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Research Article

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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Abstract

Plant-hummingbird interactions are key components of Neotropical ecosystems, yet they remain poorly documented in arid inter-Andean valleys of southern Peru, which are characterized by marked climatic seasonality. 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 reveal a temporally dynamic feeding network in which interaction frequency was concentrated around a small set of floral resources, while plants were also used as perches and sites of agonistic interactions. Overall, this study highlights the ecological importance of floral and structural resources for hummingbird activity in arid Andean landscapes.

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

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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 90% of flowering plant species are estimated to rely on animal-mediated pollination, highlighting the importance of these interactions for the maintenance of plant diversity and ecosystem functioning (Tong et al. 2023). 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 (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 hummingbirds show traits associated with the ornithophily syndrome, such as tubular flowers, conspicuous colors, low scent production, and nectar secretion, 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 regarded as a classic example of coevolution, recent syntheses indicate that the ecological and evolutionary outcomes of this mutualism are heterogeneous and 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 organized across poorly studied environments.

However, hummingbird-plant interactions do not necessarily reflect strict specialization. Hummingbirds can use both ornithophilous flowers and flowers lacking the classical traits associated with bird pollination, behaving as relatively generalist floral visitors under some ecological conditions (Dalsgaard et al. 2009; Rodrigues and Araujo 2011; Morales-Contreras et al. 2020). Such plasticity may be associated with their high energetic requirements, temporal variation in flowering, and local resource availability. Consequently, non-ornithophilous flowers may also constitute important resources in seasonal Neotropical environments or during periods of reduced floral availability (Maruyama et al. 2013).

Ecological network analysis provides a community-level framework for examining these interactions by simultaneously considering multiple plant and hummingbird species. In bipartite plant-pollinator networks, species are represented as nodes and their interactions as links, which can be weighted according to interaction frequency or intensity (Bascompte and Jordano 2007; Dormann et al. 2008). Network and species-level metrics, including connectance, specialization, nestedness, modularity, and centrality, provide complementary information on network organization and on the structural roles played by individual species (Dehling 2018; Vizentin-Bugoni et al. 2018). Importantly, these networks are not static. Their structure and the roles of individual species can change over time as species appear or disappear, interaction partners are reorganized, and resource availability and relative abundances fluctuate (Souza et al. 2018; Schwarz et al. 2020; Hervías-Parejo et al. 2023). Recent studies of plant-hummingbird and other plant-pollinator systems have documented substantial temporal variation in interaction composition, network structure, and species roles, emphasizing the importance of explicitly considering temporal dynamics rather than relying exclusively on temporally aggregated networks (Queiroz et al. 2025; Pereira-Guaqueta et al. 2026).

Temporal variation may be particularly important in arid and seasonally dry environments, where water limitation and irregular precipitation strong-

ly influence flowering phenology and the temporal availability of floral resources. Pollination networks in these environments are therefore expected to be especially dynamic, although their temporal organization remains comparatively poorly studied (Pereira-Guaqueta et al. 2026). This context is relevant to the western slopes of the southern Peruvian Andes, where arid conditions, topographic heterogeneity, and spatially heterogeneous vegetation generate strongly seasonal and locally concentrated floral resources (Weberbauer 1945; Arroyo et al. 1983; Montesinos-Tubée 2016; SENAMHI 2021). More broadly, plant-pollinator interactions in the tropical Andes may vary considerably at fine spatial and temporal scales in response to species turnover, phenology, environmental heterogeneity, and climatic variability (Rueda-Uribe et al. 2025).

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 involving 970 plant species or morphospecies and 671 animal species or morphospecies, while also revealing important geographic gaps in interaction data across the country (Bernabé Paniagua et al. 2024). In southern Peru, hummingbirds are characteristic components of arid environments, shrublands, agricultural areas, and riparian habitats along the western Andean slopes. However, available information has focused primarily on occurrence and distribution records (Villegas Paredes et al. 2025) or urban inventories (Rivero-Mamani et al. 2025), whereas the functional interactions between hummingbirds and plants remain poorly understood. In particular, little is known about how these interactions are organized through time or whether the structural importance of plant and hummingbird species remains constant during periods of changing resource availability. Addressing these dimensions is important because species that occupy central positions within interaction networks may contribute disproportionately to network connectivity and the maintenance of ecological interactions.

Floral traits provide an additional mechanistic dimension for understanding resource use by hummingbirds. Morphological characteristics such as corolla length can facilitate or restrict access to nectar and determine the degree of morphological matching between flowers and hummingbird bills, whereas nectar characteristics may influence the energetic profitability of floral resources and foraging decisions. Recent evidence indicates that plant-hummingbird interaction frequency may increase with morphological matching between bill and corolla length, although the contribution of nectar traits can be weaker or context dependent (Maglianesi et al. 2024). Evaluating these traits together with observed visitation therefore provides an exploratory means of assessing whether differences among floral resources are associated with their intensity of use.

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 set out 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 flowering plants associated with streams, irrigation canals, and crop fields. These landscape elements generate spatially heterogeneous vegetation patches that may provide floral and structural resources 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 flowering plants used as potential floral resources, accessibility for repeated surveys, and previous observations of 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.

