Nectar provision attracts hummingbirds and connects interaction networks across habitats

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Many ecosystems have been modified by humans, creating novel habitats that include human-provided resources. Gardens adjacent to native habitats may affect plant–pollinator interactions by altering the determinants of interactions and species specialization. Here, we characterized a network comprising plants and hummingbirds interacting in a birdwatching garden with human-provided resources (nectar feeders and exotic plants) and adjacent Andean cloud forest in Colombia. Specifically, we investigated the proportion of hummingbirds visiting feeders and native/exotic plants to evaluate the connection between the habitats and the ecological determinants of the interaction network. Hummingbirds relied heavily on artificial nectar feeders in the garden, leaving the natural cloud forest for resources. Morphological matching was the single most important predictor of the observed pairwise interactions, for both hummingbirds and plants. At the species level, longer flowering phenology and a higher amount of sugar in nectar led to a higher *degree* for plants (i.e. the number of visiting hummingbird species). In contrast, a longer floral corolla was associated with lower specialization. Abundance was the best predictor of the number of partners for hummingbirds. The garden created for birdwatching attracted most, but not all, hummingbird species beyond their natural cloud forest habitat. Interestingly, the most frequently visited plants in the garden were native, especially the endemic and endangered tree *Zygia lehmannii* (Fabaceae). Our results show that some ecological mechanisms determining interactions in natural communities still hold in intensively modified habitats. Furthermore, a compromise between conservation and hummingbirds' attraction to birding lodges/gardens is possible, for instance by favouring native and endemic plant species that are highly attractive for pollinators.

Keywords: cloud forest, Colombian Andes, ecological fitting, nectar feeders, networks, ornamental plants, pollination, resource provision.

Hummingbirds are the main pollinators of a broad diversity of plants in the American continent (Stiles 1978, Zanata *et al.* 2017, Dalsgaard *et al.* 2021). These birds are frequent in human-modified habitats, as they feed on diverse sources of nectar, regardless of whether these are native or artificial/exotic in origin (McCaffrey & Wethington 2008, Brockmeyer & Schaefer 2012, Maruyama *et al.* 2016, 2019, Sonne *et al.* 2016, Lanna *et al.*

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2017). Human intervention in the environment can include the provisioning of food resources to wildlife (Cox & Gaston 2018) and, for pollinators, this practice includes many ornamental plants, flower strips in urban and agricultural landscapes, and artificial nectar feeders (Webb & Kabir 2009, Doody *et al.* 2010, Tryjanowski *et al.* 2015, Maruyama *et al.* 2016, Maguiña & Muchhala 2017, Cox & Gaston 2018, Janeček *et al.* 2020). In these modified habitats, pollinators face opportunities and challenges to establish interactions with novel resources/partners. Habitat modification may, in this context, affect the local-scale importance of ecological determinants of interaction networks (Morrison *et al.* 2020). However, how habitat modification and resource provision, in combination, affect how plant–pollinator interactions are organized is not well understood.

The factors determining interactions in modified habitats with a surplus of resources may change in their relative importance compared to natural habitats. For instance, nectar feeders are readily and frequently used by pollinators (McCaffrey & Wethington 2008, Sonne *et al.* 2016, Maguiña & Muchhala 2017), and hence the feeders may affect both pollinator behaviour and their interactions. Nectar feeders have been linked to northward range expansion of migratory Anna's Hummingbird *Calypte anna* in the USA (Greig *et al.* 2017) and can facilitate/decrease flower visitation and increase local hummingbird abundance (Arizmendi *et al.* 2007, Brockmeyer & Schaefer 2012, Sonne *et al.* 2016). In addition to the feeders, human provision of resources includes the planting of ornamental/exotic plants that are integrated into plant–pollinator networks through 'ecological fitting' (Janeček *et al.* 2020), a process whereby species interact with novel partners as a result of traits they already possess (Janzen 1985). In fact, exotic plants often integrate well into local hummingbird–plant networks (Maruyama *et al.* 2016).

Hummingbird–plant interactions are strongly determined by morphological matching, and this trait-based mechanism is especially important towards the tropics (Sonne *et al.* 2020). However, because both nectar feeders and exotic plants are often highly abundant and attractive resources for hummingbirds, interactions where these are present may be strongly driven by species abundances due to the higher encounter probability of individuals (Simmons *et al.* 2019). Besides, hummingbird species respond differently to habitat modification;

for instance, morphologically specialized hermit hummingbirds are known to avoid cleared areas when moving across landscapes, whereas some non-hermit hummingbirds may tolerate or even benefit from cleared habitats (Feinsinger 1978, Hadley & Betts 2009, Hadley *et al.* 2018). In general, the absence of morphologically specialized hummingbirds can diminish the importance of morphological matching (Sonne *et al.* 2019), one of the main determinants of interaction frequencies in natural areas (Maruyama *et al.* 2014, Vizentin-Bugoni *et al.* 2014). At the same time, in cleared gardens with highly abundant nectar feeders posing no restriction to hummingbird access, other factors such as species abundances and dominance hierarchy may become relatively more important, with dominant species driving community organization (Hadley & Betts 2009, Sonne *et al.* 2016, López-Segoviano *et al.* 2018).

