

The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird–plant networks

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Abstract

1. Functional traits can determine pairwise species interactions, such as those between plants and pollinators. However, the effects of biogeography and evolutionary history on trait-matching and trait-mediated resource specialization remain poorly understood.
2. We compiled a database of 93 mutualistic hummingbird–plant networks (including 181 hummingbird and 1,256 plant species), complemented by morphological measures of hummingbird bill and floral corolla length. We divided the hummingbirds into their principal clades and used knowledge on hummingbird biogeography to divide the networks into four biogeographical regions: Lowland South America, Andes, North & Central America, and the Caribbean islands. We then tested: (a) whether hummingbird clades and biogeographical regions differ in hummingbird bill length, corolla length of visited flowers and resource specialization, and (b) whether hummingbirds' bill length correlates with the corolla length of their food plants and with their level of resource specialization.
3. Hummingbird clades dominated by long-billed species generally visited longer flowers and were the most exclusive in their resource use. Bill and corolla length and the degree of resource specialization were similar across mainland regions, but the Caribbean islands had shorter flowers and hummingbirds with more generalized interaction niches. Bill and corolla length correlated in all regions and most clades, that is, trait-matching was a recurrent phenomenon in hummingbird–plant associations. In contrast, bill length did not generally mediate resource specialization, as bill length was only weakly correlated with resource specialization within one hummingbird clade (Brilliantes) and in the regions of Lowland South America and the Andes in which plants and hummingbirds have a long co-evolutionary history. Supplementary analyses including bill curvature confirmed that bill morphology (length and curvature) does not in general predict resource specialization.
4. These results demonstrate how biogeographical and evolutionary histories can modulate the effects of functional traits on species interactions, and that traits better predict functional groups of interaction partners (i.e. trait-matching) than resource specialization. These findings reveal that functional traits have great potential, but also key limitations, as a tool for developing more mechanistic approaches in community ecology.

KEYWORDS

biogeography, island ecology, niche partitioning, plant–animal interactions, resource specialization, species traits, specificity, trait-matching

1 | INTRODUCTION

Species do not live and evolve in isolation, but are entangled within networks of interactions with other species (Bascompte & Jordano, 2007). As species' interactions play a key role in species

coexistence and speciation (Phillips et al., 2020), it is important to understand when and why co-occurring species interact and specialize on each other. Recently, there is growing interest in the role of functional traits in determining pairwise interactions between species (Maruyama et al., 2018; McGill et al., 2006; Pigot et al., 2020;

Schleuning et al., 2020; Sonne et al., 2020). If two co-occurring species have matching traits, the probability and efficiency of their interaction should increase (Eklöf et al., 2013; Maglianesi et al., 2014). Otherwise, mismatches in traits could render interactions inefficient or even impose barriers to interactions, resulting in so-called 'forbidden links' (Jordano et al., 2003). In other words, species' traits may determine whether and how frequently co-occurring species interact; thus, species' traits would be expected to match and influence resource specialization (Klumpers et al., 2019; Maglianesi et al., 2014).

Mutualistic systems of plant–pollinator interactions contain classic examples of trait-matching that have been highlighted as textbook examples of coevolution (e.g. Thompson, 2005). For instance, the length of a moth's proboscis, or the length of a hummingbird's bill, often match the corolla length of their food plants (Nilsson, 1988; Temeles & Kress, 2003). Trait-matching and floral specificity may be energetically advantageous for the pollinators and increase pollination efficiency (Montgomerie et al., 1984). Accordingly, both trait-matching and trait-mediated resource specialization have been reported in studies of local plant–pollinator interaction networks (Klumpers et al., 2019; Maglianesi et al., 2014; Stang et al., 2009; Vizentin-Bugoni et al., 2014; Weinstein & Graham, 2017). However, drawing general conclusions in community ecology requires comparative studies of local communities across biogeographic regions (Lessard et al., 2012), and biogeographical history has been suggested to influence the role traits play in mediating plant–pollinator interactions (Dalsgaard et al., 2018). Notably, theory predicts that biogeographical regions where species have co-occurred for longer should contain species with more specialized associations and greater trait-matching (Dalsgaard et al., 2011; Sonne et al., 2016, 2020). At the other extreme, pollinators on oceanic islands are predicted to have generalized feeding behaviours, probably because it is advantageous to be a generalist to colonize and establish on islands (Olesen et al., 2002). Moreover, as oceanic islands have an impoverished insect pollinator fauna (Olesen & Jordano, 2002), evolutionary processes may drive island pollinators, especially vertebrates, to evolve novel and generalized feeding niches (Olesen et al., 2002; Olesen & Valido, 2003; Traveset et al., 2015). Taken together, theory suggests that biogeographical history may influence trait-matching and how well traits predict resource specialization in plant–pollinator networks, but large-scale analyses across biogeographical regions are rare (Dalsgaard et al., 2018; Sonne et al., 2020).

