


ORIGINAL ARTICLE

The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient

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Abstract

Morphological trait matching between species affects resource partitioning in mutualistic systems. Yet, the determinants of spatial variation in trait matching remain largely unaddressed. Here, we generate a hypothesis that is based on the geographical distributions of species morphologies. To illustrate our hypothesis, as a study system we use hummingbirds in the tropical Andes. Hummingbirds with specialized morphologies (i.e., long or curved bills) may forage on flowers that are inaccessible to hummingbirds with generalized bill morphologies (i.e., small-to-medium-sized bills with no curvature), yet the vast majority of hummingbirds have generalized bill morphologies. Thus, we propose that trait matching across space is determined by the distribution of morphological specialists. In the Andes, we observe the richness of specialized hummingbird morphotypes to peak at high and low elevations. Therefore, we hypothesize that trait matching should be most influential in predicting pairwise interactions at high and low elevations. We illustrate our hypothesis by field observations along an elevational gradient in Podocarpus National Park (Ecuador). Using Bayesian hierarchical modeling of interaction frequencies in combination with network analyses, we found that hummingbirds at high and low elevations contributed to resource partitioning by foraging on morphologically close-matching flowers. Moreover, at high and low elevations, hummingbirds with specialized morphologies showed a stronger tendency to visit close-matching flowers than morphological non-specialists did. In contrast, at mid-elevations, hummingbirds were not attracted to morphologically close-matching flowers. These results suggest that the spatial distribution of specialized morphotypes determines trait matching and the partitioning of interactions within hummingbird-plant communities.

Abstract in Spanish is available with online material.

KEYWORDS

Ecuador, modularity, mutualism, networks, plants, Podocarpus National Park, pollination, resource partitioning, specialization

1 | INTRODUCTION

The partitioning of resources among species within ecological communities has implications for co-existence and may thereby affect geographical patterns in species richness (Dobzhansky, 1950; Michalet et al., 2006; Schemske, 2002). Resource partitioning among species having different morphological traits is thought to enable them to specialize on resources that are inaccessible or energetically less favorable to competitors (Dehling, Jordano, Schaefer, Böhning-Gaese & Schleuning, 2016; Grant & Grant, 2006; Maruyama et al., 2018; Stang, Klinkhamer & Van Der Meijden, 2006; Temeles & Kress, 2003). For instance, within mutualistic systems, such as flowering plants and their pollinators, morphological co-adaptations may result in plants having floral corolla shapes matching the feeding apparatus of their most effective animal pollinators (e.g., Darwin, 1862; Rothschild, 1903; Temeles & Kress, 2003).

The significance of trait matching for the assembly of plant-pollinator interaction networks has been documented in previous studies (Dehling et al., 2014; Maglianesi, Blüthgen, Böhning-Gaese & Schleuning, 2014; Sazatornil et al., 2016; Soteras, Moré, Ibañez, del Rosario Iglesias & Cocucci, 2018; Vizentin-Bugoni, Maruyama & Sazima, 2014; Weinstein & Graham, 2017). Several of these feature hummingbirds and their flowering plants, which exhibit the most specialized co-adaptations and greatest niche partitioning of any avian-plant mutualistic association (Fleming & Muchhala, 2008; Stiles, 1981; Zanata et al., 2017). Recent studies showed that resource partitioning in hummingbird-plant networks correlates positively with the local diversity of hummingbird morphologies (Maruyama et al., 2018), but that hummingbird traits matter less for resource partitioning in areas with limited trait evolution (Dalsgaard et al., 2018). These results accord with the idea that hummingbird traits and hummingbird-plant trait matching impact niche partitioning, but also suggest that the spatial distribution of hummingbird morphologies may influence the level of trait matching and niche partitioning.

Here, we propose a hypothesis on how the distribution of morphological traits impacts trait matching and niche partitioning. Based on variation in hummingbird morphologies (Figure 1a), we make two observations that underlie our hypothesis for the mechanism of trait matching. First, the vast majority of species have the same generalized bill morphology: small-to-medium-sized bills with slight or no curvature (del Hoyo, Elliott & Sargatal, 1999; Figure 1a). Secondly, hummingbirds with long or curved bills are those with the potential of consuming resources that are inaccessible to small-and-straight billed hummingbirds—but not *vice versa* (Feinsinger & Colwell, 1978; Snow & Snow, 1972). Together, these two observations imply that morphological generalists predominate in hummingbird-plant communities, whereas unique floral morphologies are exploited by the minority of morphological specialists with long or curved bills (Figure 1b). Therefore, we hypothesize that geographical variation in trait matching and niche partitioning could be attributed to the geographical distribution of hummingbirds that evolved specialized bill morphologies (i.e., long or curved).

To examine this hypothesis, we combine the morphologies and elevational ranges of hummingbirds in the east Andes to propose expectations for their trait matching with flowering plants. We then examine whether level of trait matching coincides with level of niche partitioning. Our methodology involves three phases. First, based on the elevational distribution of morphologically specialized hummingbirds, we formulate a prediction on elevational variation in trait matching. According to our hypothesis, trait matching should be more pronounced at elevations where the richness of morphologically specialized hummingbird species is higher than expected based on total hummingbird richness alone. Second, we evaluate trait matching using field observations of three spatially distinct interaction networks in Podocarpus National Park, Ecuadorian east Andes. The detection of trait matching is challenging, owing to the potential presence of equally important, interacting processes. To begin with, phenological turnover imposes constraints on the timing of species interactions (Morente-López, Lara-Romero, Ornos & Iriondo, 2018). Thus, limited seasonal co-occurrence between morphologically suitable partners may explain why they interact infrequently. At a given point in the phenological cycle, a neutral model would constrain the outcome of pairwise interactions to be a simple product of the species' abundances (Dáttilo, Marquitti, Guimarães & Izzo, 2014; Simmons et al., 2018). Thus, if interactions happen at random, the network would be expected to show a core of frequent interactions between common species, within which the rare species' interactions are nested. To disentangle the influence of trait matching from neutrality and phenological overlap, we use predictive models of pairwise interactions based on morphological matching, while accounting for species phenologies and encounter rates (abundances). Finally, we assess whether hummingbird-flower trait matching coincides with the observed level of niche partitioning, as quantified in the three plant-hummingbird interaction networks.

2 | METHODS

2.1 | Elevational distributions of specialized hummingbird morphologies

Biogeographically, the fauna and flora of Podocarpus National Park are associated with most the eastern high Andes (Bloch, Poulsen, Carsten & Rasmussen, 1991; Madsen, 1989). Thus, to assess the representation of morphological specialists, our hummingbird morphological data comprise bill length and bill curvature measured on museum specimens for the 115 species of hummingbirds known to occur in this region, following the IOC World Bird List v.7.3 (Gill & Donsker, 2017). We focus on these traits, as they are well-known to associate with hummingbird foraging patterns (Dalsgaard et al., 2009; Feinsinger & Colwell, 1978; Maglianesi, Blüthgen, Böhning-gaese & Schleuning, 2015; Maglianesi et al., 2014; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira & Dalsgaard, 2014; Snow & Snow, 1972; Stiles, 1981; Vizentin-Bugoni et al., 2014). The data consist of sex-level averages of bill length and curvature measured on up to

ten adult males and females when possible (S1a). Our hummingbird–plant interaction data do not capture differences in flower interactions between the sexes of conspecifics. Therefore, we averaged trait values to species level by taking the weighted intersexual mean, in which weights are given by the number of measured individuals

of each sex. To explore the possibility that the elevational distribution of long-straight-bill specialists might be driven by variation in body mass, we collected data on hummingbird body mass from the literature (S1b). Five species remained with missing body mass information.