Evaluation period and observation schedule

Field evaluations were conducted from March to August 2025, covering the period following the main rainy season in the region. This sampling period was selected to encompass the post-rainy-season flowering period and to increase the probability of recording interactions between hummingbirds and flowering plants. It also coincided with the local occurrence of several hummingbird species in the study area. A total of 24 surveys were conducted across the six-month study period, with one survey per week and four surveys per month. The same sampling route was followed during each survey to minimize variation associated with sampling effort. Each survey lasted approximately 5 h, resulting in a total sampling effort of approximately 120 observation hours over the six-month study period. 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 survey, the previously delimited sectors were traversed slowly, prioritizing areas with flowering plants and visible hummingbird activity. Observations were conducted at a sufficient distance to observe hummingbirds without altering

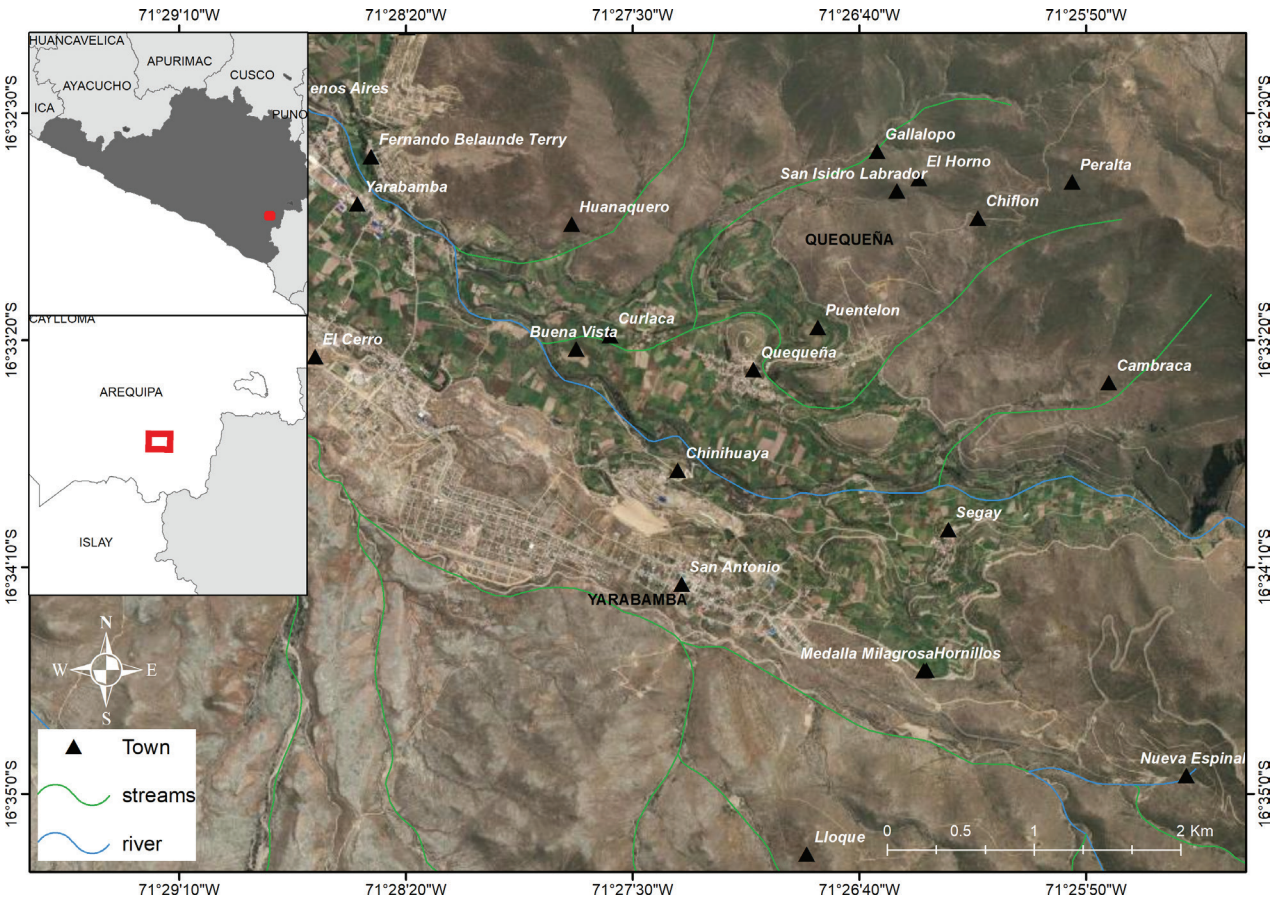

Figure 1. Location of the study area in the Sogay-Quequeña valley, Arequipa, southern Peru. The map shows the evaluated valley sector, nearby towns, streams and the main river corridor associated with the observation area.

their behavior or interrupting their interactions. When an individual was detected, the survey was temporarily paused, and the observation distance was increased whenever behavioral changes attributable to the observer were detected.