One of the ecosystems with the highest diversity of hummingbirds and hummingbird-pollinated plants is the Andean cloud forest, which is a hotspot for endangered and endemic species at a global scale (Foster 2001, Bubb *et al.* 2004, Morales & Armenteras 2013, Ramírez-Burbano *et al.* 2017, Serrano-Serrano *et al.* 2017). This ecosystem currently faces degradation by deforestation, forest fragmentation and climate change, which can disrupt local plant–animal interactions (Still *et al.* 1999, Foster 2001, Bubb *et al.* 2004). Moreover, birdwatching is a common activity in this region, frequently using artificial nectar feeders and ornamental/exotic plants to attract hummingbirds to gardens and lodges (Snow & Snow 1980, Poulsen & Krabbe 1998, Brockmeyer & Schaefer 2012).

Here, we investigated the ecological determinants regulating hummingbird–plant interactions in an Andean cloud forest community, dramatically transformed by human intervention. Our main objectives were to characterize the integration of human-provided resources into a hummingbird–plant network and evaluate whether the same determinants of interactions usually reported for natural areas still hold in a heavily modified cloud forest habitat.

METHODS

Study area and data collection

We conducted fieldwork during 3–10 days per month from March 2015 to January 2017 in the

'finca Zíngara' (3°32'N, 76°36'W), a private property located at the eastern slope of the Western Cordillera of the Colombian Andes, in the Valle del Cauca department, Colombia (Supporting Information Fig. S1). Elevation varies between 1900 and 2000 m asl. The area has a bimodal precipitation regime, with the highest precipitation during April–May and October–November. Annual rainfall is about 1650 mm, and annual mean temperature is 16 °C (Giraldo 1990). The area harbours a typical cloud forest vegetation, mainly composed of patches of primary forest in the highest elevations with trees reaching 23 m in height (Giraldo 1990). The study site belongs to the Bosque San Antonio/Km18 Important Bird Area (IBA) catalogued by BirdLife International, with A1 IBA criteria, as it holds significant numbers of globally threatened species (BirdLife 2021). Since 1938, this region has been established by the Colombian government as a natural protected area, and there are few or no farming activities. However, illegal wood extraction and traffic of forest products, including ornamental orchids and heliconias, persist (BirdLife 2021). Specifically, as other properties in the area, Zíngara has a garden patch of about 2500 m², which includes exotic and native plant species as well as artificial nectar feeders that have been placed there for the past 12 years (four to seven nectar feeders with *c.* 230 mL of *c.* 23% sucrose solution). Data sampling was carried out in the whole area of Zíngara's garden (hereafter 'garden'), the borderline of 150 m between the garden and the forest (garden/forest border, hereafter 'border'), and inside the forest in a longitudinal transect of 420 × 6 m (hereafter 'forest', a total of 2520 m²) located 10 m from the border and heading towards the forest core (Fig. S1).

Hummingbirds and visited plants

We sampled all the plants with nectar accessible to a hummingbird, regardless of specialized adaptation to hummingbird pollination, in the garden, forest and border transects. Plant samples were collected and taken to the CUVC Herbarium of the Universidad del Valle for identification with the aid of local specialists. We classified plants as native or exotic using the online database from Universidad Nacional de Colombia (Bernal *et al.* 2019).

Along the transects, we quantified the hummingbirds' visitation frequencies with nectar plants by using video recordings. Each plant species and the feeders were recorded for between 10 and 15 h, accumulating a total of 825 recording hours to quantify hummingbird visitation, using five video cameras each day (Replay XD video cameras with a 10 000 mah Adata power bank to enhance battery duration). Each video camera was placed on a different plant species/feeder on the same day, and we recorded each plant species for 3–5 h on a specific day. We used the MotionMeerkat software (Weinstein 2015) to detect hummingbird visitation to each individual plant from the video recordings. Here, we determined the hummingbird species, the number of flowers visited (as *frequency of visitation*) and whether the visit was legitimate or illegitimate (considering when the hummingbird inserted its bill into the corolla opening as a legitimate visitation). In the case of the feeders, we counted each time a bird arrived and drank nectar until it left as a visit. We also carried out direct observations of hummingbird visitation using binoculars (Vortex Diamondback 8 x 42 mm) for 99 h to characterize their behaviour, so that total sampling hours amounted to 924 h. Hummingbirds were identified using a field guide (Ayerbe-Quiñones 2015).

For both hummingbirds and plants, we recorded abundances and traits relevant to their interactions to evaluate their associations with plant and hummingbird species roles. For *plant abundance*, every month in the field, we counted all the flowers of each plant species available for hummingbirds in the whole area of the transects established in the three habitats (garden, border and forest). Each nectar feeder was considered a single 'flower'. For *hummingbird abundance*, we calculated the relative abundance using the frequency of recorded days for each species, including visitation to flowers and other sightings over the total number of days of fieldwork (Vizentin-Bugoni *et al.* 2014).

The following plant traits were considered:

- Sugar in nectar (natural and artificial): measured for the plants as the mean nectar production from six to 10 flowers, from previously isolated flower buds or just opened flowers, which were covered with nylon mesh bags for 24 h. Nectar volume was assessed using 30-µL glass micro-capillaries and concentration was measured with a pocket

refractometer with automatic temperature compensation (0–32 Brix). From the mean values across different samples, we calculated the total amount of sugar in nectar per flower as a measure of energetic reward (Galetto & Bernardello 2005). For the nectar feeders, sugar in the artificial nectar was calculated from the total volume of artificial nectar available per day of sampling. Then, we calculated the *sugar in nectar* (*per* plant population), as sugar per flower × the mean number of flowers per plant individual × the number of plant individuals (estimated by counting flowers and plant individuals each month as previously explained). To calculate the amount of sugar in the group of feeders, we multiplied the amount of sugar in each one by the total number of feeders in the garden.