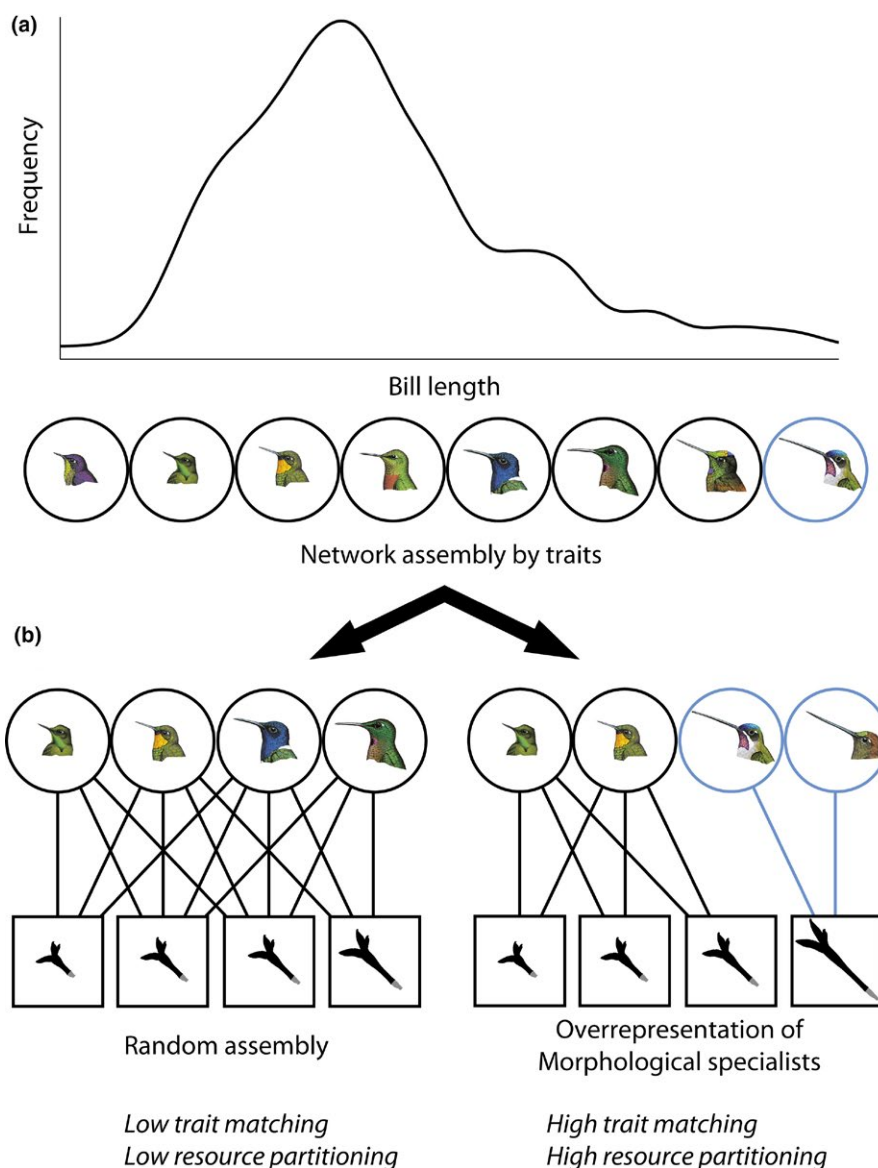


FIGURE 1 Conceptual figure illustrating our hypothesis that morphologically specialized hummingbirds are important for trait matching and resource partitioning. The vast majority of hummingbird species have the same, generalized bill morphology: small-to-medium-sized bills. Panel a shows the distribution of bill lengths among east Andean hummingbirds (excluding the extremely long-billed *Ensifera ensifera*). Circles show examples of different hummingbird bill lengths. The blue circles indicate morphological specialists (in this case, species with exceptionally long bills). Panel b shows two hummingbird–plant networks assembled from the regional species pool. The connecting lines illustrate interactions between plant and hummingbird species. Because of the right-skewed distribution of hummingbird morphologies, a random sample of hummingbirds from the source pool will most likely comprise species with generalized morphologies (left). In this case, the low diversity of bill morphologies implies that species are unlikely to feed on specialized floral morphologies that are inaccessible to other species in the community. Thus, communities comprising generalized morphologies should have low trait matching and low resource partitioning. Morphological specialists with long or curved bills are those with the potential of utilizing floral resources that are inaccessible to small-and-straight billed hummingbirds—but not vice versa (Feinsinger & Colwell, 1978; Snow & Snow, 1972). Thus, when the minority of morphological specialists are overrepresented (right), they should impose high trait matching and high resource partitioning. Imaged hummingbirds are reproduced with permission from J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana (Eds.). (2018). Handbook of the Birds of the World Alive. Barcelona, Spain: Lynx Edicions. (Retrieved from <http://www.hbw.com/> on 7 January 2019) [Colour figure can be viewed at wileyonlinelibrary.com]

In the process of mapping the elevational distributions of hummingbird morphologies, we categorized two morphotypes as “specialized”: curved bills and long-straight bills. The curved-bill morphotype was established as the 10% of species with most strongly curved bills ($n = 12$). The long-straight-bill morphotype was established as the 10% of species with longest bills. From this latter group, we removed those species assigned as having specialized curved bills, leaving seven species assigned to the long-straight-bill morphotype. To assess the sensitivity of results to the 10% threshold of each specialized morphotype, the procedure was repeated by applying alternative thresholds of 5% and 15% (Table S3, Figure S4).

According to our hypothesis, strong trait matching should occur in areas where the richness of morphologically specialized species is higher than expected based on total richness alone. To identify such areas, first we compiled information on each hummingbird species’ observed elevational range, that is, elevations between its minimum and maximum elevational range (S2). We then stacked the elevational ranges and extracted hummingbird richness along the gradient. Within intervals of 50 m elevation, we compared the observed richness of morphological specialists to the expected number generated by a null model. The null model randomly sampled, from the complete regional pool of hummingbird species, a number of species equal to the total observed richness of a given elevational 50 m band. Species with wide elevational ranges contribute more records to the elevational richness gradient than species with narrow elevational ranges (Colwell & Lees, 2000). To accommodate this bias, the probability of sampling a species in a given elevational band was proportional to the extent of its elevational range. After running the null model 1000 times, for each 50-m interval, we determined the proportion of random hummingbird assemblages, generated by the null model, that contained fewer species of each specialized morphotype than empirically observed. We name this proportion the *rank-order richness* of specialized morphotypes.