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 a fixed transect with variable width, established during a preliminary survey in which the presence of floral resources and hummingbird activity was assessed. The transect followed the local topography and spatial distribution of floral resources and covered approximately 3 km during each survey. Because floral resources were heterogeneously distributed along the route, sampling was conducted continuously rather than by delimiting floral patches as independent sampling units. 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 sugar concentration was evaluated in the plant species recorded as floral resources used by hummingbirds. Measurements were conducted between 07:00 and 09:00 h to standardize the time of nectar sampling. For each plant species, recently opened flowers were selected for nectar extraction.

Nectar was extracted directly from the base of the corolla using 5 µL capillary tubes, a procedure commonly used to characterize floral nectar in pollination and floral-visitor studies (Kearns and Inouye 1993; Dafni et al. 2005). Because the nectar volume obtained from individual flowers was insufficient for refractometric measurement in several species, nectar from multiple flowers of the same species was pooled until a sufficient volume was obtained. Nectar sugar concentration was estimated using a portable 0–30 °Brix refractometer, with five replicate measurements obtained for each floral resource evaluated. °Brix values were used as an approximation of the relative sugar concentration of nectar and were subsequently evaluated as a potential correlate of hummingbird visitation frequency (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, fol-

lowing 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 (Blüthgen et al. 2006; Bascompte and Jordano 2007; Dormann et al. 2008; Martínez-García and Ortiz-Pulido 2014).

At the network level, we calculated plant and hummingbird richness, the number of observed and possible links, connectance, interaction evenness, nestedness (NODF and weighted NODF), complementary specialization H2', hummingbird generality, and plant vulnerability. Generality and vulnerability are standard quantitative metrics for bipartite networks implemented in the bipartite package. Hummingbird generality represents the weighted mean effective number of plant species used by hummingbirds, whereas plant vulnerability represents the weighted mean effective number of hummingbird species interacting with each plant. 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 (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. The composite index was interpreted as a relative measure of structural importance within each analyzed network and trophic level. Therefore, its values were used to rank and compare species within the same network rather than as absolute centrality values directly comparable among networks of different size or composition. Species with higher composite values were considered to have a greater relative contribution to network connectivity and interaction intensity (Csárdi and Nepusz 2006; Bascompte and Jordano 2007; Dormann et al. 2008).

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. Interaction asymmetry was calculated as the difference between plant-to-hummingbird and hummingbird-to-plant dependence. Accordingly, values close to zero indicate relatively balanced dependence between the two interacting species, positive values indicate greater dependence of the plant on the hummingbird, and negative values indicate greater dependence of the hummingbird on the plant.

Sampling sufficiency was evaluated using complementary incidence and abundance-based approaches. First, an incidence matrix was constructed in which sampling dates represented sampling units and each unique plant-hummingbird combination represented an interaction unit. For each sampling date, interactions were coded as present (1) or absent (0), regardless of the number of feeding events recorded on that date. This incidence matrix was used to estimate total interaction richness using the Chao, first-order Jackknife, second-order Jackknife, and Bootstrap estimators implemented in the specpool function of the vegan package (Oksanen et al. 2025). The ratio between the number of observed links and the Chao richness estimate was additionally calculated as an incidence-based measure of observed interaction richness relative to the estimated total richness.

Second, sample-size-based rarefaction and extrapolation were performed using an abundance-based approach. For this analysis, each unique plant-hummingbird combination (i.e., each network link) was treated as an interaction richness unit analogous to a species, whereas the number of feeding records observed for each plant-hummingbird pair represented its abundance. Thus, the input data consisted of abundance vectors containing the frequency of each unique interaction. Rarefaction and extrapolation curves were generated for the accumulated network and separately for each month to evaluate the number of observed and expected plant-hummingbird links at different sampling sizes. Sample coverage was also estimated as the proportion of individual interaction records belonging to the plant-hummingbird links represented in the sample. These analyses were performed using the iNEXT package (Hsieh et al. 2016), following an abundance-based approach previously applied to plant-hummingbird interaction networks (Queiroz et al. 2025).

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. Because the composite index was standardized separately within each monthly network, temporal comparisons focused on changes in the identity and relative ranking of central species rather than on direct comparisons of absolute index magnitudes among months.

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 have remained undetected. The estimated interaction richness was 51.55 links according to Chao, 28.64 according to Jackknife 1, 35.04 according to Jackknife 2, and 24.22 according to Bootstrap, compared with the 21 links observed in the accumulated network (Fig. 2). Thus, the observed links represented 40.7% of the interaction richness estimated by Chao, suggesting that additional low-frequency interactions may occur in the system. In contrast, monthly sample coverage was high on average (94.48%; range: 77.41–100%), with the lowest value recorded in July (77.41%) and the highest in August (100%).