- Corolla length: measured in 10–15 flowers of each plant species, considering the morphological restriction imposed on hummingbirds (effective corolla length, *sensu* Wolf *et al.* 1976). We adopted a corolla length of zero for nectar feeders, as these consisted of red dishes filled with sucrose solution and imposed no restriction to hummingbirds (Fig. 1).
- Flowering phenology: measured as the proportion of sampling months in which plant species flowered (August 2015 to January 2017).

For hummingbirds, we considered:

- Bill length: measured in voucher specimens from the ornithology collection at the Universidad Nacional de Colombia (*n* = c. 10 for each species).
- Hummingbird phenology: measured as the proportion of sampling months in which each species was recorded from August 2015 to January 2017.
- Dominance hierarchy: calculated as the dominance behaviour, as dominant hummingbirds may restrict the interactions of other species and affect community-level hummingbird–plant interactions (López-Segoviano *et al.* 2018). We used the agonistic encounters data observed during visitation to plants and feeders, where we recorded the species involved, the aggressive behaviour and the interaction outcome. From each interaction, a species was considered a winner when it excluded the other from the nectar source. We calculated David's score (DS) as a dominance index for

each hummingbird species (David 1987). This metric is based on an interspecific dominance matrix of the hummingbird species resulting from the agonistic encounters. The matrix entries reflect the win proportion of species i when it interacts with species j following the formula:

$$DS = W + W_2 - L - L_2$$

where W is the sum of wins of species i over species j, and W_2 is the sum of wins of j over i, and L and L_2 are their respective losses. DS indicates the range of dominance of the species in the assemblage, with a value for each species in a range with the higher values for the most dominant ones (positive values are for winners and negative values for losers). We calculated the dominance index using the *Steepness* package (Leiva & de Vries 2014) in R 3.4.2 (R Development Core Team, 2016).

Hummingbird–plant interaction network

Using the frequency of visitation (i.e. the number of flowers or feeders visited), we constructed quantitative hummingbird–plant interaction networks. The interaction matrices included all the hummingbird species and resources of the three habitats studied. We discriminated legitimate visits and visitation to the feeders and elaborated three sets of networks:

- including only the legitimate visitation to flowers, indicating the potential for pollination (Pollination);
- legitimate visitation to flowers plus visitation to the feeders (+ Feeders);
- all visits to plants and feeders, including illegitimate visitation (Visitation).

As studies on plant–animal interactions may disregard the presence of artificial food sources in the study area, we evaluated how the inclusion or exclusion of the nectar feeders could affect the characterization of the networks. To analyse the overall interaction network characteristics, we calculated the following network-level metrics:

- *Complementary specialization* (H'_2), which quantifies the exclusivity of the interactions in the networks, i.e. how species interact with their partners more or less than expected based
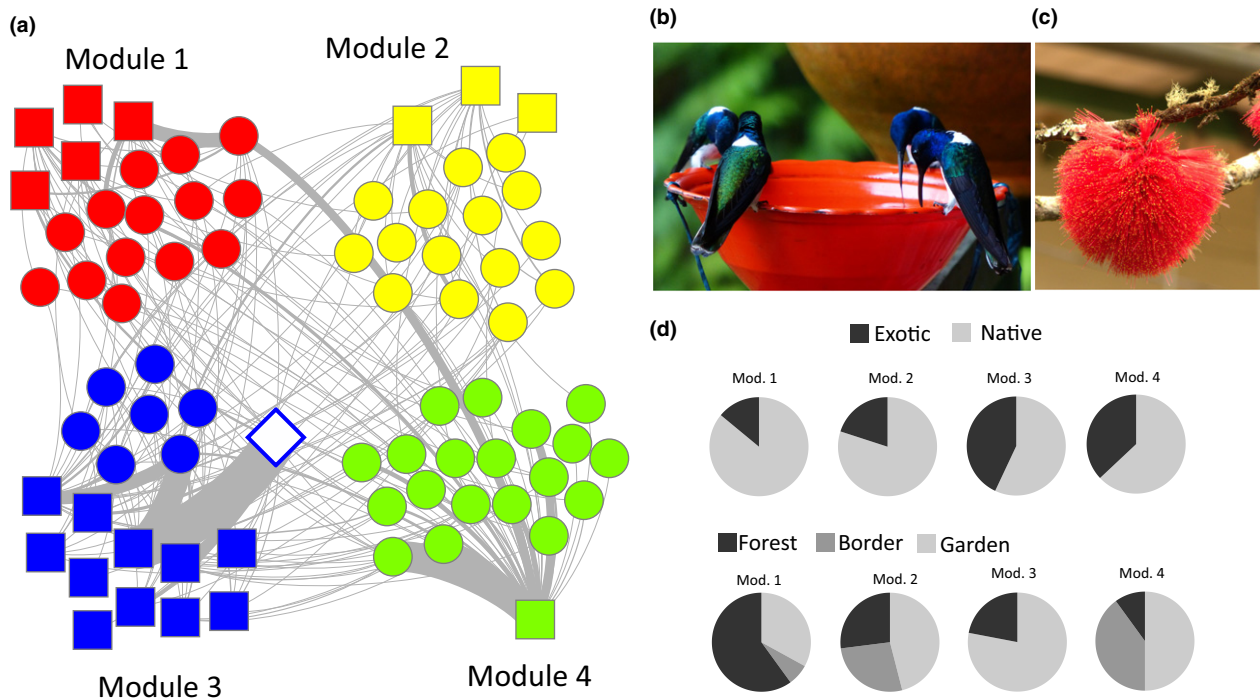
Figure 1. Hummingbird–plant interaction network from the forest–garden transition area in the Andean cloud forest of Colombia. (a) Hummingbird–plant interaction network, with squares indicating hummingbirds, circles indicating plants and the diamond indicating the artificial nectar feeders. Different colours illustrate different modules, and the nectar feeders were included in Module 3. (b) White-necked Jacobin *Florisuga mellivora,* the most common hummingbird in the study area visiting nectar feeders, included in Module 3. (c) The endemic and endangered *Zygia lehmannii* (Fabaceae) was the most visited plant species and was included in Module 3. (d) The proportion of exotic/native plant species and their distribution in the forest, garden and transition area in the interaction modules. [Colour figure can be viewed at wileyonlinelibrary.com]