The elevational distribution of each of the two specialized morphotypes could be driven by geographical turnover in phylogenetic lineages. In this case, curved-bill specialists are dominated by the Phaethorninae clade, which predominates in the lowlands. In contrast, the genus *Coeligena* predominates in highlands and comprises a clade of six species with the highest concentration of long-straight-bill specialists (Fjelds  & Krabbe, 1990). We assessed the contributions of these two clades to the distribution of specialized morphotypes by removing them from the dataset and then recalculating, for each 50 m elevational interval, the rank-order richness of each specialized morphotype. Next, as a previous study found hummingbird body size to increase systematically with elevation, likely due to selective advantages in thermoregulation (Altshuler, Dudley & McGuire, 2004), we explored the possibility that the elevational distribution of long-straight-bill specialists was driven by variation in body mass. To the degree that larger hummingbirds are isometric with smaller ones (larger hummingbirds having longer bills), elevational variation in body mass could explain the predominance of long-straight-bill specialists in the highlands. We investigated this

possibility by regressing the median body mass for hummingbirds against the rank-order richness of long-straight-bill specialists.

Finally, we explored the contribution of the two specialized morphotypes to overall diversity in hummingbird bill traits—measured by the standard deviation in hummingbird bill traits for each 50 m elevational interval. We do this because morphological diversity has previously been shown to correlate with hummingbird resource partitioning (Maruyama et al., 2018), and could have implications for trait matching.

2.2 | Study area and sampling design

Field data were collected at three elevations in and around Podocarpus National Park (Southern Ecuador; 4°21’S, 78°58’W). The park itself has a highly irregular topography, encompassing elevations from 950 to 3700 m. It is traversed by the main eastern Cordillera Real, although the principal faunal-floral composition is east Andean (Bloch et al., 1991; Madsen, 1989). The lowland site (Bombuscaro) was sampled between 950 and 1000 m.a.s.l. along an 1800 m. transect (04°08’S, 78°58’W). The high frequency of landslides seems to be limiting forest successional stage to mainly late second growth, with an average tree height between 10 and 25 m, with some trees up to 35 m. The vegetation is humid subtropical *tierra firme* (Beck, Bendix, Kottke, Makeschin & Mosandl, 2008). Here, some abundant nectar-producing plant families include Bromeliaceae, Fabaceae, Gentianaceae, and Rubiaceae. The mid-elevation site is located outside the National Park adjacent to the San Francisco biological station “ECSF” (1800 to 2100 m a.s.l.; 03°58’S, 79°04’W). The sampled transect extends 800 m. along a mountain ridge stretching between 1250 and 1800 m.a.s.l. The forest is a mix of old growth and second growth with a characteristic thick humus layer (Beck et al., 2008). Tree height is principally determined by distance from ridge-tops, ranging drastically between 5 m on ridge-tops and 20 m in valleys. The majority of nectar-producing plants are epiphytes of the families Bromeliaceae, Ericaceae and Gesneriaceae and shrubs of the family Rubiaceae. The highland site (Cajanuma; 03°06’S, 79°10’W) was sampled between 2700 and 2850 m a.s.l. across a 600 m transect limited at the upper end by transition to tree-line vegetation. The transect stretches entirely through old-growth montane forest with trees averaging 5–7 m in height. Plants of the family Ericaceae are particularly prominent, but Bromeliaceae, Campanulaceae, Melastomataceae, Orchidaceae, Rubiaceae, and Solanaceae were also numerous. Of the three sites, Cajanuma is the most species-rich in terms of hummingbird-pollinated plants. All three sites are characterized by humid tropical climate (Kottke, Grieser, Beck, Rudolf & Rubel, 2006). Mean annual temperature varies elevationally from 9.4°C in Cajanuma up to 19.4°C in Bombuscaro, and mean annual precipitation ranges from 2000 mm in Bombuscaro to 4500 in Cajanuma (Emck, 2007; Moser, Hertel & Leuschner, 2007). Climate seasonality differs between the eastern and western side of Cordillera Real. The wettest season in Bombuscaro and ECSF (east) occurs between April and July, in contrast to Cajanuma (west), where the wettest period is between December and March (Beck et al., 2008).

Data collection took place in two seasons (February – May 2017 and October 2017 – January 2018). Throughout each season, we

worked at one site per day and changed site after, typically, 3–5 days. The data collected in the field consisted of: (1) records of hummingbird–plant interactions, (2) hummingbird and plant encounter rates, and (3) measurements of flower morphologies. Hummingbird–plant interactions were quantified by combining video recordings and visual observations. To represent our interaction networks, within each study site we selected a 200 m transect segment (ground distance) to sample hummingbird–plant interactions. On each day of sampling, we selected six flowering plant individuals to be filmed for five hours (camera model JVC GZR 415 GE). We prioritized filming flowers just starting to flower or those about to end their flowering. Otherwise the selection was made at random. As hummingbirds may visit both core ornithophilous syndrome flowers (e.g., red to purple color, with tubular corolla shape) as well as a range of flowers with floral traits that fall outside the ornithophilous pollination syndrome (Dalsgaard et al., 2009), we carefully evaluated all plants in flower for hummingbird visitation. We also consulted a local expert on hummingbird-pollinated flowers (Jürgen Homeier, *personal communication*). Only herbs with neither nectar nor tubular corollas were eliminated as candidates for hummingbird pollination. The remaining flowering plants were all observed for hummingbird visitation, but were excluded as candidates if no interactions were observed after 20 hr of video recording. For the three sites combined, the video recordings summed to cover 2269 hr: Bombuscaro (729 hr), ECSF (799 hr), and Cajanuma (740 hr).

The abundances of hummingbirds and plants were determined by morning surveys in 100 m segments (ground distance) covering the entire range of each transect. Birds were counted on the way out from base camp in the early mornings, whereas the floral abundance of all plant species was recorded on the way back to camp after the cameras had been placed (approximate 06:30–07:00 hr). For each flowering plant individual, the number of open flowers was counted directly. Their morphology was measured from photographs taken of the flower, together with a ruler for scale reference. Corolla length was measured as the straight distance from the bottom of the nectary to the corolla opening. The frequently complex shapes of flowers made angular measures of flower curvature difficult to interpret. Thus, we measured corolla curvature as the ratio between corolla length and length of a freehand line drawn between bottom of the nectary to the corolla opening, along the corolla centerline. We attempted to obtain flower morphologies from at least three individuals per species. However, the inaccessibility of flowers on tall trees and epiphytes made this objective impossible for a few species: Bombuscaro (singletons = 1), ECSF (singletons = 1, doubletons = 1), and Cajanuma (singletons = 1). Additionally, for two species in Cajanuma, we were unable to obtain any field measurements. For these, we used scaled photographs of herbarium sheets from the collection at the Universidad Técnica Particular de Loja.

2.3 | Processing of interaction data

We used the video motion software MotionMeerkat to screen videos for movement and isolate candidate frames to detect visiting hummingbirds (Weinstein, 2015). Using video recordings to quantify

interactions raises concerns about pseudo-replication by territorial hummingbirds, which repeatedly visit the same flowers, causing statistical inflation in species-level foraging preferences. To minimize pseudo-replication, interaction networks were assembled by including only one interaction between hummingbird i and plant j per survey day k unless: (1) plant j interacted with both sexes of hummingbird species i on day k , adding one extra interaction; or (2) interactions between hummingbird i and plant j were visually observed in other transect sections on the same survey day k (i.e., separated by at least 100 m distance), adding one extra interaction for each unique section in which the interaction was observed.