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. Network connectance was 0.525, complementary specialization was H2' = 0.550, interaction evenness was 0.612, and modularity was Q = 0.386. Presence-absence nestedness was NODF = 65.23, whereas weighted nestedness was lower when interaction frequencies were considered. Hummingbird generality was 2.54, whereas plant vulnerability was 2.19 (Fig. 3). These values indicate that hummingbirds used, on average, slightly more than two effective floral-resource partners, while plants interacted with approximately two effective hummingbird partners when interaction

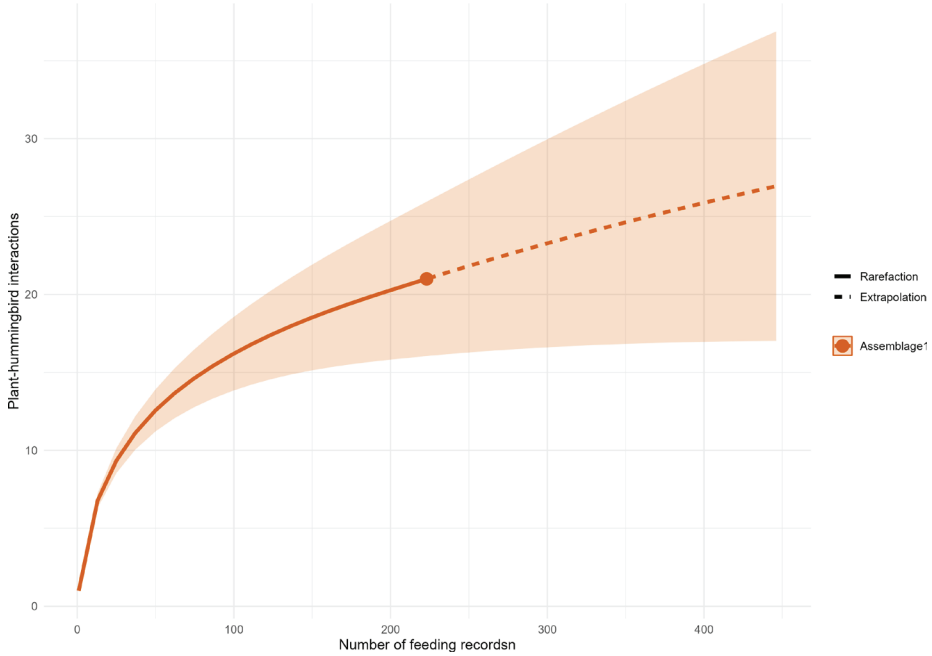

Figure 2. Sample-size-based rarefaction and extrapolation curve of plant-hummingbird interaction richness recorded in Sogay.

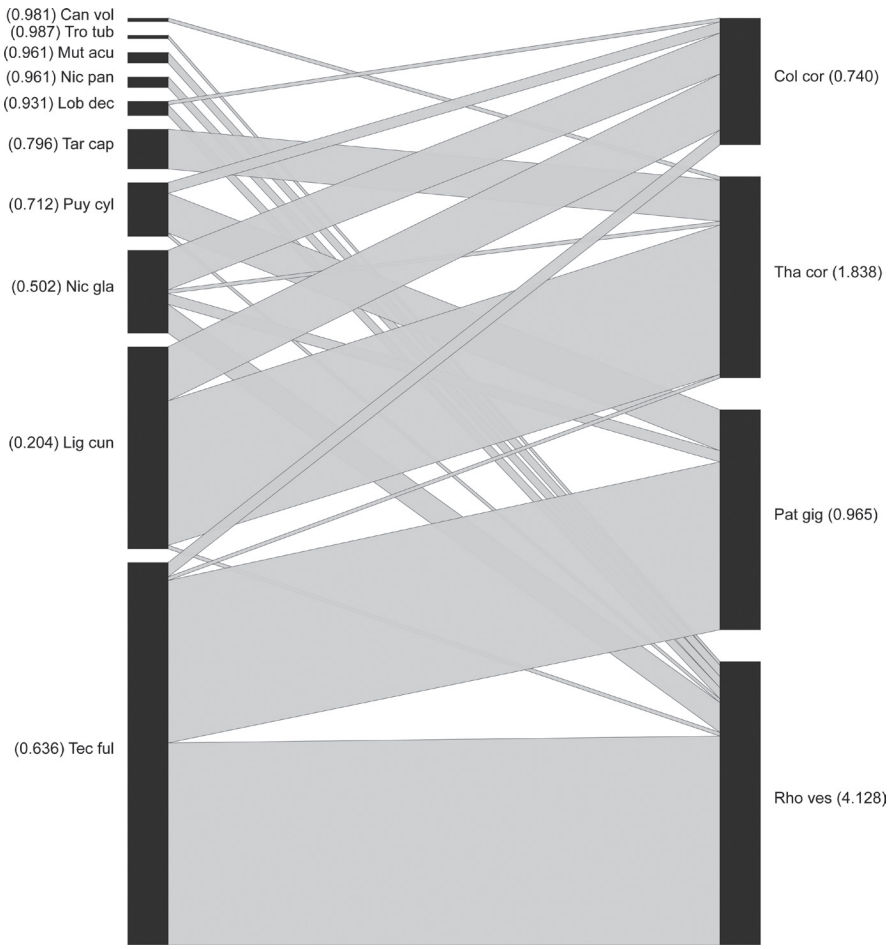

Figure 3. Accumulated bipartite network representing interactions between plant species (left) and hummingbird species (right) recorded in the Sogay valley, southern Peru. Box width represents the degree of each species, defined as the number of interaction links. Line thickness indicates the frequency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

frequencies were considered. Overall, these metrics indicate a network with moderately high connectivity and intermediate specialization, in which several hummingbird species shared floral resources but interaction frequencies were unevenly distributed among plant-hummingbird pairs. The moderate modularity suggests some internal organization into subsets of more strongly interacting species, whereas the higher presence-absence nestedness relative to weighted nestedness indicates that nested organization was more evident in interaction occurrence than in interaction intensity.