on the abundances of the partners, here approximated by their total number of interactions, where H'_2 ranges from 0 to 1, with higher values indicating higher specialization (Blüthgen *et al.* 2006).

- *Modularity* (Q), which quantifies the extent of the division of a network into modules, i.e. subsets of species interacting more among themselves than with other species in the network. Modularity was estimated using the DIRTLPA+ algorithm, repeating it 50 times to find the optimal solution (Beckett 2016). To evaluate the significance of the network metrics, we generated 1000 simulated matrices with the same dimensions as the original matrices using the Patefield algorithm – which keeps the same marginal totals – and the *vaznull* algorithm – which keeps the connectance (Vázquez *et al.* 2007, Blüthgen *et al.* 2008). The network indices were also calculated for the simulated matrices, and we estimated the

significance of the observed metrics by counting the number of times the simulated matrices generated values equal to or higher than the values obtained for the observed networks.

Determinants of pairwise interactions

To evaluate the relative importance of morphological matching, phenological overlap and abundance as predictors of hummingbird–plant interactions, we modelled the pairwise interaction frequencies using a Bayesian generalized linear mixed effect model, similar to the one used in Sonne *et al.* (2020) and adapted from Weinstein and Graham (2017). We determined morphological matching (**M**) as the standardized difference in length between the hummingbird's bill and the plant's floral corolla, using the average for each species (Sonne *et al.* 2019). Hence, plants and hummingbirds had a higher probability of interaction if their bill and corolla were relatively more similar in

relation to other species in the community (Sonne *et al.* 2019, 2020). For phenological overlap (**P**), we expect a pair of species to interact proportionally with the amount of time they co-occur in the community. Thus, the pairwise phenological overlap was calculated for each hummingbird–plant pair by counting the number of months in which each pair of hummingbird and plant co-occurred over the total of months of fieldwork. Finally, for abundance (**A**), the pairwise interaction probability is proportional to the product of the relative abundances of each hummingbird and plant (+ Feeder). While **M** and **P** represent the niche/trait-based mechanisms determining the interactions, **A** represents a neutral model for interaction frequencies (Sonne *et al.* 2020).

The importance of each mechanism was modelled separately for the hummingbird and plant guilds. To minimize the uncertainty associated with poor sampling, three plant species that interacted only once were excluded when modelling the plants' interactions. The predictors **M**, **P** and **A** were first scaled to zero mean and unit variance. Our model assumes that the interaction frequency (N) between focal species i and its partner j follows a Poisson distribution with mean λ_i, with the log link function of λ_i predicted by the covariates: M_i, P_i and A_i.

$$N_{ij} \sim \text{Poisson}(\lambda_i)$$

$$\text{Log}(\lambda_{ik}) \sim \alpha_{ik} + \beta_{ik}^A \times A_{i,j} + \beta_{ik}^P \times P_{i,j} + \beta_{ik}^M \times M_{i,j}$$

These covariates were parametrized by the slope coefficients β_i^M, β_i^P and β_i^A as estimated using the following uninformative priors:

$$\alpha_i \sim \text{Normal}(\mu_\alpha, \tau_\omega)$$

$$\beta_i^A \sim \text{Normal}(\mu_{\beta_{iA}}, \tau_{\beta_{iA}})$$

$$\beta_i^P \sim \text{Normal}(\mu_{\beta_{iP}}, \tau_{\beta_{iP}})$$

$$\beta_i^M \sim \text{Normal}(\mu_{\beta_{iM}}, \tau_{\beta_{iM}})$$

$$\beta_i^D \sim \text{Normal}(\mu_{\beta_{iD}}, \tau_{\beta_{iD}})$$

where

$$\mu_\alpha \sim \text{Normal}(0, 0.01)$$

$$\mu_{\beta_{iA}} \sim \text{Normal}(0, 0.01)$$

$$\mu_{\beta_{iP}} \sim \text{Normal}(0, 0.01)$$

$$\mu_{\beta_{iM}} \sim \text{Normal}(0, 0.01)$$

$$\mu_{\beta_{iD}} \sim \text{Normal}(0, 0.01)$$

$$\tau_\omega \sim \text{half} - \text{caunchy}(0, 1)$$

$$\tau_{\beta_{iA}} \sim \text{half} - \text{caunchy}(0, 1)$$

$$\tau_{\beta_{iP}} \sim \text{half} - \text{caunchy}(0, 1)$$

$$\tau_{\beta_{iM}} \sim \text{half} - \text{caunchy}(0, 1)$$

$$\tau_{\beta_{iD}} \sim \text{half} - \text{caunchy}(0, 1)$$

The normal distributions are parametrized by precision rather than standard deviation (precision = $1/\sigma^2$; e.g. precision 0.001 is equal to a standard deviation of 31.6). μ states the parameters' means centred on zero with low precision. τ states the precision of the parameter represented by a half-Cauchy distribution, which decreases away from zero.