We used the resulting interaction networks to quantify resource partitioning at both the community level and at the species level. At the community level, we used the complementary specialization index H'_2 (Blüthgen, Menzel & Blüthgen, 2006) and modularity index (Q ; Dormann & Strauss, 2014). The complementary specialization index H'_2 determines the partitioning of interactions relative to their availability (i.e., network marginal sums). Thus, this metric reflects resource specialization among all community members (Blüthgen et al., 2006). The modularity index Q quantifies the tendency of species to form subgroups of species that interact more with one another than with other species from the network (Dormann & Strauss, 2014). We used this index because mutualistic networks, including weighted plant–hummingbird networks, are known to have a modular structure (Martín González et al., 2015; Maruyama et al., 2018), which is partly associated with differences in species traits (Maruyama et al., 2014). At the species level, we used specialization index d' , which quantifies the division of interactions between a focal hummingbird and all other hummingbirds relative to a neutral scenario that assumes interactions are simply determined by partner availability (Blüthgen et al., 2006). In our case, the hummingbird's partner availability was defined by the floral abundance of each plant species. All three measures, H'_2 , Q , and d' , were calculated in R using the “bipartite” package (Dormann, Gruber & Fründ, 2008). To calculate Q , we used the Beckett algorithm (Beckett, 2016) and selected the maximum modularity structure from five independent runs (Schleuning et al., 2014). H'_2 , Q , and d' range between zero and one, with higher values indicating, respectively, higher specialization and modularity of interactions. To account for intrinsic network properties and differences in sampling effort that are known to influence Q , we compared the empirical values to a null model consisting of 1000 null networks, which randomize interactions while preserving each species' summed number of interactions (i.e., the Patefield algorithm in the bipartite package; Vázquez, 2005). We avoided using null models that constrain network connectance because of studies showing that morphological trait matching has implications for species' degree distributions (i.e., morphological generalists species have high degree, morphological specialists have low degree; Vázquez, Chacoff & Cagnolo, 2009; Vizentin-Bugoni et al., 2014). Thus, by constraining connectance in a null model, we might risk masking the effect of trait matching. In contrast, the marginal totals that the Patefield algorithm constrains are not

affected by any niche-based processes. The observed value for Q was subtracted from means of 1000 values generated by the null model to obtain ΔQ (Dalsgaard et al., 2017; Martín González et al., 2015; Schleuning et al., 2012). In contrast to Q , H'_2 and d' are already corrected for species availability in the network and were therefore not adjusted for the null model (Blüthgen et al., 2006).

2.4 | Predicting interactions by morphological match, phenological overlap, and neutrality

Hummingbird–plant trait matching was determined using a standardized method that builds upon the assumption that the hummingbirds with relatively longest and most-curved bills have the highest probability of interacting with plants with the longest and most-curved corollas. Likewise, the interaction frequency is assumed to be high for the shortest and straightest bill and corolla morphologies. Pairwise morphological match was calculated by first standardizing all trait variables to zero mean and unit variance. For these standardized variables, we calculated morphological match as the Euclidean distance in traits between each hummingbird–plant pair. Previous studies have calculated morphological trait matching as either the Euclidean distance between the raw trait measures (e.g., Weinstein & Graham, 2017) or via the concept of “forbidden links”—assuming a hummingbird is able to access all flowers with corollas shorter than its bill length (e.g., Vizentin-Bugoni et al., 2014). We favor the standardized approach, detailed above, because of three benefits: 1) it minimizes assumptions about the significance of hummingbird tongue lengths, which are poorly known between species (Rico-Guevara, 2014); 2) it allows for implementation of more than one trait dimension, that is, we are able to include both bill–corolla length and curvature; and 3) species with interactions that are influenced by trait matching can be more directly interpreted as contributing to resource partitioning. If plant and hummingbird traits do not have similar mean and variance, species with extreme morphologies may not have any close-matching partners, and their traits are thus assumed not to be relevant for niche partitioning (Figure S5a). As a result, if species do not have traits with equal mean and variance, and interact proportionally to the similarity in their traits, quantified niche partitioning will be not much greater than if species interacted randomly (Figure S5b).

In addition to morphological match, we considered phenological overlap and a neutral model based on variation in abundances. The model for phenological overlap is based on the rationale that interaction probabilities should increase with the extent of temporal co-occurrence (Vázquez et al., 2009). We define phenological overlap as the number of unique survey days on which i and j were encountered together. The neutral model relied upon the expectation that species with higher encounter rates are expected to interact more frequently (Simmons et al., 2018; Vázquez et al., 2009). Thus, the neutral model assumes pairwise interaction frequencies to be proportional to the multiplied relative abundances for individual hummingbird and plant species (See S6 for details).

2.5 | Hierarchical Bayesian models for species interaction frequencies

The significance of morphological match, phenological overlap, and neutrality in determining realized pairwise interaction frequencies were evaluated using hierarchical N -mixture models following the approach of Weinstein and Graham (2017). Their model is built on the assumption that sampling constraints cause empirically observed interactions to represent a subset of a true underlying interaction network (Chacoff et al., 2012; Weinstein & Graham, 2017). This assumption is particularly true for biodiversity hotspots where many species occur at low densities (Terborgh, Robinson, Parker, Munn, & Pierpont, 1990). For each hummingbird i in each network, we fitted a model that explicitly estimated daily hummingbird detection probability. Underlying the daily observed interaction frequencies, the model assumes a true number of pairwise interactions. The detectability of this frequency is parametrized by the probability of detecting hummingbird i . All model parameters are estimated by assuming non-informative prior knowledge about the systems. Model standardized coefficients reflect the estimated influence of, respectively, morphological match (β_i^M), phenological overlap (β_i^P) and neutrality (β_i^N), in determining the underlying true interaction frequencies for hummingbird i . Here, more negative values of β_i^M indicate greater trait matching, whereas more positive values of β_i^P and β_i^N indicate greater influence of phenological overlap and neutrality, respectively. Covariates were considered important if the posterior distribution of their β parameter did not overlap zero (Weinstein & Graham, 2017). All models were run using Markov chain Monte Carlo (MCMC) procedures in the software JAGS (Plummer, 2003, 2012). To obtain posterior parameter distributions, we ran three MCMC chains for 100,000 draws, and we applied a thinning of 10 to reduce autocorrelation among individual MCMC draws. For a more detailed description, see S7 and Weinstein and Graham (2017).

3 | RESULTS

Elevational ranges of hummingbirds with specialized morphologies revealed strong discrepancies between long-straight and curved-bill specialists. Figure 2 shows that curved-bill specialists were overrepresented from low elevations up until 2000 m, above which they became replaced by long-billed specialists. This trend was insensitive to different thresholds used for defining morphological specialists (Figure S4). The trend also coincided with the composition of hummingbird morphotypes that we recorded at a local scale along the elevational gradient in Podocarpus National Park: of the 17 hummingbirds recorded at the lowland site, one (6%) was a long-billed specialist and three (18%) were curved-bill specialists. At mid-elevation, 17 hummingbirds were recorded, including two (11%) long-straight-bill specialists and one curved-billed specialist (6%). At the highland site, we recorded 12 hummingbird species, of which four (33%) were long-straight-bill specialists and one (8%) was a curved-bill specialist (Table S8). The ecological significance of these