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, accounting for 47.5% of all feeding records, followed by *Ligaria cuneifolia* (25.1%) and *Nicotiana glauca* (10.3%). Together, these three species accounted for 83.0% of all feeding records, whereas each of the remaining floral resources contributed less than 7% of visits (Fig. 4A). At the hummingbird level, *Rhodopis vesper* showed the highest visitation frequency, followed by *Patagona gigas*, *Thaumastura cora*, and *Colibri coruscans* (Fig. 4B). The most frequent interactions were *Tecoma fulva-Rhodopis vesper* (25.1% of feeding records), *Tecoma fulva-Patagona gigas* (20.2%), and *Ligaria cuneifolia-Thaumastura cora* (17.9%). Together, these three links accounted for 63.2% of all feeding records, demonstrating that interaction intensity was strongly concentrated in a small subset of plant-hummingbird pairs.

Interaction dependence and asymmetry

Dominant interactions showed different patterns of dependence between plants and hummingbirds (Table 1). 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*, resulting in an asymmetry value of –0.209. This negative value

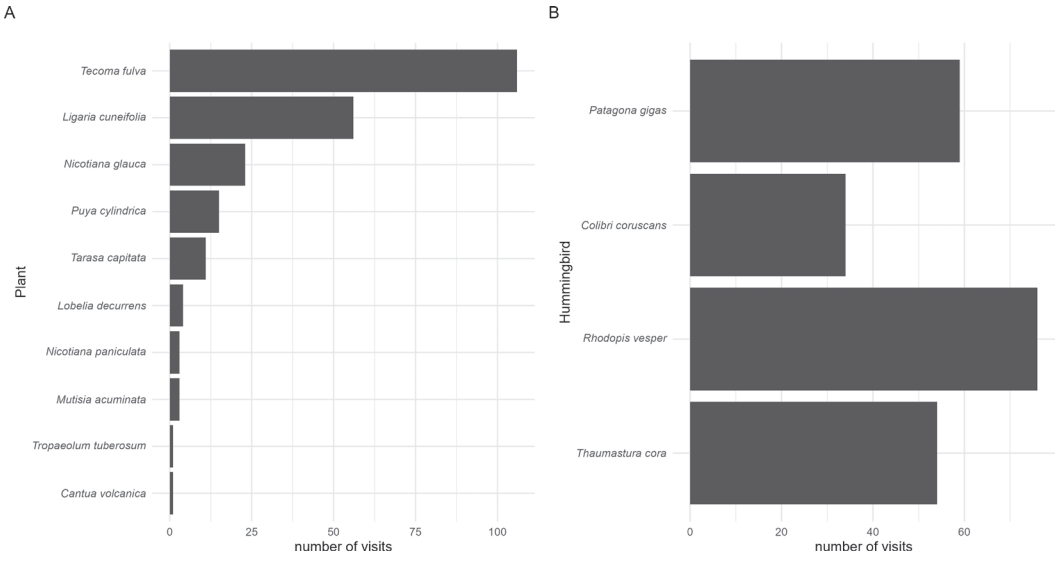

Figure 4. Frequency of floral visits by plant species and hummingbird species in Sogay. **A.** Number of visits recorded for each plant species used as floral resource; **B.** Number of visits recorded for each hummingbird species. Bars represent total feeding records during the study period.

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

Plant (P)	Hummingbird (H)	Visits	Dependence P – H	Dependence H - P	Asymmetry*
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

*Positive asymmetry values indicate greater plant dependence on the hummingbird, negative values indicate greater hummingbird dependence on the plant, and values close to zero indicate relatively balanced dependence.

indicates greater proportional dependence of *R. vesper* on *T. fulva* than of *T. fulva* on *R. vesper*. 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), indicating relatively balanced proportional dependence between the two 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.

Central species in the network

The centrality analysis identified *Rhodopis vesper* as the most central hummingbird species within the accumulated network. This species had the highest degree among hummingbirds (degree = 8), weighted strength (strength = 76), betweenness (0.705), and closeness (2.694). Its composite centrality index

was 1.184, the highest value among hummingbird species. Together, these metrics indicate that *R. vesper* occupied the most central relative structural position among hummingbirds, combining a high number of floral partners, high interaction frequency, and a comparatively important position connecting different nodes within the observed network.

Among plants, *Tecoma fulva* showed the highest relative centrality, with degree = 4, strength = 106, betweenness = 0.218, closeness = 2.616, eigenvector centrality = 1.000, and a composite centrality index of 1.748. It was followed by *Nicotiana glauca* (0.926) and *Ligaria cuneifolia* (0.748). These results identify *T. fulva* as the most central floral resource within the accumulated network, whereas *N. glauca* and *L. cuneifolia* occupied secondary positions according to the composite centrality index.