We then estimated β_i^M, β_i^P and β_i^A as posterior parameter distributions in Markov chain Monte Carlo (MCMC) simulations with three independent runs over 100 000 iterations. All parameters were specified with non-informative priors (i.e. zero mean and low precision; precision = 1/variance). We used a burn-in of 2000 iterations and subsequently kept one of every 10th draw for downstream analyses. We fitted the model with all parameter combinations, including an intercept-only model as a baseline comparison. We selected the best-fitting model using the deviance information criterion (DIC; Spiegelhalter *et al.* 2002). As with other information criteria, models with lower DIC are preferred over models with higher DIC. Models with ΔDIC ≤ 2 were considered equally fit (Spiegelhalter *et al.* 2002). All Bayesian analyses were run in the JAGS software (Plummer 2003, 2012) and were executed from R using the function 'jags' in the *R2jags* package (Su & Yajima 2015).

Determinants of interaction specialization

Finally, we evaluated the determinants of species-level specialization of the interaction networks

constructed. We calculated: *Degree (k)*, which describes the number of partners a species links to, and *Complementary specialization (d')*, which measures how specialized the interaction of a species is according to the availability of interacting partners (Blüthgen *et al.* 2006). To calculate *d'* values for hummingbirds and plants, instead of using the marginal totals as a surrogate for the availability of partners, we included the availability of nectar, expressed as the amount of sugar per species, and hummingbird abundance, respectively, as vectors. We used the *bipartite* package (Dormann *et al.* 2008) in R 3.4.2 (R Development Core Team, 2016) to perform all network calculations.

We then tested how species abundance, phenology, and morphological, energetic and behavioural traits predict degree and species-level specialization. We fitted linear models with a Gaussian distribution of errors for all the combinations of predictor variables. The predictors were bill length (morphology), abundance, phenology and dominance hierarchy as predictors for hummingbird models, and corolla length (morphology), sugar in nectar (as a measure of the abundance of the resource), phenology and the exotic or native status (origin) for plant models (variables measured as explained above). The amount of sugar was log_{10}-transformed to improve the distribution of the residuals. All data were standardized to zero mean and unit variance with the *decostand* function in the *vegan* package (Oksanen *et al.* 2020) before analyses. Model performance was assessed based on the Akaike information criterion with correction for small samples (AIC_C) and model selections were conducted using the *dredge* function in the *MuMIn* package (Barton 2017) in R 3.4.2 (R Development Core Team, 2016). If the intercept-only model (null model) had $\Delta AIC_C \leq 2.0$, we considered that all predictors showed poor performance. When multiple models had ΔAIC_C values ≤ 2.0, we chose the model with the least number of predictors as the minimum adequate model. We verified for multicollinearity between the predictor variables in the models by checking that variance inflation factor (VIF) ≤ 5 and condition number < 30 (Dormann *et al.* 2013), using *vif* and *kappa* functions in the *car* package, respectively (Fox & Weisberg 2011). All analyses were conducted using R 3.4.2 (R Development Core Team, 2016). As for the analysis with probabilistic models, only the +Feeder network was used for species-level analyses.

RESULTS

We recorded 20 hummingbird species and 55 plant species plus the nectar feeders, with a total of 10 856 interactions (Tables S1–S3). Most plants were native (72.7%), with Gesneriaceae, Ericaceae and Bromeliaceae the most diverse plant families. Most (76.1%) hummingbird visits to flowers were legitimate, but 0.9% were illegitimate, and visits to feeders accounted for 23.0% of the total. Most hummingbird species (75%) visited the feeders, with variable frequencies (Tables S3 and S4). The forest and border transects supported most of the native plant species, and only three species were found flowering in both the garden and forest (*Ornithidium aureum* – Orchidaceae, *Guzmania multiflora* – Bromeliaceae and *Cavendishia adenophora* – Ericaceae). Some native species, such as the endemic and endangered tree *Zygia lehmannii* (Fabaceae), were only recorded flowering in the garden, despite their occurrence inside the forest. One plant species, *Columnea dimidiata* (Gesneriaceae), was only visited illegitimately (Table S4). Exotic plants were only recorded in the garden, with 16 species visited by hummingbirds. Two of these, *Crocosmia x crocosmiiflora* (Iridaceae) and *Streptosolen jamesonii* (Solanaceae), are categorized as naturalized species in Colombia (Bernal *et al.* 2019; Table S2).