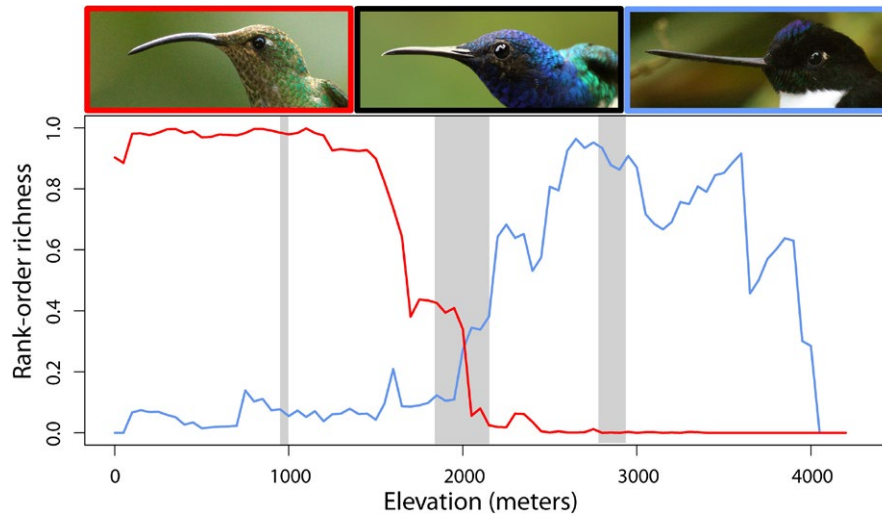


FIGURE 2 Elevational turnover in the richness of curved-billed specialists ($n = 11$, red) and long-straight-billed specialists ($n = 7$, blue) in the eastern high Andes. Within elevational bands of 50 meters, the richness of each specialized morphotype is compared to the expected number generated by a null model. The rank-order richness determines the proportion of 1000 randomly generated species compositions that contained fewer of each specialized morphotype than observed. Gray fragments mark elevations of the sampling sites within Podocarpus National Park (Ecuador). Photos by JS. From left: an example of a curved-billed specialist (*Lafresnaya lafresnayi*), a species with medium bill length and curvature (*Florisuga mellivora*), and an example of a long-straight-billed specialist (*Coeligena torquata*) [Colour figure can be viewed at wileyonlinelibrary.com]

specialists is evident from their contribution to total morphological diversity (Figure S9). Among east Andean hummingbirds, we found that the elevational variation in morphological diversity was explained solely by the morphological diversity of species with specialized morphotypes (Figure S9).

As expected, the overrepresentation of curved-bill specialists in the lowlands disappeared after removing the Phaethornithinae clade (Hermits; Figure 3). The only remaining curved-bill specialist was *Lafresnaya lafresnayi*, which therefore alone explains the appearance of curved-bill specialists in the highlands in Figure 3C. Long-straight-bill specialists, in contrast, are dispersed more widely in the phylogeny, comprising five independent evolutionary trajectories (Figure 3A). The highest concentration of long-straight-bill specialists is found in a clade within the highland genus *Coeligena* (clade Y in Figure 3a). Upon removing this clade, long-straight-bill specialists nonetheless remained overrepresented in the highlands (Figure 3c). The overrepresentation of long-straight-bill specialists in the highlands also remained when accounting for the overall increase in hummingbird body mass toward higher elevations (Figure S10).

If our hypothesis about the role of morphologically specialized hummingbirds holds, we would expect trait matching to reach a maximum at low and high elevations where they are overrepresented. Local-scale field observations corroborated this expectation (Table 1). At the highland site, six out of the eight hummingbirds had posterior parameter distributions for morphological matching not overlapping with zero. That is, these species tended to visit morphologically close-matching flowers. The same tendency applies to four of the seven species in the lowland site. Conversely, at mid-elevation, none of the nine hummingbirds were influenced by morphological matching. Moreover, at high and low elevations,

trait-matching parameters for realized interactions were more negative for morphological specialists than for non-morphological specialists, whereas at mid-elevation, both morphological specialists and non-morphological specialists had trait-matching parameters equally close to zero (Table 1). Phenological overlap influenced three species at mid-elevation and four species at low elevation (Table S11). Neutrality played a minor role in predicting interaction frequencies, influencing the interactions for just two species at the highland site (Table S11).

Community-level modularity (Q) and complementary specialization (H'_2) followed elevational trends similar to trait matching. The mid-elevation network was less modular and specialized than the highland and lowland networks (Table 2, S12). In all three networks, the observed value of modularity is $> 95\%$ of the null model values (S12). In regard to the species-level specialization index (d'), morphological specialists had on average more specialized foraging preferences than non-specialists in the highland and lowland networks (Table 2). At mid-elevation, there was less difference in degree of specialization between the two morphotypes. The observed interaction networks, including the foraging preferences of each specialized hummingbird morphotype, are illustrated in Figure 4.

4 | DISCUSSION

We showed that morphological specialists prevail at low and high elevations in the eastern high Andes (Figure 2). Conversely, mid-elevation (~ 2000 m) represents a transition zone from the pre-montane forest into the cloud forest, where long-straight-billed specialists replace curved-billed specialists. If the distribution of