In addition to biogeographical history, if trait-matching and trait-mediated resource specialization are invariant properties of pollination networks, they should manifest repeatedly among distinctly related groups within a pollination system. For example, the mutualistic association between hummingbirds and their nectar-food plants is the most specialized avian pollination system (Fleming & Muchhala, 2008; Zanata et al., 2017), largely manifested in the match between the length of hummingbird bills and the length of the flowers they feed on (Cotton, 1998; Dalsgaard et al., 2009; Feinsinger & Colwell, 1978; Maruyama et al., 2014; Sonne et al., 2020; Stiles, 1981; Vizentin-Bugoni et al., 2014; Weinstein

& Graham, 2017). However, hummingbirds consist of nine evolutionary distinct clades (McGuire et al., 2014), which differ greatly in their bill morphology and floral preferences (Bleiweiss, 1998; Feinsinger & Colwell, 1978). Thus, if trait-matching is universal for hummingbird–plant associations, bill length and corolla length of visited flowers should co-vary between hummingbird clades. In other words, hummingbird clades consisting of long-billed species should prefer flowers with long corollas and *vice versa* for clades with shorter bills. Moreover, bill length should correlate with corolla length both across all hummingbird species and across the species within each hummingbird clade. Likewise, if bill length predicts resource specialization (Maglianesi et al., 2014), then bill length should co-vary with resource specialization both between and within hummingbird clades. However, although evolutionary relatedness is known to structure plant–pollinator interaction networks (Martín González et al., 2015; Rezende et al., 2007), the role of evolutionary history in influencing trait-matching and trait-mediated resource specialization remains poorly understood.

To examine whether evolutionary and biogeographical histories influence the generality of trait-matching and trait-mediated resource specialization in assemblages of plants and pollinators, we compiled a database of 93 quantitative hummingbird–plant networks distributed widely across continental America and the Caribbean islands. Each network represents the mutualistic interactions occurring within local assemblages of hummingbirds and their food plants (Dalsgaard et al., 2011), for which we gathered data on hummingbird bill length and the effective floral corolla length (*sensu* Wolf et al., 1976). To test the generality of trait-matching and trait-mediated resource specialization across evolutionary and biogeographical histories, we divided the hummingbirds into their nine principal clades and used knowledge on hummingbird biogeography to divide the networks into four biogeographical regions: Lowland South America, Andes, North & Central America, and the Caribbean islands (McGuire et al., 2014). We used this unique set of hummingbird–plant networks and trait data to test: (a) whether hummingbird clades and biogeographical regions differ in hummingbird bill length, corolla length of visited flowers and resource specialization, and (b) whether hummingbirds' bill length correlates with the corolla length of their food plants and with their level of resource specialization, which we examined both for the entire dataset and within each hummingbird clade and biogeographical region.

2 | MATERIALS AND METHODS

2.1 | Datasets: Hummingbird–plant networks and traits

We compiled a dataset of 93 quantitative hummingbird–plant interaction networks from localities distributed widely across the Americas. Each of the 93 networks describes interaction frequencies within assemblages of hummingbirds and their food plants in a

specific location. We only included mutualistic interactions in which a given hummingbird was observed drinking nectar and touching the stigma/anthers of the given flower, thereby potentially acting as a pollinator (see Appendix S1). The networks were sampled to represent all hummingbird clades and hummingbird-visited plant families without any taxonomic bias. Species names of the hummingbirds follow the International Ornithological Committee World List (IOC version 9.2; www.worldbirdnames.org; Appendix S2). Hummingbirds were divided into nine clades following McGuire et al. (2014). Species names and families of the plants follow 'The Plant List' (TPL version 1.1; www.theplantlist.org), with a few exceptions where species names of recorded plants were not found in TPL (specified in Appendix S3). The networks can be downloaded from Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd7n> (Dalsgaard et al., 2021).

We compiled two trait datasets: one for all hummingbird species and one for all plant species observed in the 93 networks (Appendices S2 and S3). In total, the datasets contained 181 hummingbird species and 1,256 plant species for which we gathered data on hummingbird bill length and the effective floral corolla length (*sensu* Wolf et al., 1976). Data on hummingbird bill length were based on museum specimens, most averaged across five males and five females (specified in Appendix S2). In total, we obtained bill length estimates for 180 of the 181 hummingbird species (~99% of the species; Appendix S2). Data on floral corolla length were based on measurements in the field. Apart from a few cases (~1% of the species), data on floral corolla length were collected at the same locality as the network. For plant species present in more than one network, if data on floral corolla length were collected in several localities (~19% of the species), we calculated species averages across localities. In total, we obtained floral corolla length estimates for 962 plant species (~76% of the species; Appendix S3). As a supplement to bill and corolla length, we attempted to gather data on bill and corolla curvature, as these traits may also match and the combination of bill length and curvature may better predict hummingbird resource specialization than bill length alone (Maglianesi et al., 2014; Sonne et al., 2019). There were insufficient data available on floral curvature to be included in our analyses, but we were able to gather a comprehensive dataset for bill curvature (~99% of the species; Appendix S2); this we used in supplementary analyses to validate our main focus on bill length. The bill length, bill curvature and corolla length trait data can be downloaded from Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd7n> (Dalsgaard et al., 2021).

2.2 | Measuring resource specialization

For each hummingbird species within the 93 hummingbird-plant networks, we calculated resource specialization using two metrics, one reflecting niche overlap and one reflecting niche breadth. As a measure of niche overlap, we used the complementary specialization index d' (Blüthgen et al., 2006). We used this index as it is

robust to variation in sampling effort, more than other measures of resource specialization (Fründ et al., 2016). The index derives from Shannon's entropy and quantifies the extent to which observed interaction frequencies differ from random encounter probabilities of species, as derived from species' total interaction frequencies (Blüthgen et al., 2006). This follows the assumption that if species specialize on specific interaction partners, these preferences should be captured as deviations from random encounters given by partner availability (Blüthgen et al., 2006). The index d' ranges between 0 and 1 for extreme generalization and extreme specialization, respectively (Blüthgen et al., 2006). As a measure of hummingbird niche breadth, we used the proportional generality index; a quantitative version of proportional resource use (normalized degree in binary networks), making it suitable for comparisons between networks (Cusser et al., 2019). A proportional generality value at or close to zero indicates a narrow niche breadth (i.e. a specialized species), whereas higher values indicate a broader niche breadth. Note that the proportional generality index may be larger than one. For each hummingbird species in each network, we calculated species-level specialization d' and proportional generality using the BIPARTITE package in R (Dormann et al., 2008).