Hummingbird–plant networks were more specialized and modular than expected by the null model. Network indices were not strongly affected by including visits to nectar feeders and illegitimate visitations, in addition to legitimate visits (Table 1). Hence, we focus our analysis on the network considering only the legitimate and nectar feeder visits. The optimal solution for modularity identified four modules, but modules did not reflect the habitat division among forest interior, garden and border (Fig. 1). About half of the hummingbird species (52.6%), including the White-necked Jacobin *Florisuga mellivora*, were grouped into a single module, including the feeders (module 3 in Fig. 1a,b). This module also included the plant species most frequently visited by hummingbirds, *Z. lehmannii* (Fig. 1c). Morphologically specialized hermits, with long and curved bills (the Tawny-bellied Hermit *Phaethornis syrmatophorus* and the Green Hermit *Phaethornis guy*) were grouped with the Black-throated Mango *Anthracotorax nigricollis* in a single module (module 2 in Fig. 1a). One module with five

hummingbird species had the lowest proportion of exotic plant species and simultaneously included the highest proportion of plants from the natural forest, with the Greenish Puffleg *Haplophaedia aureliae* as the main visitor (module 1 in Fig. 2a, see also Fig. 2d). Interestingly, there was a module including only one hummingbird species, the Speckled Hummingbird *Adelomyia melanogenys*, which interacted with many plant species in the community, mainly the exotic *Streptosolen jamesonii* (Solanaceae) (module 4 in Fig. 1a).

We found that morphological matching was the best predictor of pairwise interaction frequencies for hummingbirds and plants (Fig. 2). On the other hand, model selection indicated that hummingbird degree was best predicted by their abundance, with more abundant species having more interaction partners ($R^2_{adj} = 0.41$, Fig. 3a, $n = 20$ hummingbird species). None of the predictors was associated with hummingbird species-level complementary specialization. For plants, the best model predicting the degree included the phenology and the amount of sugar as predictors ($R^2_{adj} = 0.50$), with positive effects for both phenology ($R^2_{adj} = 0.30$, Fig. 3b) and amount of sugar ($R^2_{adj} = 0.37$, Fig. 3b, $n = 55$ plant species and the feeder). The positive association with the amount of sugar was consistent, albeit weaker when removing the nectar feeders, which was an outlier ($R^2_{adj} = 0.20$, $n = 54$). Complementary specialization in plants decreased with corolla length, with longer flowers showing lower levels of specialization ($R^2_{adj} = 0.20$, Fig. 3d, $n = 55$).

DISCUSSION

Nectar feeders attracted hummingbirds beyond the natural forest habitat, with most hummingbird

Table 1. Complementary specialization (H'₂) and Modularity (Q) metrics of the interaction networks between hummingbirds and plants, Andean Cloud Forest of Colombia. Pollination network, with only the legitimate visits to flowers; +Feeders, also including the nectar feeders; and all visitation, also including illegitimate visitation to flowers.

Network	Specialization (H_2')	Modularity (Q)
Pollination	0.48*	0.51*
+Feeders	0.51*	0.51*
All visits	0.50*	0.50*

All metrics were significant (*) according to Patefield and Vaz-null null models, $P < 0.0001$.
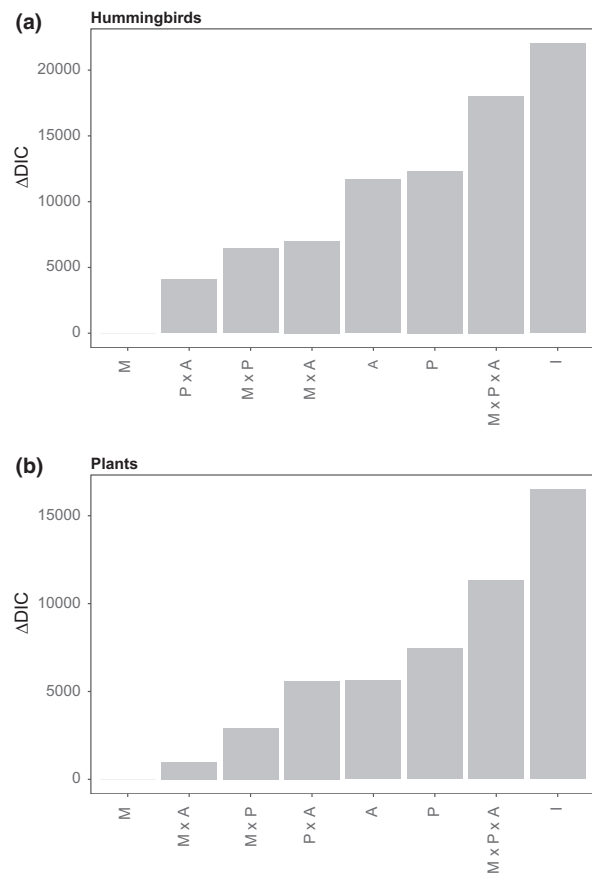

Figure 2. Barplots showing DIC values of models with every parameter combination subtracted by the lowest DIC value (ΔDIC). Models with low DIC were preferred over models with high DIC. The model with ΔDIC = 0 was selected as the best-fitting model. M - Morphology, A - Abundance, P - Phenology, I – Intercept.