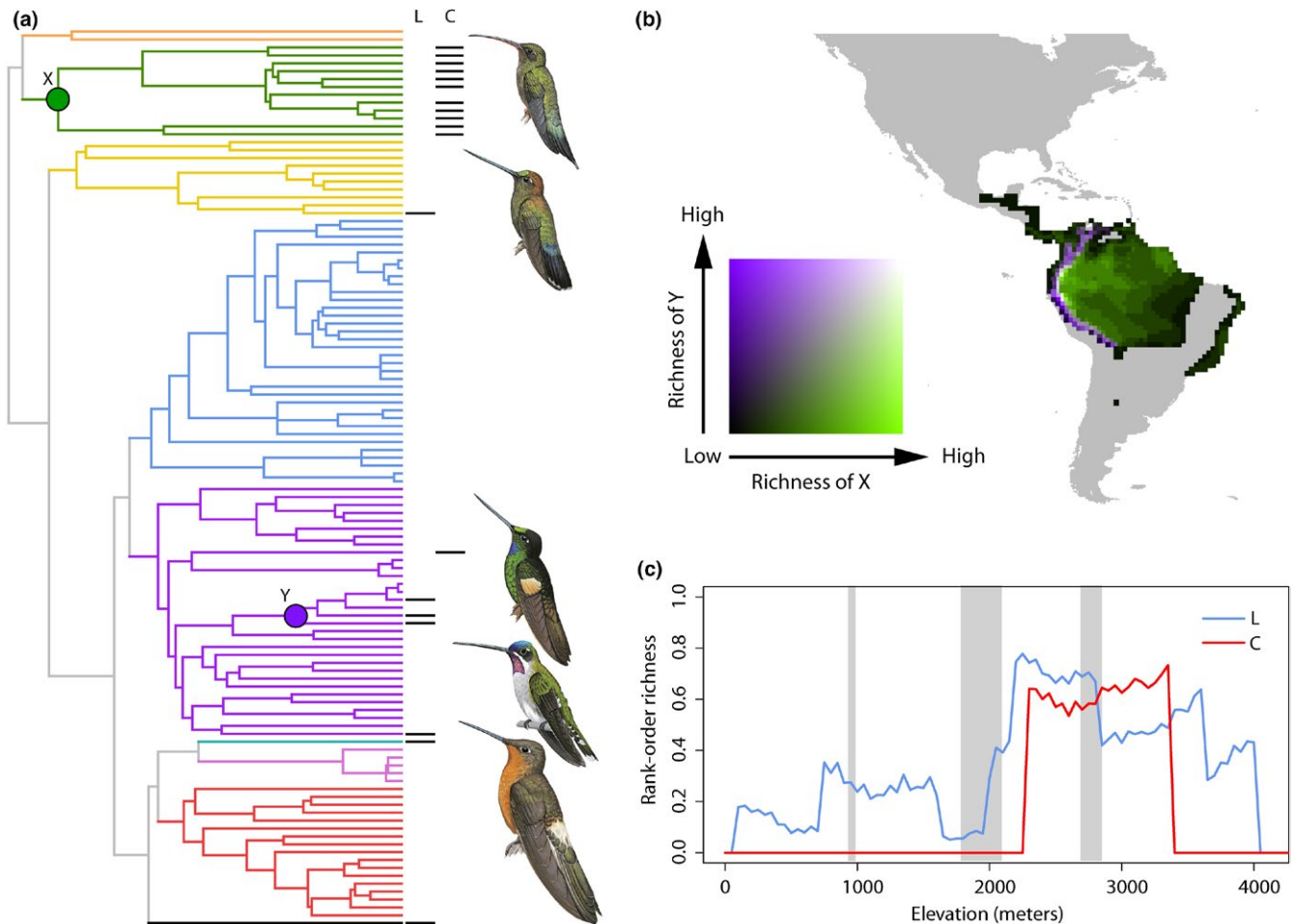


FIGURE 3 Phylogenetic distribution of the morphologically specialized species: 7 long-straight billed (L) and 11 curved-billed specialists (C) occurring in the eastern Andes. Colors represent the major hummingbird clades, as identified by McGuire et al. (2014). (a) Clade X marks the Phaethorninae subfamily (Hermits), which dominates the curved-billed morphotype. Clade Y marks a lineage within the genus *Coeligena*, which has the highest concentration of long-straight-billed morphotypes. (b) Geographical pattern in the richness of clades X and Y. (c) The pattern of Figure 2 after removing clades X and Y from the dataset. Specifically, clade X was removed when calculating rank-order richness of curved-billed specialists (red), whereas clade Y was removed when calculating rank-order richness of long-straight-billed specialists (blue). As in Figure 2, the rank-order richness determines the proportion of 1000 randomly generated species compositions that contained fewer of each specialized morphotype than observed. Note that the overrepresentation of curved-billed specialists in the lowlands from Figure 2 disappears after removing clade X. Likewise, the overrepresentation of long-straight-billed specialists in highlands persists after removing clade Y. Gray fragments mark elevations of the sampling sites within Podocarpus National Park (Ecuador). The phylogeny derives from McGuire et al. (2014). Data on hummingbird geographical distributions consists of 1×1 longitude-latitude resolution presence-absence maps for the 115 extant hummingbird species. The data derive from a database that has been continuously updated since its original presentation by Rahbek and Graves (2000, 2001). Imaged representatives of morphological specialists are reproduced with permission from J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie and E. de Juana (Eds.). (2018). Handbook of the Birds of the World Alive. Barcelona, Spain: Lynx Edicions. (Retrieved from <http://www.hbw.com/> on 21 February 2018). From top: curve-billed specialist *Phaethornis guy*, long-straight billed specialists *Doryfera ludovicae*, *Coeligena lutetiae*, *Heliomaster longirostris*, and *Patagona gigas* [Colour figure can be viewed at wileyonlinelibrary.com]

morphologically specialized species has relevance for variation in trait matching, we expect morphological trait matching to be least important for interaction frequencies at mid-elevation (around 2000 m) and to increase toward low and high elevations. Field investigations in three sites along an elevational gradient in southern Ecuador (~1000, 2000 and 3000 m) were in accord with this expectation (Table 1). We found that hummingbirds at low and high elevations had a stronger tendency to visit morphologically matching flowers than hummingbirds at mid-elevations. Moreover,

morphologically specialized hummingbirds in these networks showed a greater tendency to visit well-matched flowers than morphological non-specialists. At mid-elevation, the two long-straight-bill species (*Coeligena torquata* H11, *Doryfera ludovicae* H13) showed no particular preference for the long-corolla flowers (*Bomarea pardina*, *Guzmania squarrosa*, and *Orthaea abbreviate*). The hummingbird with the smallest bill (*Oreotus underwoodii* H16) was observed visiting only *Palicourea stenosepala*, which had the fifth shortest corolla length in the mid-elevation network. *Adelomyia melanogenys* (H9),

TABLE 1 Summary statistics for trait-matching parameters (β_i^M) from hierarchical Bayesian models. Specialist morphotypes: (L) Long-straight-bill specialist, (C) Curve-bill specialist. Hummingbirds for which the posterior parameter distribution did not overlap zero were considered to favor morphologically close-matching flowers. These hummingbirds are indicated by boldface font.

ID	Species by locality	Specialist Morphotype	β_i^M Z score (mean; SD)
Cajanuma (2700–2850 m)			
H1	<i>Boissonneaua matthewsii</i>		–1.98 (–1.21; 0.61)
H2	<i>Coeligena lutetiae</i>	L	–5.07 (–1.58; 0.31)
H3	<i>Coeligena torquata</i>	L	–2.85 (–2.03; 0.71)
H4	<i>Doryfera ludovicae</i>	L	–1.70 (–1.22; 0.72)
H5	<i>Eriocnemis vestita</i>		–4.05 (–1.69; 0.42)
H6	<i>Heliangelus micraster</i>		–4.78 (–1.03; 0.21)
H7	<i>Lafresnaya lafresnayi</i>	C	–4.60 (–1.57; 0.34)
H8	<i>Metallura tyrianthina</i>		–3.88 (–2.56; 0.66)
	Mean		–2.28 (–1.61; 0.71)
	Morph. specialists		–2.55 (–1.60; 0.63)
	Non-morph. specialists		–2.08 (–1.62; 0.78)
ECSF (1800–2100 m)			
H9	<i>Adelomyia melanogenys</i>		–2.31 (–0.77; 0.33)
H10	<i>Coeligena coeligena</i>		–2.12 (–0.51; 0.24)
H11	<i>C. torquata</i>	L	–1.93 (–0.99; 0.52)
H12	<i>Colibri thalassinus</i>		–1.63 (–1.11; 0.68)
H13	<i>D. ludovicae</i>	L	–1.78 (–0.97; 0.55)
H14	<i>Haplophaedia aureliae</i>		–2.07 (–0.85; 0.41)
H15	<i>Heliangelus amethysticollis</i>		–1.95 (–1.02; 0.52)
H16	<i>Ocreatus underwoodii</i>		–2.05 (–1.16; 0.56)
H17	<i>Phaethornis syrmatorophorus</i>	C	–2.23 (–1.44; 0.65)
	Mean		–1.72 (–0.98; 0.57)
	Morph. specialists		–1.61 (–0.98; 0.61)
	Non-morph. Specialists		–1.82 (–0.98; 0.54)
Bombuscaro (950–1000 m)			
H18	<i>Doryfera ludovicae</i>	L	–3.53 (–1.08; 0.31)
H19	<i>Eutoxeres aquila</i>	C	–3.67 (–1.90; 0.52)
H20	<i>Heliodoxa leadbeateri</i>		–2.61 (–1.33; 0.51)
H21	<i>O. underwoodii</i>		–1.42 (–0.74; 0.52)
H22	<i>Phaethornis guy</i>	C	–3.72 (–1.32; 0.35)
H23	<i>Phlogophilus hemileucurus</i>		–3.65 (–1.70; 0.47)
H24	<i>Thalurania furcata</i>		–2.29 (–1.04; 0.45)
	Mean		–2.23 (1.30; 0.58)
	Morph. specialists		–2.72 (–1.43; 0.53)
	Non-morph. Specialists		–1.99 (–1.20; 0.60)

with the second smallest bill, visited a wide range of different flowers shapes (Figure 4B). By the differences in the elevational distribution of long-straight-billed and curve-billed morphotypes, we speculate that east Andean highlands and lowlands may represent two distinct regimes for hummingbird–plant coevolution. The species composition at mid-elevation represents mixed subsets of hummingbirds and plants from the two regimes, which may lead morphological

specialists in mid-elevation to adopt more opportunistic foraging preferences. From the plant perspective, this explanation accords with our observation that the most extreme corolla lengths were found in the highlands (Figure S13a), and that the most extreme corolla curvatures were found in the lowlands (Figure S13b).