2.3 | Biogeographical regions

The datasets were separated into four major biogeographical regions: Lowland South America, Andes, North & Central America, and the Caribbean (Figure 1). This separation is based on the division of hummingbirds into biogeographical regions, as extant hummingbirds supposedly originated in lowland South America ~22 million years ago, then expanded into the Andes (~16 million years ago) and north of the Isthmus of Panama (~12 million years ago), arriving in the Caribbean region more recently ~5 million years ago (McGuire et al., 2014). Our 'Lowland South America' region includes all networks south of the Isthmus of Panama, excluding networks located in the Andean mountains. The 'Andes' region includes all networks within the Andean mountains as defined by Rahbek et al. (2019). The 'North & Central America' region includes all networks located on the mainland north of the Isthmus of Panama. Finally, the 'Caribbean' region includes all networks located on oceanic islands in the Caribbean Basin, excluding the continental island of Trinidad located south of Bond's line, which for biogeographical reasons was included in the 'Lowland South America' region (Carstensen et al., 2012). The 93 hummingbird-plant interaction networks were distributed as follows: 41 in Lowland South America, 22 in North & Central America, 21 in the Andes, and nine in the Caribbean (Figure 1). We observed most hummingbird species in the Andean networks (76 species), followed by Lowland South America (55 species), North & Central America (53 species) and the Caribbean island networks (12 species). With respect to hummingbird-visited plant species, we recorded 641 species in Lowland South America, 367 species in the Andes, 233 species in North & Central America, and 65 species in the Caribbean.