species frequently recorded drinking artificial nectar. Nevertheless, both exotic and native plants in the garden and in the forest were still frequently visited. The endemic tree *Z. lehmannii* in the garden received most of the visits, second only to the feeders. Hence, plants still potentially experience pollination services by the hummingbirds. Although our study only considered one study site, the results suggest that hummingbird–plant interactions can interconnect the Andean cloud forest and the adjacent human-made garden. Moreover, morphological matching was the most important determinant of the pairwise interactions, as often observed in natural communities. At the species level, hummingbird abundance and the amount of sugar for plants and feeders (which can be considered as a measure of the abundance of the
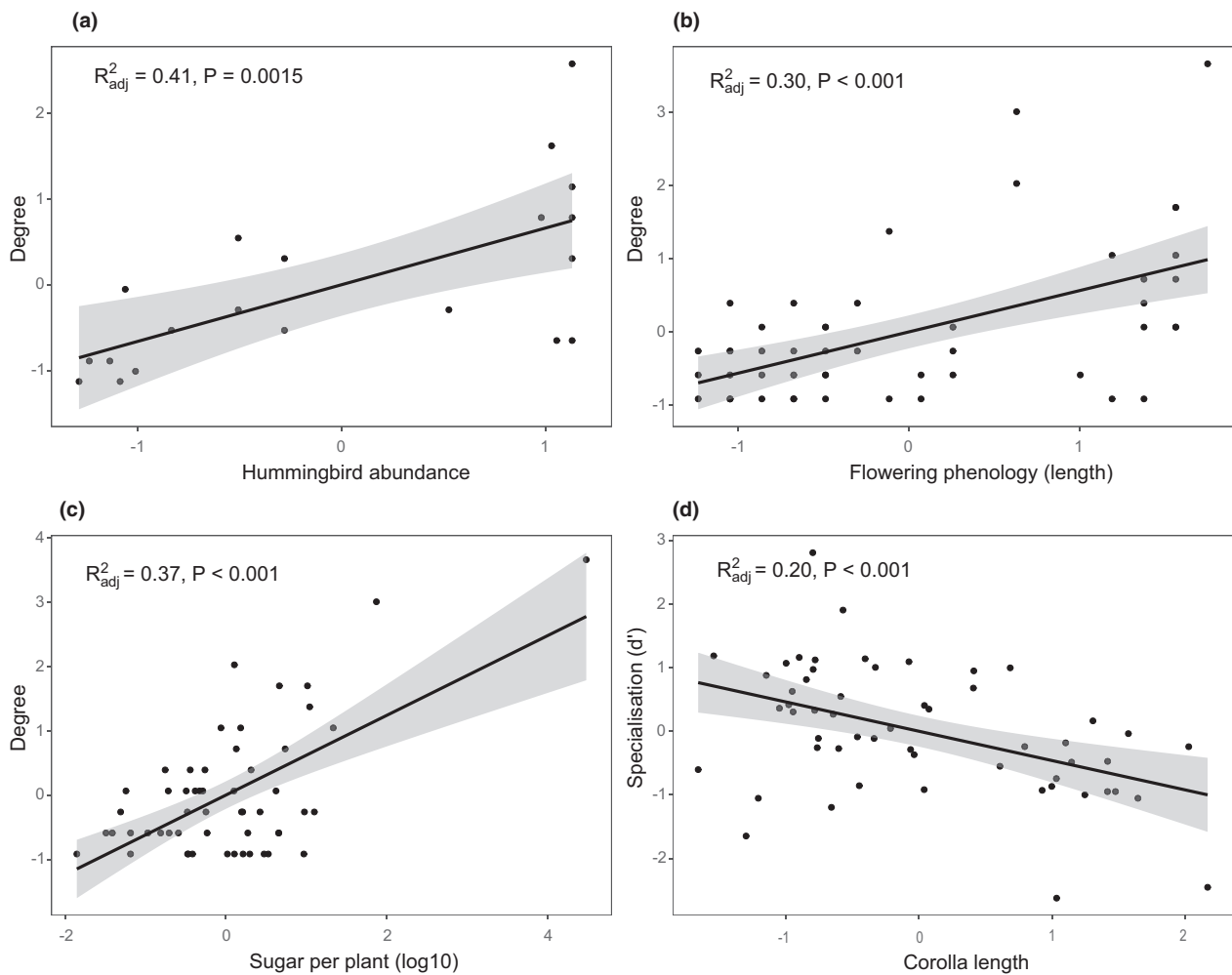
Figure 3. Determinants of plant and hummingbird interaction specialization, showing the association with predictors in the best-selected models. (a) Hummingbird abundance as a predictor of the number of interacting plant species, i.e. degree, $n = 20$. (b) Flowering phenology length (number of months) as a predictor of hummingbird species richness associated with plants, degree, $n = 55$. (c) The amount of sugar per plant, estimated from nectar volume and concentration, as a predictor of hummingbird richness associated with a plant, degree, $n = 55$. Note that this association was consistent, albeit less strong when removing the outlier (nectar feeders). (d) Floral corolla length as a predictor of plant species complementary specialization, *d'*, $n = 55$. Sugar per plant was $\log_{10}$-transformed and all variables were standardized to zero mean and unit variance before analysis to improve fit.

resource) were important determinants of the number of partners (degree). Additionally, for plants, the number of hummingbird partners increased with longer flowering phenology, whereas flowers with longer corollas showed lower complementary specialization. Our results indicate different mechanisms determining species interactions at the network and species levels. These are generally the same ecological determinants previously reported for more natural hummingbird–plant communities in the Neotropics (see below).