An important assumption in our concept of trait matching is that morphologically specialized hummingbirds should avoid visiting

TABLE 2 Differences in community-level specialization (H'_2) and modularity (Q) among the three sites. H'_2 determines the partitioning of interactions relative to their availability (i.e., network marginal sums), and Q quantifies the tendency of species to form subgroups of species that interact more with one another than with other species in the network. Δ sign indicates a correction by the Patefield null model. The species-level specialization index (d') is compared between morphological specialists and non-morphological specialists according to the 10% threshold. The index determines the division of interactions between a focal hummingbird and its competitors relative to a neutral scenario that assumes interactions to be solely determined by partner availability. In the species-level index, partner availability is quantified by the plant encounter rate.

Site	Community level			Species level (mean \pm SD)	
	Obs. H'_2	Obs. Q	Δ Q	d' (morphological specialists)	d' (non-morphological specialists)
Cajanuma	0.53	0.51	0.30	0.63 \pm 0.34	0.46 \pm 0.21
ECSF	0.38	0.35	0.15	0.56 \pm 0.26	0.48 \pm 0.29
Bombuscaro	0.53	0.47	0.30	0.39 \pm 0.10	0.25 \pm 0.09

plants with generalized floral morphologies (i.e., short, straight floral corollas). This avoidance could be driven by resource competition with hummingbirds having generalized morphologies (Tinoco, Graham, Aguilar & Schleuning, 2017). A flower's morphology may also be linked to its nectar secretion, so that flowers with generalized morphologies produce less nectar and, thus, are less profitable for morphologically specialized hummingbirds (Dalsgaard et al., 2009; Feinsinger & Colwell, 1978; Kodric-Brown, Brown, Byers & Gori, 1984; Maglianesi et al., 2014). For these reasons, the significance of trait matching for resource partitioning is likely a product of both mechanical constraints on flower handling time and variation in nectar production (Wolf, Stiles & Hainsworth, 1976). At the network level, we found that the degree of modularity was highest in the networks at low and high elevation where morphological specialists contributed more to specialization than morphological non-specialists (Table 2). Together, these results are in accord with the idea that morphological specialists at low and high elevations are the main drivers of trait-determined resource partitioning.

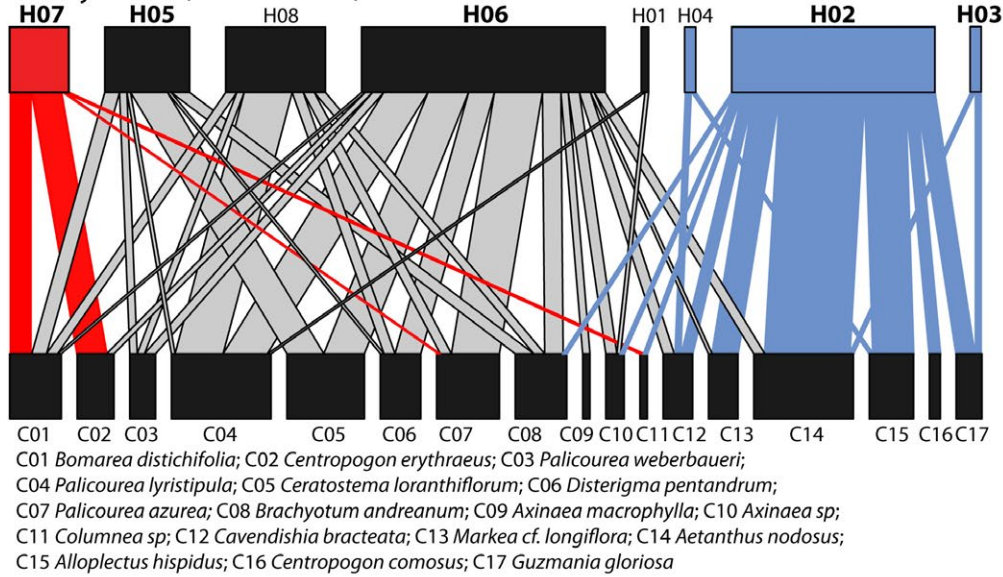
In the highland site, more than half of the hummingbird species tended to visit a subset of available flowers that matched their bills closely in morphology (Table 1). In the lowland site, we found only one case in which a hummingbird (*Eutoxeres aquila*; H19) was completely isolated from others in the network (Figure 4). Even though the remaining two lowland morphological specialists, *D. ludovicae* (H18), and *Phaethornis guy* (H22), tended to forage on morphologically matching flowers, their interactions overlapped with three hummingbirds with no noticeable trait-matching: *Heliodoxa leadbeateri* (H20), *O. underwoodii* (H21), and *Thalurania furcata* (H24). Therefore, although morphological specialists may contribute to network-wide resource partitioning, species with specialized

morphologies and foraging strategies may utilize the same flowers as morphological generalists and thereby diminish resource partitioning. Nevertheless, specialization and modularity in the lowland site were high because the two morphological specialists and the three generalists had limited or no connection with *Phlogophilus hemileucurus* (H23; a morphological generalist) and the morphological specialist *E. aquila* (H19). Finally, at mid-elevation, the lack of trait matching resulted in high resource overlap, as reflected in the specialization metrics. With these observations, we conclude that morphological specialists within Podocarpus National Park contribute to trait-determined resource partitioning at high and low elevation.