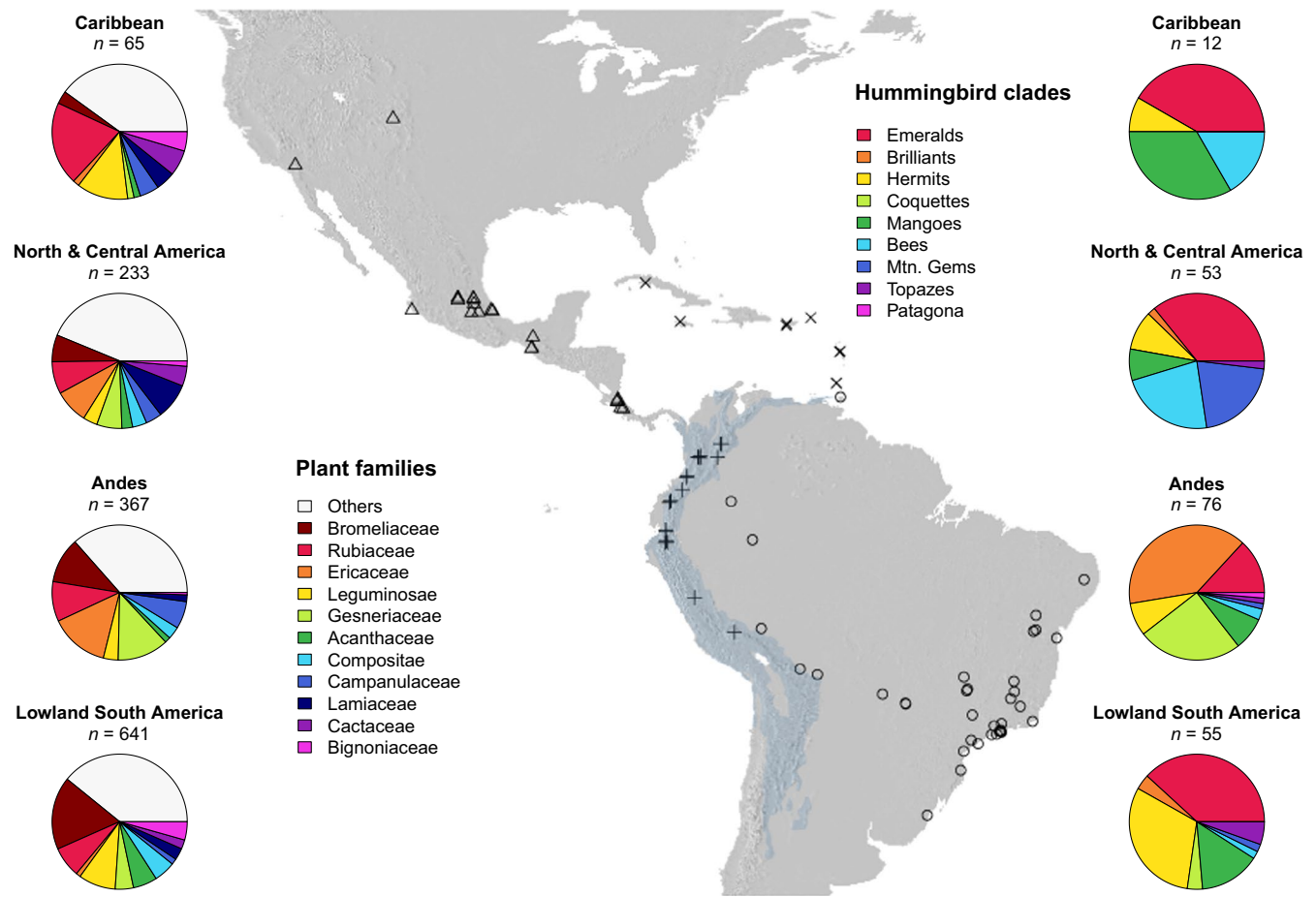


FIGURE 1 The distribution of 93 hummingbird–plant interaction networks across four biogeographical regions (O = Lowland South America, + = Andes, Δ = Central & North America, x = Caribbean). The pie charts visualize the distribution of species of all nine hummingbird clades (right) and the 11 most frequently visited hummingbird–plant families (left) within each biogeographical region. The category ‘others’ includes the rest of the plant families visited by hummingbirds. Within a given pie chart, the size of a clade/family reflects the number of species observed in the networks within a given region. Fisher’s exact test showed that all regions differed in respect to plant family distribution ($p < 0.05$ for all pairwise comparisons). For hummingbirds, all mainland regions differed significantly in clade distribution ($p < 0.05$), but the Caribbean was not significantly different from North & Central America and Lowland South America ($p > 0.05$), the two regions from where hummingbirds colonized the Caribbean (Dalsgaard et al., 2018)

2.4 | Statistical analyses

First, we explored whether the hummingbird clades and plant families were distributed randomly across the four biogeographical regions. To examine whether differences in hummingbird clade and plant family distribution were statistically different between the four biogeographical regions, we used Fisher’s Exact Test followed by False Discovery Rate (FDR) adjusted pairwise comparisons between all regions for both hummingbird clades and plant families. Significance levels were calculated with the function ‘fisher.test’ in R (R Development Core Team, 2016) using Monte Carlo simulations with 10,000 replicates. For plants, to focus on the main families, only the five most frequent families in each region were chosen, which across the four regions gave a total of 11 families (plus the category ‘others’ containing the rest of the plant families).

Second, we used one-way ANOVA tests followed by FDR adjusted multiple comparisons to examine whether functional traits

(hummingbird bill length, floral corolla length) and hummingbird resource specialization (complementary specialization d' , proportional generality) varied between (a) biogeographical regions and (b) hummingbird clades. When performing the one-way ANOVAs between hummingbird clades, the comparison was based on all observed species within each clade, irrespective of regional affinities. We only used the seven most species-rich clades in our dataset, excluding the species-poor clades Topazes (three species) and Patagona (one species). When performing the one-way ANOVAs between biogeographical regions, the comparison was based on all species observed within each region, that is, we allowed species to be affiliated with multiple biogeographical regions (only 13 hummingbird species, i.e. ~7%, occurred in two regions; four species, i.e. ~2%, in three regions, and no species occurred in four regions). For all analyses, we log-transformed bill and corolla length. Supplementary one-way ANOVAs showed that bill curvature varied significantly between hummingbird clades and regions (for details, see Figure S3), but there

was no indication that this caused clade and regional differences in resource specialization (compare Figures 2 and 3 with Figure S3). The ANOVA tests were run using the 'ANOVA' function in R. We also constructed linear mixed-effect models with the aim to control for

clades as a random intercept (when examining how regions differ in traits and specialization level) and regions as a random intercept (when examining how clades differ in traits and specialization level). However, these models did not converge due to singularities (see

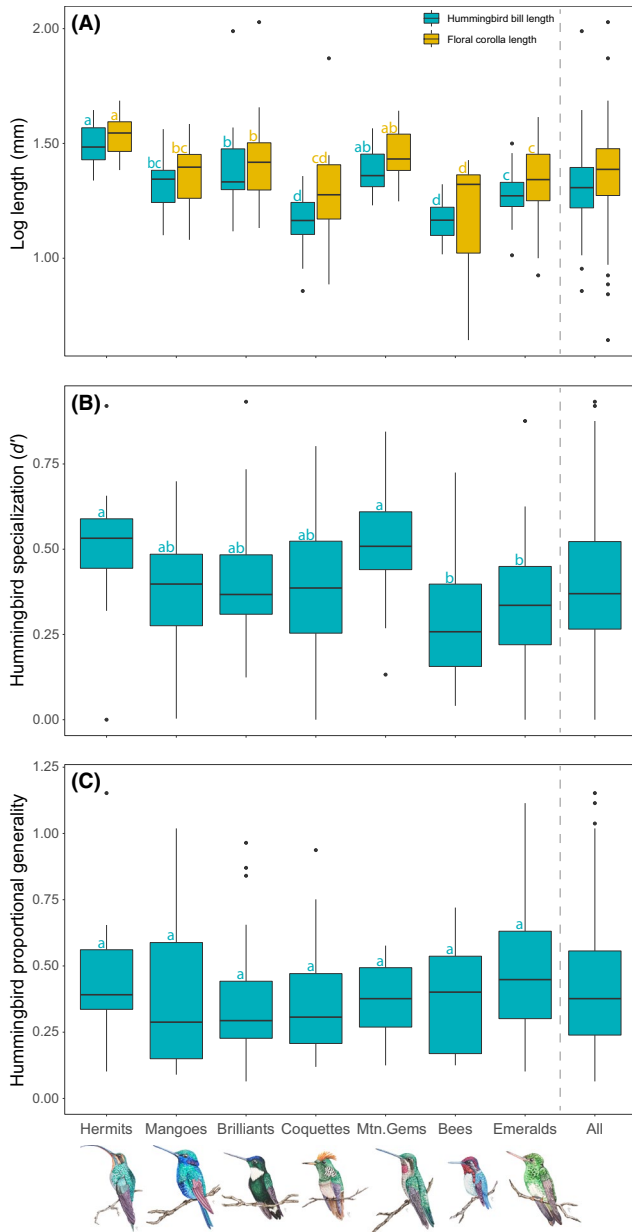


FIGURE 2 Hummingbird clade-specific differences in (A) hummingbird bill length (turquoise) and mean corolla length of visited flowers (yellow), and (B) mean hummingbird specialization d' , and (C) mean hummingbird specialization measured as proportional generality. This comparison was based on all species within each clade, irrespectively of regional affinities. Boxes indicate the first and third quartiles (Q1 and Q3), horizontal lines inside boxes are medians, vertical lines indicate Q1/Q3 + 1.5 × interquartile ranges (IQR), and circles are outliers. Different letters represent statistical difference ($p < 0.05$) according to one-way ANOVAs with multiple post-hoc comparisons using the False Discovery Rate (FDR). For comparison, on the right in all figures we show boxplots across all species. Hummingbird paintings by Katrine Hansen

