not having the highest nectar concentration, whereas *Nicotiana paniculata* showed high °Brix values but low visitation frequency. This contrast indicates that the dominance of *T. fulva* within the network was not determined by nectar concentration alone, but probably by a combination of floral morphology, accessibility, local availability, temporal persistence, plant architecture, and behavioral use by hummingbirds.

The observed pattern also supports the idea that hummingbirds do not exclusively use flowers with classic ornithophilous traits. Although many hummingbird-visited plants have tubular flowers, conspicuous colors, and nectar accessible to birds, several studies have shown that hummingbirds can also use non-ornithophilous flowers when these provide accessible rewards or are available during periods of lower floral supply (Dalsgaard et al. 2009; Maruyama et al. 2013; Morales-Contreras et al. 2020). Similarly, studies on nectar characteristics in flowers visited by hummingbirds have indicated that nectar volume, sugar concentration, and energetic content may not clearly differ between ornithophilous and non-ornithophilous flowers, reinforcing the idea that floral classification does not always predict the intensity of use by nectar-feeding birds (de Araújo et al. 2021).

Therefore, the use of floral resources by hummingbirds in Sogay should be interpreted as a multidimensional process rather than as a direct response to a single floral variable. The high use of *T. fulva*, *L. cuneifolia*, and *N. glauca* likely reflects the combined influence of floral traits, nectar rewards, accessibility, temporal availability, and the behavior of the visiting hummingbirds. Because floral availability was not systematically quantified, these patterns should be interpreted as observed resource use and visitation frequency, rather than as floral preference or resource selection.

Ecological and conservation implications

The results of this study have ecological and conservation implications for nectar-feeding birds and their resources in arid inter-Andean valleys of southern Peru. The identification of *T. fulva* as the main floral resource, together with the secondary importance of *L. cuneifolia* and *N. glauca*, suggests that a reduced set of plant species can sustain a large proportion of plant–hummingbird interactions during the period following the rainy season. In environments where floral resources may be seasonal and spatially concentrated, maintaining these resources could be important for conserving the functional connectivity between nectar-feeding birds and flowering plants.

However, the conservation value of plants in this system was not limited to their role as nectar sources. The frequent use of *Schinus molle* as a perch indicates that plant species with low or no contribution to the feeding network may still provide important structural functions within the habitat. Perches can facilitate resting, vigilance, territorial behavior, and proximity to feeding areas, especially when floral resources are patchily distributed. Likewise, *T. fulva* fulfilled a dual role as both the most visited floral resource and one of the most frequently used perch plants, reinforcing its importance as a functional resource within the valley.

These findings suggest that conservation or habitat management actions in arid Andean landscapes should not focus exclusively on increasing floral abundance, but also on maintaining heterogeneous vegetation structure. Trees, shrubs, and plants from different vertical strata may provide complementary resources for feeding, resting, territorial defense, and reproduction. In Sogay, the combined use of floral resources, perches, and sites associated with agonistic or reproductive behavior indicates that hummingbirds rely on vegetation patches as multifunctional habitat units rather than only as nectar sources.

Future studies should incorporate floral abundance, flowering phenology, nectar volume, nectar renewal rates, pollen transfer, and repeated annual sampling to evaluate whether the central species identified here maintain their importance under different environmental conditions.

Despite this limitation, this study provides baseline information for a poorly documented inter-Andean system in southern Peru. This is particularly relevant in the Peruvian context, where interaction records remain

spatially uneven despite recent national syntheses of pollination and floral-visitor interactions (Bernabé Paniagua et al. 2024). At broader scales, projected changes in species co-occurrence under climate change are expected to alter plant–hummingbird network size, number of links, and robustness (Restrepo-González et al. 2026). Although the present study did not evaluate climate change scenarios, the temporal variation observed in Sogay highlights the importance of maintaining diverse floral and structural resources that can buffer seasonal changes in resource availability.

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Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

This study did not involve human participants or animal experimentation.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.

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Author contributions

MAQ-P, CRL-F: Conceptualization, Investigation, Data Curation, Funding Acquisition, Writing-Editing and Review; MAQ-P, CRL-F: Data Analysis and Writing-Original Draft

Data availability

All of the data that support the findings of this study are available in the main text

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