Morphological matching has been reported as an influential predictor of pairwise interactions in many hummingbird–plant interaction networks (Maruyama *et al.* 2014, Vizentin-Bugoni *et al.* 2014, Weinstein & Graham 2017, Sonne *et al.* 2020), and here we found a similar result. Morphology was also important in determining complementary specialization for plants but, unexpectedly, flowers with longer corollas were less specialized in their interactions. Previous studies had found that morphologically more specialized hummingbirds, i.e. with longer bills, show

higher complementary specialization in their interactions (Maglianesi *et al.* 2014, Tinoco *et al.* 2017, Sonne *et al.* 2019). Our opposing result seems related to the fact that morphologically specialized plants with longer flowers were associated with very abundant long-billed Hermit hummingbirds, the Tawny-bellied Hermit and the Green Hermit. Therefore, plants showed lower complementary specialization (Blüthgen *et al.* 2006).

Longer flowering phenology was associated with a tendency for plants to interact with a higher richness of hummingbirds. This is the case of the native plants in the garden, such as *Cavendishia quereme, Cavendishia adenophora, Guzmania multiflora* and *Z. lehmannii*, which make them useful as garden plants for attracting hummingbirds as well as nectar feeders. Dominance hierarchy had a negligible effect on determining hummingbird specialization. Despite the recognized importance in affecting community dynamics of hummingbird communities (Justino *et al.* 2012, Sonne *et al.* 2016, López-Segoviano *et al.* 2018), it seems that dominance hierarchy does not relate to specialization, as even non-dominant species can use highly rewarding resources as territory intruders (Justino *et al.* 2012, Sonne *et al.* 2016). Lastly, the positive association between abundance and degree for both hummingbirds and plants (plus feeders) confirms previous findings that locally abundant species tend to be ecologically more generalist (Simmons *et al.* 2019).

We showed that feeders attract a wide range of hummingbird species, but not all. One of the detected interaction modules was formed by a hummingbird rarely recorded at the feeders, the Speckled Hummingbird, and a diverse number of plant species from the forest and garden associated with it. Because visitation to native plants was still very frequent, it is possible that with proper management, the recreational attraction of hummingbirds may be reconciled with the maintenance of pollination services. Furthermore, generalist plants such as the endemic and endangered tree *Z. lehmannii* were visited by the highest number of hummingbird species, second only to the nectar feeders. Although almost no information on its general biology is available (Calderón 1998), the brush-like flowers of *Z. lehmannii* characterize an ecologically and functionally generalist species (Amorim *et al.* 2013). Such generalist species provide cohesion to the whole interaction network and may be regarded as keystone species (Martín

González *et al.* 2010), suggesting that this species is potentially an important resource for pollinators. Interestingly, open gardens may even enhance the reproductive output of this endangered species, as *Z. lehmannii* only flowered in the garden during our study and not in the forest where individuals of similar sizes were also found. This is in line with recent suggestions that gardens may be more suitable habitats than completely deforested areas, large crop fields or other types of anthropogenic matrices in fragmented landscapes (Hagen *et al.* 2012). Thus, gardens may be effectively managed as potential tools in conservation practices (Webb & Kabir 2009, Doody *et al.* 2010, Cammack *et al.* 2011, Samnegård *et al.* 2011, Lindemann-Matthies & Marty 2013).

In summary, the opportunistic behaviour of hummingbirds facilitates the integration of human-provided resources into interaction networks with plants, connecting natural and human-modified habitats. Because our study is limited to a single study site, general conclusions should be drawn with caution. Nevertheless, the finding that morphological matching was the most important predictor of pairwise interactions, similarly to what has been reported for more 'pristine' natural environments, may indicate that fundamental rules governing hummingbird–plant interactions are maintained at some level of disturbance. Moreover, it stresses the importance of ecological fitting on structuring community interactions between avian pollinators and plants in altered habitats (see also Janeček *et al.* 2020). Finally, our study suggests that nectar supplementation with feeders for sustainable ecotourism could be accompanied by an encouragement to use native flora to attract hummingbirds and other pollinators, supporting the conservation of species and their interactions while providing benefit for local landowners.

AUTHOR CONTRIBUTIONS

Mónica Beatriz Ramírez-Burbano: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (supporting); Writing-original draft (lead); Writing-review & editing (equal). **Felipe Amorim:** Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (equal); Supervision (equal); Visualization (equal); Writing-review & editing (supporting). **Alba Marina Torres-González:** Conceptualization (equal); Investigation (supporting); Methodology (equal); Supervision (equal); Writing-review & editing (supporting). **Jesper Sonne:** Formal analysis (equal); Methodology (equal); Visualization (equal); Writing-review & editing (supporting). **Pietro Maruyama:** Conceptualization (equal); Formal analysis (equal); Investigation (supporting); Methodology (equal); Supervision (equal); Visualization (equal); Writing-review & editing (equal).

Data availability statement

The data supporting this study are available in the online supplementary material.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Characterization of the study area (source Google MAPS®). Geographical location of the study and transect location inside the 'Finca Zíngara' are shown to illustrate our sampling procedure.

Table S1. List of hummingbird species, with information on their bill length, phenology and abundances.

Table S2. List of plant species, with information on their origin, whether found in the garden forest or edge, corolla length, phenology, amount of sugar produced per flower, floral and individual abundances.

Table S3. Hummingbird–plant interaction matrix, considering only the legitimate interactions and visits to nectar feeders (+ Feeders).

Table S4. Hummingbird–plant interaction matrix considers all interactions, including visits to nectar feeders and illegitimate access to the flowers (Visitation).