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 according to the month, 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.

The identity of the most central species varied according to the months (Fig. 5). *Thaumastura cora* was the most central hummingbird in March, followed by *Rhodopis vesper* in April and *Colibri coruscans* in May. *Rhodopis vesper* regained the highest centrality from June onward. Among plants, *Ligaria cuneifolia* was the most central species in March, whereas *Tecoma fulva* occupied this role consistently from April to July before being replaced by *Nicotiana glauca* in August. Overall, *T. fulva* was the most persistent central floral resource during the period of greatest network activity, whereas *R. vesper* was the hummingbird that most consistently occupied a central structural position across months.

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. Orni-

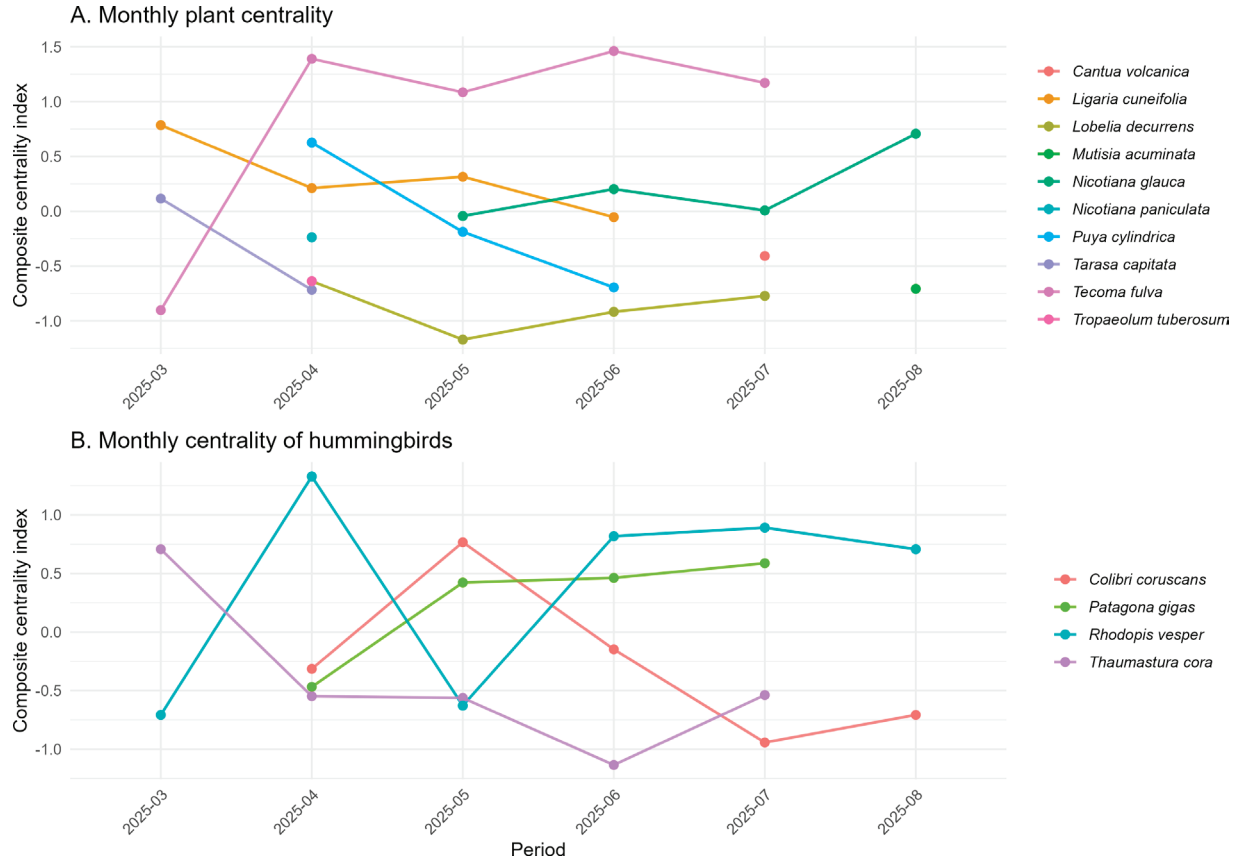

Figure 5. Temporal variation in plant and hummingbird centrality within the plant-hummingbird interaction network of Sogay. **A.** Monthly composite centrality index for plant species; **B.** Monthly composite centrality index for hummingbird species. The index summarizes the relative structural importance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

thophilous 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 TL1 and visitation frequency was positive but not significant (Spearman ρ = 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 ρ = 0.285, p = 0.458), as did TL2 (Spearman ρ = 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 TL1. In the quasi-Poisson models, the null model showed the best relative fit (QAIC = 7.30), followed by TL1 (ΔQAIC = 1.04), °Brix (ΔQAIC = 1.11), and °Brix + TL1 (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 + TL1 (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 TL1 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), TL1 showed a non-significant positive trend (ρ = 0.504; p = 0.166; n = 9), and °Brix was not related to TL1 (ρ = 0.214; p = 0.645; n = 7). Overall, visitation frequency was not clearly explained by either nectar sugar concentration or the floral-length variables evaluated.