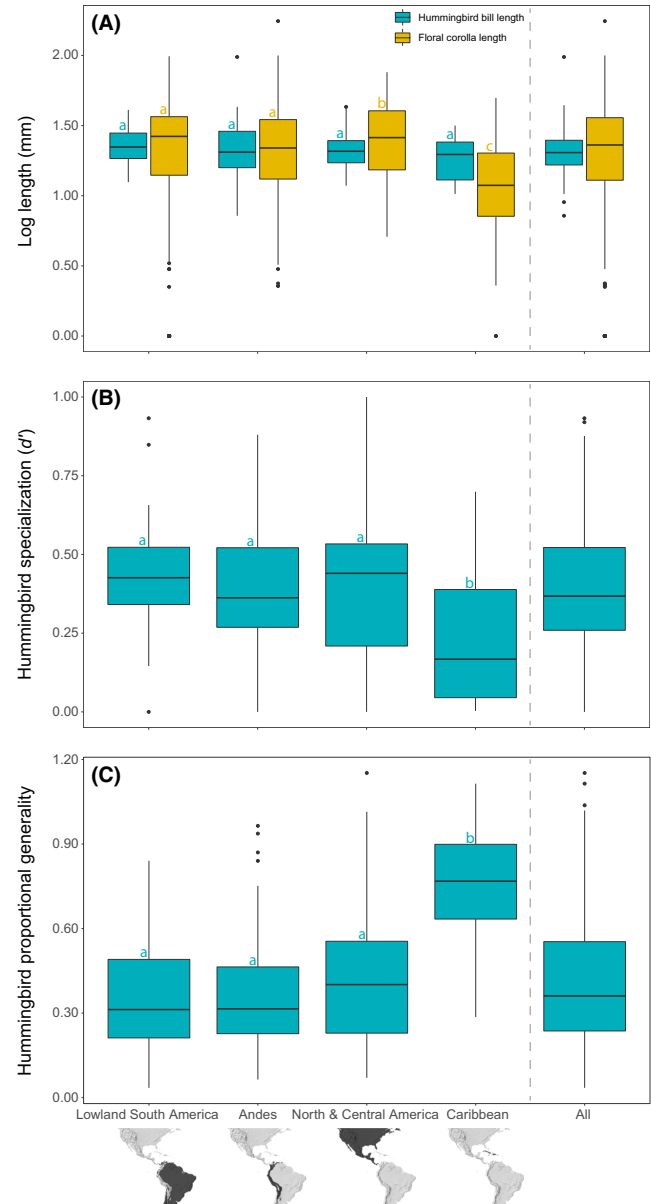


FIGURE 3 Differences in (A) hummingbird bill length (turquoise) and mean floral corolla length (yellow), (B) mean hummingbird specialization d' , and (C) mean hummingbird specialization measured as proportional generality between biogeographical regions: Lowland South America, Andes, Central & North America, and the Caribbean. The comparison was based on the species pool for each region, as extracted in the networks within each region. Boxes indicate the first and third quartiles (Q1 and Q3), horizontal lines inside boxes are medians, vertical lines indicate Q1/Q3 + 1.5 × interquartile ranges (IQR), and circles are outliers. Different letters represent statistical difference ($p < 0.05$) according to one-way ANOVAs with multiple post-hoc comparisons using the False Discovery Rate (FDR). For comparison, on the right in all figures, we show boxplots across all species

Bates et al., 2015), probably caused by hummingbird clades being non-randomly distributed across regions (see the Results of Fisher's Exact Test).

Third, we investigated whether the length of hummingbird bills was associated positively with: (a) the mean corolla length of the flowers they visit, and (b) their degree of resource specialization (complementary specialization d' , proportional generality) averaged across networks. We tested these potential associations with linear mixed-effects models (LMMs) using the `nlme` package in R (Pinheiro et al., 2019). Models simultaneously including hummingbird clade and biogeographical region as random effects did not converge, so for each response variable we built two sets of models both with bill length as a fixed effect: one considering hummingbird clades and another considering biogeographical regions as random intercepts. When using clades as a random factor, mean corolla length and resource specialization were estimated for each species irrespective of regional affinity. When using regions as random factor, mean corolla length and resource specialization were estimated for each species within each region. For each of these analyses, we constructed both unweighted and weighted models, the latter weighted with the square root number of plants visited (when predicting mean corolla length) and the square root number of networks (when predicting mean resource specialization; Maglianesi et al., 2014). The weighting procedure gave higher weight to hummingbird species that visited more plants and occurred in more networks, respectively. We constructed both weighted and unweighted LMMs because estimates of mean corolla length and mean resource specialization may be more reliable when based on larger sample sizes, however, it may also bias the results towards frequent and geographically widespread species. To estimate the significance of bill length in the LMMs, we used the function 'ANOVA' from the `CAR` package in R (Fox & Weisberg, 2019). We estimated the proportion of variance explained by bill length in the LMMs as marginal R^2 , and the proportion of variance explained by both fixed and random factors as conditional R^2 with the function 'r.squaredGLMM' in the `MuMIn` package (Barton, 2020; Nakagawa et al., 2017).