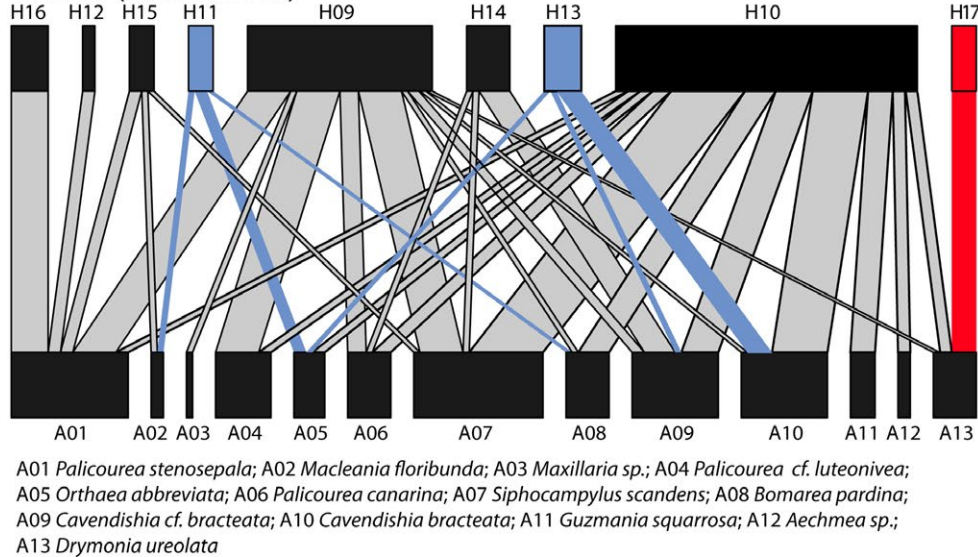
Implications of trait matching for pairwise interactions within mutualistic networks have been underlined by several recent studies (Maglianesi et al., 2014, 2015; Soteras et al., 2018; Vizentin-Bugoni et al., 2014; Weinstein & Graham, 2017). Yet, none has specifically addressed the determinants of trait matching at an assemblage level across space. Here, we have proposed a mechanistic hypothesis suggesting that the level of trait matching is facilitated by the elevational distribution of species morphologies. Specifically, based on the observation that the vast majority of hummingbird species have rather generalized bill morphologies (del Hoyo et al., 1999), and that morphologically specialized hummingbirds with long or curved bills are those with the potential of utilizing unique floral resources, we propose that the distribution of morphological specialists underlies geographical patterns in hummingbird-plant trait matching. What determines the distribution of morphological specialists at the biogeographical scale remains an open question. The overrepresentation of curved-bill specialists in the lowlands coincides with the ancient radiation of the primarily lowland Phaethorninae subfamily (Figure 3c). Thus, there is no direct indication that the lowland

FIGURE 4 Hummingbird-plant interaction networks. (a) Cajanuma 2700–2850 m; (b) ECSF 1800–2100 m; and (c) Bombuscaro 950–1000 m. Boxes indicate individual species: hummingbirds (above) and plants (below). Box width reflects the total number of interactions recorded for each species. Width of the connecting lines indicates the frequency of pairwise interactions. Hummingbird identification numbering follows that in Table 1. Curved-billed morphological specialists are marked in red and long-straight-billed specialists are marked in blue. Hummingbirds for which posterior parameter distribution did not overlap with zero were considered to favor morphologically close-matching flowers. These species are indicated by boldface font. Our concept of trait matching assumes that hummingbirds with the relatively longest and most-curved bills interact most frequently with plants having the longest and most-curved corollas. Likewise, the interaction frequency is assumed to be high for the shortest and straightest bill and corolla morphologies [Colour figure can be viewed at wileyonlinelibrary.com]

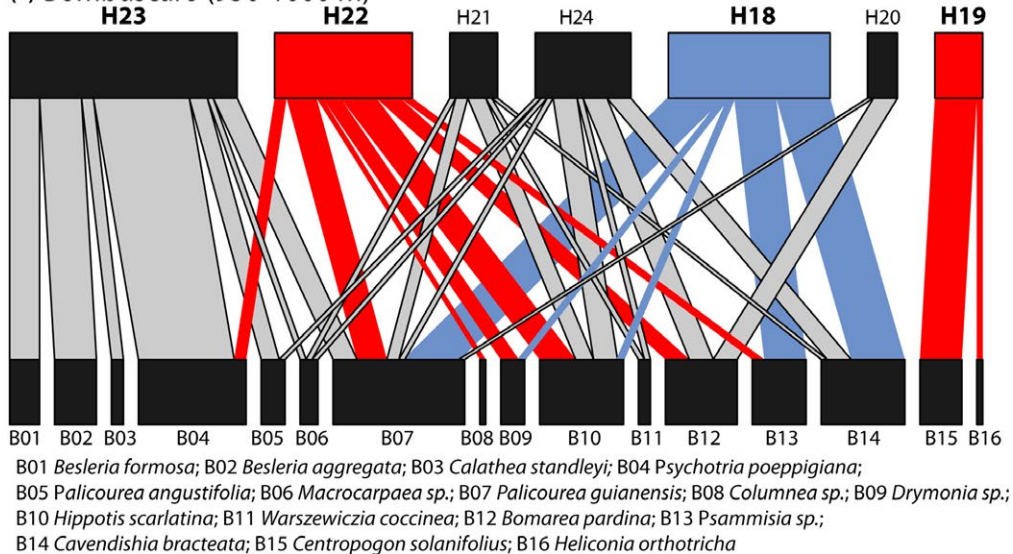
(a) Cajanuma (2700–2850 m)



(b) ECSF (1800–2100 m)



(c) Bombuscaro (950–1000 m)



environmental setting should have selected for specialized bill curvatures. On the other hand, long-straight-billed specialists have evolved numerous times in the high Andes. Thus, the question is why the environmental setting in the highlands has favored evolution of long-billed hummingbirds. One suggestion is that bill length is simply a body mass covariant. Altshuler et al. (2004) found that mean hummingbird body size increases steadily with elevation, likely due to the selective advantage of larger body size for thermoregulation. To the degree that hummingbird bill length correlates with body mass, abiotic factors favoring adaptations in body size could perhaps explain the overrepresentation of long-straight-billed specialists in the highlands. We found, however, that the increase in body mass toward high elevations does not explain the overrepresentation of long-straight-billed specialists around 3000 meters elevation in the eastern high Andes (Figure S10). An alternative explanation suggests that hummingbird-plant coevolution and resource partitioning are greater in mountain environments characterized by rainy and cold conditions (Dalsgaard et al., 2009, 2018; Sonne et al., 2016; Stiles, 1978), possibly because such conditions are unfavorable to large, pollinating insects, especially bees and lepidopterans (Aizen, 2003; Cruden, 1972; Dalsgaard et al., 2009, 2018; Poulsen, 1996). Annual precipitation increases and temperature decreases with elevation, toward our highland site in Podocarpus National Park (Emck, 2007; Moser et al., 2007). Thus, a limitation of pollinating insects in the highlands may have caused hummingbirds to diversify as the principal pollinators of many highland flowers (Aizen, 2003; Cruden, 1972; Dalsgaard et al., 2009, 2018; Poulsen, 1996), resulting in greater hummingbird-plant coevolution with several hummingbird lineages developing long bills from short-billed ancestors. In this respect, it is noticeable that numerous Andean highland flowers have extremely long corollas (e.g., *Aetanthus*, *Brugmansia*, *Passiflora*, and *Tristerix*), which was also the case in our networks (Figure S13a). This observation supports the idea of high coevolution and trait matching in the Andean highlands (Soteras et al., 2018).

With this study, we add to the growing literature linking up biogeography and community ecology. Here, we hope to raise awareness of the biogeographical processes that may underlie patterns in trait matching within local plant-animal communities. Specifically, we propose that the spatial distribution of morphotypes could be a candidate determinant of variation in trait matching across environmental gradients. As this result has implication for trait-driven resource partitioning, and given the small sample size of our data set, we hope our study will stimulate others to test the generality of our hypothesis that the distribution of morphotypes determines trait matching within local communities.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.16837bf> (Sonne et al., 2019), and Figshare: <https://doi.org/10.6084/m9.figshare.6151196.v3>

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SUPPORTING INFORMATION

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

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