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 measurements 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 participations, equivalent to 28.2%, and *Thaumastura cora*, with 10 participations, equivalent to 25.6%. *Rhodopis vesper* recorded eight participations, equivalent to 20.5%, whereas *Colibri coruscans* showed six participations, equivalent to 15.4%. Competitive events for floral resources involving another floral visitor were also recorded, as in the case of *Conirostrum cinereum*, which accounted for four participations (10.3%) (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*, *Ophryosporus peruvianus*, and *Viguiera* sp.

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

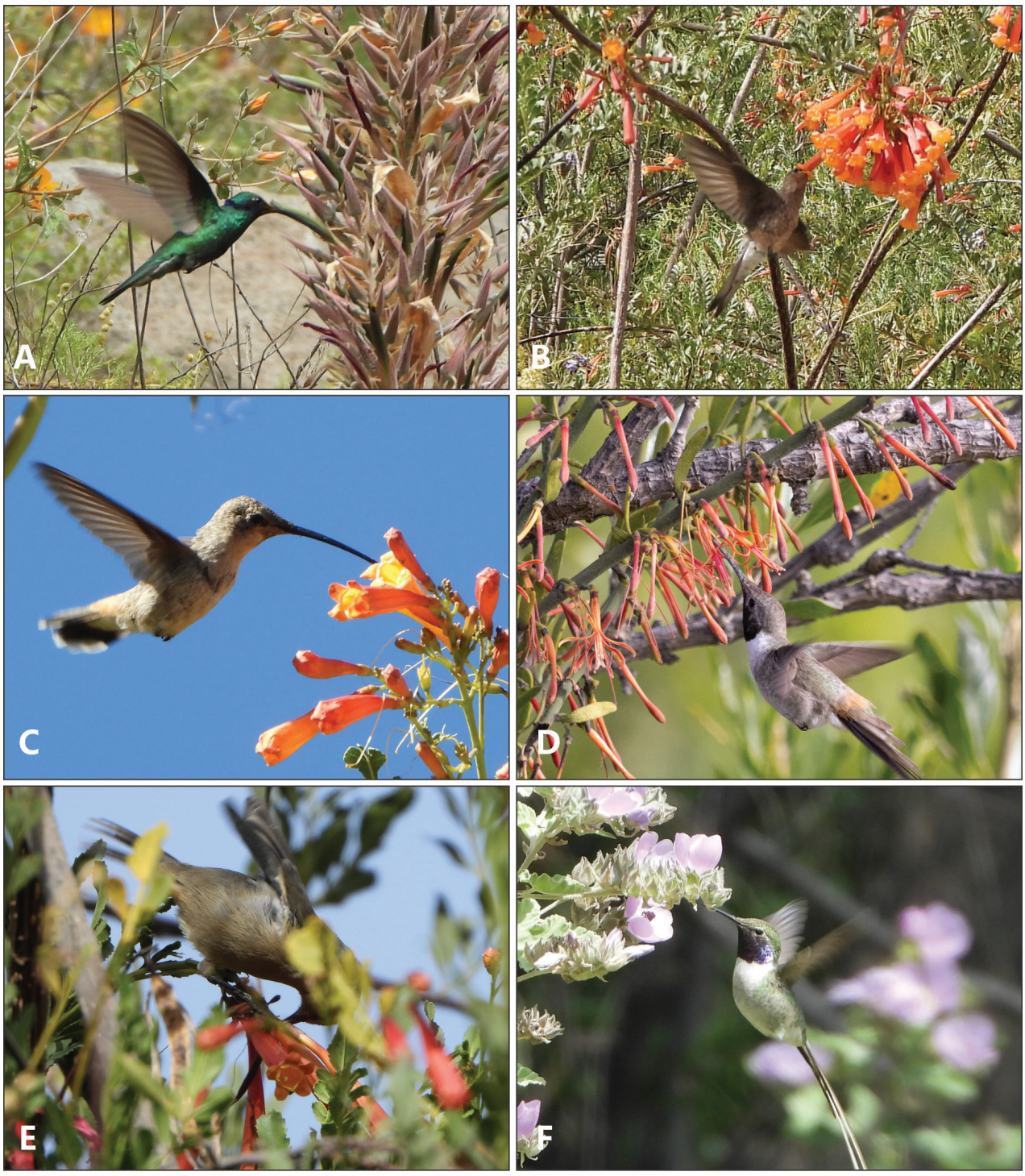

Figure 6. Use of floral resources by hummingbirds recorded in Sogay, Arequipa, Peru. **A.** *Colibri coruscans-Puya cylindrica*; **B.** *Patagona gigas-Tecoma fulva*; **C.** *Rhodopis vesper-Tecoma fulva*; **D.** *Rhodopis vesper-Ligaria cuneifolia*; **E.** *Conirostrum cinereum* stealing nectar from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

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 analyses identified *Rhodopis vesper* and *Tecoma fulva* as the hummingbird and plant species, respectively, occupying the most central relative positions within the accumulated network. *Rhodopis vesper* combined a high number of floral partners with high interaction frequency and comparatively high betweenness and closeness, whereas *T. fulva* combined high visitation frequency with interactions involving all four hummingbird species. Species-level network metrics provide complementary information on the structural position of species and can reveal taxa that contribute disproportionately to the observed pattern of interactions (Dehling 2018). In the present study, however, centrality should be interpreted as relative structural importance within the sampled network.