In addition to the LMMs, we estimated Pagel's lambda λ to assess how well evolutionary relatedness explains the distribution of bill length, mean corolla length and resource specialization among hummingbird species (Pagel, 1999). Subsequently, to account for the non-independence of the species-level data in our regression analyses, we repeated these using phylogenetic least squares regression (PGLS) with the function 'pgls' in the R package `CAPER` (Orme et al., 2018). In these analyses, we derived the expected covariances among all species using the maximum clade credibility tree of McGuire et al. (2014). To reconcile our trait dataset with the McGuire et al. (2014) phylogeny we: (a) excluded species included in our networks but not sampled in the tree, (b) dropped species that McGuire et al. (2014) showed evidence as being either paraphyletic or polyphyletic with respect to other taxa included in our networks, and (c) used the mean bill/corolla length and specialization value for species pairs that represent recent taxonomic splits only represented by a single tip in the McGuire et al. (2014) phylogeny. These

amendments reduced our dataset to 155 species (bill vs. corolla length) and 158 species (bill vs. specialization) in the PGLS regressions. As additional analyses, we repeated the unweighted/weighted and PGLS regressions separately for each of the seven hummingbird clades (not for *Topazes* and *Patagona* with only three and one species, respectively) and for each of the four biogeographical regions. Finally, we constructed supplementary LMM and PGLS regressions to examine whether bill curvature provides additional explanatory power in predicting resource specialization. These analyses showed negligible effects of bill curvature (for details, see Table S1).

3 | RESULTS

3.1 | Hummingbird clade and plant family distribution across regions

There was a clear difference in the distribution of hummingbird clades between the four regions ($p < 0.05$; Figure 1). Notably, the *Brilliant*s and *Coquette*s dominated the Andean networks and appeared in very low numbers outside of the Andes. In the other three regions, *Emerald*s were the most species-rich group, along with *Hermits* (Lowland South America), *Mountain Gems* and *Bees* (North & Central America) and *Mangoes* (Caribbean). Likewise, there were clear differences in plant family distribution between the four regions ($p < 0.05$; Figure 1). The *Ericaceae* dominated the Andean networks, and were well represented in North & Central America, but had few species in the Lowland South American and the Caribbean networks. The *Bromeliaceae* dominated in the Lowland South American networks, and were well represented in the Andean and North & Central American networks, but were poorly represented in the Caribbean. The Caribbean networks were dominated by the *Rubiaceae*, which were also well represented in the other regions (Figure 1).

3.2 | Comparing traits and resource specialization between clades and between regions

The hummingbird clades differed significantly in bill length and the length of the flowers visited (bill length: $F_{6,165} = 25.29$, $p < 0.001$; corolla length: $F_{6,165} = 12.64$, $p < 0.001$; Figure 2A). The *Hermits* and *Mountain Gems* had the longest bills, although the bill length of *Mountain Gems* was not significantly longer than those of *Mangoes* and *Brilliant*s. The shortest bills were those of the *Coquette*s and *Bees*, whereas *Emerald*s had bills of intermediate length, only overlapping with those of *Mangoes*. The *Hermits* and *Mountain Gems* visited the longest flowers, although the flowers visited by *Mountain Gems* were not significantly longer than those visited by *Brilliant*s and *Mangoes*. The *Coquette*s and *Bees* visited the shortest flowers, although the *Coquette*s' flowers were not significantly shorter than those visited by *Emerald*s and *Mangoes* (Figure 2A). Hummingbird resource specialization d' largely differed among clades in accordance

with differences in bill/corolla length: the Hermits and Mountain Gems were the most specialized clades (i.e. species in these clades were most exclusive in their resource use), significantly more specialized than the Bees and Emeralds, with intermediate levels of specialization shown by Mangoes, Brilliants and Coquettes ($F_{6,169} = 4.29$, $p < 0.001$; Figure 2B). The hummingbird clades showed a similar level of proportional generality, that is, niche breadth did not differ significantly between clades ($F_{6,169} = 1.19$, $p = 0.32$; Figure 2C).

Hummingbird bill length was similar across regions ($F_{3,191} = 1.15$, $p = 0.33$), but there were regional differences in the corolla length of hummingbird-visited flowers ($F_{3,575} = 10.15$, $p < 0.001$): North & Central American flowers were the longest, whereas the Caribbean flowers were significantly shorter than flowers in all mainland regions (Figure 3A). There were also regional differences in hummingbird resource specialization, both when measured as d' ($F_{3,192} = 2.82$, $p < 0.05$) and proportional generality ($F_{3,192} = 13.35$, $p < 0.05$). Notably, the Caribbean hummingbirds were more generalized than mainland hummingbirds, both in terms of niche overlap (d') and niche breadth (proportional generality; Figure 3B,C).

3.3 | Associations between traits and between traits and resource specialization

In LMMs across all hummingbird species, when including region as a random factor, bill length was strongly and positively associated with mean corolla length (Table 1; Figure 4B), weakly related to mean resource specialization when measured as d' (Table 1; Figure 4D), but unrelated to mean proportional generality (Table 1;

Figure 4F). When including clade as a random factor, hummingbird bill length was also strongly positively associated with mean corolla length (Table 1; Figure 4A), but bill length was not associated with neither measure of resource specialization (Table 1; Figure 4C,E). The species-level variation in bill length, mean corolla length of visited flowers, and both measures of resource specialization displayed a phylogenetic signal that was significantly greater than zero ($p < 0.001$ in all cases). In particular, closely related hummingbird species are likely to be similar in bill length ($\lambda = 0.97$), more so than the corolla length of visited flowers ($\lambda = 0.59$), with weaker phylogenetic signals for resource specialization: proportional generality ($\lambda = 0.51$) and d' ($\lambda = 0.23$). When accounting for this phylogenetic non-independence using PGLS, we continued to detect a strong positive association between bill length and mean floral corolla length ($\beta = 0.83$, $R^2 = 0.32$, $p < 0.001$), but there was no association between bill length and mean resource specialization, both measured as d' ($\beta = 0.05$, $R^2 = 0.00$, $p = 0.70$) and proportional generality ($\beta = 0.01$, $R^2 = 0.00$, $p = 0.94$).

Analysing the individual hummingbird clades separately showed that most clades had a moderate to strong positive association between bill length and mean corolla length, although relationships for some clades were weak and non-significant (Figure S1a). Only Brilliants showed a weakly positive association between bill length and mean resource specialization d' (Figure S1b). For all other clades, there were no significant associations between bill length and both measures of resource specialization (Figure S1b).

For all four regions analysed separately, there was a strong positive association between hummingbird bill length and the mean corolla length of their flowers (Figure S2a). The association between

TABLE 1 Linear mixed-effects models (LMMs), analysing the association between hummingbird bill length and (a) mean corolla length of visited flowers, and mean resource specialization, measured both as (b) complementary specialization d' and (c) proportional generality. For each response variable, we built two sets of models: one considering hummingbird clades and another considering biogeographical regions as random intercepts, with bill length as a fixed effect. For each of these analyses, we constructed both unweighted and weighted models, the latter weighted with the square root number of plants visited (when predicting mean corolla length) and the square root number of networks (when predicting mean specialization d' and mean proportional generality). Unweighted models are in bold. We estimated the proportion of variance explained by bill length in the LMMs as marginal R^2 , and the proportion of variance explained by both bill length and random factors as conditional R^2 . We also report standardized coefficient estimates as well as corresponding p -values and standard errors

Model	Random factor	R^2 marginal	R^2 conditional	Coefficient	SE
(a) Corolla length	Clade	0.45	0.45	0.80**	0.07
	Clade	0.11	0.11	0.87**	0.08
	Region	0.41	0.50	0.78**	0.06
	Region	0.11	0.13	0.86**	0.07
(b) Specialization d'	Clade	0.01	0.10	0.13^{NS}	0.11
	Clade	0.00	0.01	0.09 ^{NS}	0.12
	Region	0.04	0.04	0.25*	0.09
	Region	0.00	0.02	0.18 ^{NS}	0.10
(c) Proportional generality	Clade	0.00	0.02	0.07^{NS}	0.12
	Clade	0.00	0.01	0.14 ^{NS}	0.14
	Region	0.00	0.43	0.10^{NS}	0.10
	Region	0.00	0.10	0.10 ^{NS}	0.11