The interaction between *R. vesper* and *T. fulva* also showed marked asymmetric dependence. A larger proportion of the feeding records of *R. vesper* involved *T. fulva* than the proportion of visits to *T. fulva* attributable to *R. vesper*, resulting in negative interaction asymmetry. Thus, within the observed network, *R. vesper* showed greater proportional dependence on *T. fulva* than *T. fulva* showed on *R. vesper*. Such asymmetric dependencies are common in mutualistic networks and indicate that the consequences of an interaction may differ between the two partners according to the availability and use of alternative interaction partners (Martínez-García and Ortiz-Pulido 2014).

The *Ligaria cuneifolia-Thaumastura cora* interaction showed a contrasting pattern, with an asymmetry value close to zero, indicating relatively balanced proportional dependence between the two species within the observed network. However, the mechanisms underlying this pattern cannot be determined from the present data because floral availability, morphological matching, and resource accessibility were not quantified specifically for this interaction. 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 contained the highest number of feeding records and unique interactions and also showed the greatest temporal similarity, indicating that a relatively stable set of dominant interactions characterized the period of highest network activity. In contrast, August showed fewer records and interactions and low similarity with previous months, indicating a marked reorganization of the observed interaction structure toward the end of the study period. Temporal variation of this kind is consistent with previous studies showing that plant-hummingbird and plant-pollinator networks can change substantially among months or seasons through shifts in species phenology, relative abundance, resource availability, and visitor activity (Fonseca et al. 2015; Schwarz et al. 2020; Hervías-Parejo et al. 2023; Queiroz et al. 2025). In Sogay, the persistence of interactions involving *Tecoma fulva*, *Ligaria cuneifolia*, *Nicotiana glauca*, and *Puya cylindrica* contributed to the similarity observed between May and June. However, because floral availability was not systematically quantified, the temporal patterns detected here should be interpreted as changes in observed resource use and interaction structure.

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 humming-

birds 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 detect statistically significant differences in visitation frequency between ornithophilous and non-ornithophilous plants, or a significant association between floral length and visitation frequency. Therefore, the floral variables evaluated here did not independently explain the observed variation in resource use. In plant-hummingbird networks, interaction frequencies can arise from multiple, potentially interacting factors, including floral morphology, phenological overlap, flower abundance, nectar characteristics, accessibility, plant architecture, and spatial overlap between plants and hummingbirds (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 TL1 did not improve the explanation of the number of visits relative to the null model. Together, these results indicate, on a preliminary basis, that the sugar concentration in the nectar was not a strong predictor of visitation frequency among the floral resources evaluated in Sogay. The weak relationship between nectar sugar concentration and visitation frequency observed here is consistent with recent evidence indicating that nectar traits do not necessarily predict plant-hummingbird interaction frequency. For example, Maglianesi et al. (2024) found that interaction frequency increased with morphological matching between hummingbird bill length and floral corolla length, whereas nectar traits were unrelated to interaction frequency. In the present study, *T. fulva* was the most frequently visited floral resource despite not having the highest nectar sugar concentration, whereas *Nicotiana paniculata* showed relatively high °Brix values but low visitation frequency. This contrast further indicates that nectar sugar concentration alone did not explain the observed differences in floral resource use. Other factors known to influence plant-hummingbird interactions, such as flower abundance, phenological overlap, accessibility, plant architecture, and hummingbird foraging behavior, were not comprehensively evaluated here and therefore remain potential explanations to be tested in future studies.

The occurrence of hummingbird visits to non-ornithophilous plants is also consistent with evidence that hummingbirds do not exclusively use flowers exhibiting the classical ornithophilous syndrome. 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 observed use of floral resources by hummingbirds in Sogay cannot be attributed to a single floral variable. The high visitation frequencies recorded for *T. fulva*, *L. cuneifolia*, and *N. glauca* identify these species as the most frequently used floral resources during the study period, but the mechanisms underlying this pattern cannot be established from the variables measured here.

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*, shows that a reduced set of plant species accounted for a large proportion of the observed plant-hummingbird interactions during the period following the rainy season. In environments where floral resources are seasonal and spatially concentrated, maintaining these frequently used resources may contribute to preserving feeding opportunities and plant-hummingbird interactions.

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 and habitat-management actions in arid Andean landscapes should consider not only floral resources but also the structural characteristics of the vegetation. Preserving heterogeneous vegetation may therefore help maintain a broader range of resources used by hummingbirds beyond nectar alone. Future studies should incorporate floral abundance, flowering phenology, 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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Additional information

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The authors have declared that no competing interests exist.

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Data availability

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