** $p < 0.001$, * $p < 0.05$, ^{NS} $p > 0.05$.

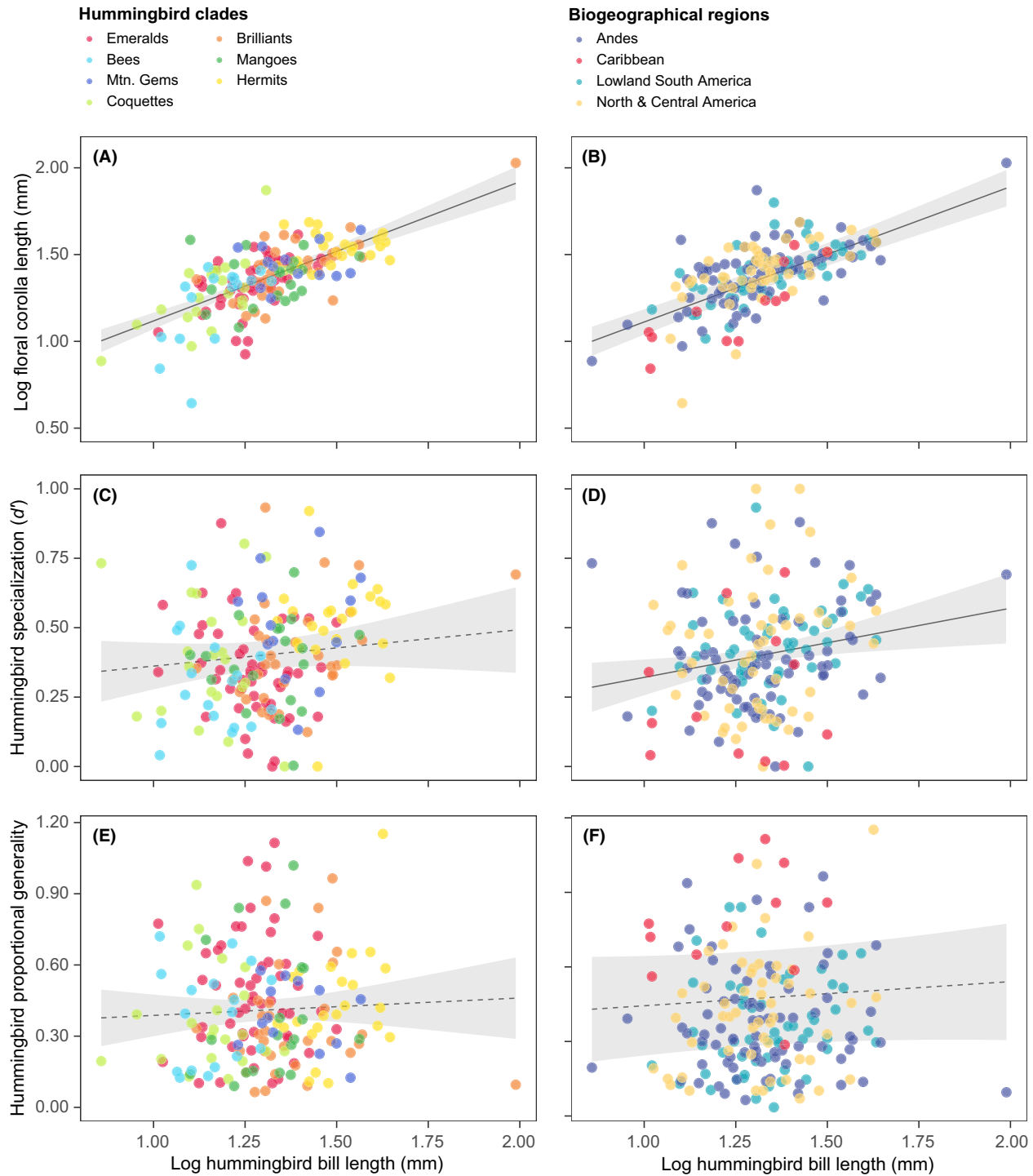


FIGURE 4 Associations between hummingbird bill length and (A, B) mean floral corolla length, (C, D) mean hummingbird specialization d' and (E, F) mean hummingbird specialization measured as proportional generality, when using hummingbird clades as a random factor (clades in different colours: A, C and E; $n = 172$ and $n = 177$) and when using biogeographical regions as a random factor (regions in different colours: B, D and F; $n = 191$ and $n = 195$). The black lines (with grey 95% confidence intervals) represent the overall fits of unweighted linear mixed-effects models; the dotted lines represent non-significant fits. Note that a few hummingbird species were recorded in more than one region and, thus, appear more than once in the analyses including regions as a random factor (B, D and F). See Figure S1 for individual plots for each hummingbird clade and Figure S2 for individual plots for each biogeographical regions

bill length and resource specialization d' was non-significant for all four regions when using unweighted regressions and PGLS, but weakly positive for Andes and Lowland South America when using

weighted regressions (Figure S2b). There was no association between bill length and proportional generality, that is, niche breadth, in any of the regions (all fits had $p > 0.05$).

4 | DISCUSSION

We demonstrate that morphological trait-matching is a recurrent phenomenon in hummingbird–plant networks throughout the Americas, that is, the length of hummingbirds' bill correlates with the corolla length of the flowers they visit (Figure 4A,B). This result was repeated within all biogeographical regions and within most hummingbird clades (Figures S1 and S2). Trait-matching was also evident when comparing between clades, as clades dominated by long-billed hummingbirds (e.g. Hermits) generally visited longer flowers and *vice versa* for clades with shorter bills (Figure 2A). These recurrent patterns of trait-matching may have been even stronger if we had local trait measurements for all hummingbird-visited flowers and local measurements of hummingbird traits (rather than from museum specimens). When comparing between clades, traits also largely co-varied with resource specialization (niche overlap d'), for example, the long-billed Hermits were also the most exclusive in their resource use (Figure 2B). However, there was no difference in niche breadth between clades (Figure 2C) and morphological traits did not generally mediate resource specialization, as bill length was only a weak predictor of both measures of resource specialization (Figure 4C–F; bill curvature had only negligible additional explanatory power in predicting resource specialization, see Table S1). Notably, bill length was associated with resource specialization only within the Brilliants and within the regions of Lowland South America and the Andes (Figures S1 and S2). Taken together, these results demonstrate the strong influence of biogeographical and evolutionary histories on recurrent patterns of morphological trait-matching, and the weak relationships between hummingbird bill length and resource specialization.

The recurrent patterns of trait-matching show that hummingbirds feed on flowers approximately similar in length to their bills, even though long-billed hummingbirds are able to access nectar from flowers with shorter corollas. This may be because long-billed hummingbirds minimize competition with short-billed hummingbirds by primarily feeding on flowers inaccessible to short-billed hummingbirds (Maglianesi et al., 2015; Sonne et al., 2020). It may also be related to nectar production, as longer flowers often offer more nectar than shorter flowers (Buzato et al., 2000; Dalsgaard et al., 2009; Ornelas et al., 2007; Stiles, 1981), making it energetically optimal for longer-billed hummingbirds to feed on flowers with longer corollas, up to a given corolla length threshold (Montgomerie et al., 1984). From the plant's perspective, it may also be an advantage to attract hummingbirds with matching traits, thereby increasing pollination efficiency (Montgomerie et al., 1984). Therefore, there is a clear association between functional traits of hummingbirds and plants. Similar patterns have been reported for other plant–pollinator systems, such as hawkmoths and other insect pollinators visiting flowers approximately similar in length to their proboscises (Klumpers et al., 2019; Sazatornil et al., 2016; Stang et al., 2009). Interestingly, on average, species in all hummingbird clades visited flowers with slightly longer corollas than their bills (Figure 2A), reflecting that hummingbirds extend their tongues while drinking

nectar (Hainsworth, 1973; Montgomerie et al., 1984). Notably, the Bees and the Coquettes – the two clades with the shortest bills – visited flowers considerably longer than their bills (Figure 2A). This may be because short-billed hummingbirds have evolved the ability to extend their tongues proportionally longer than long-billed hummingbirds (Hainsworth, 1973), allowing short-billed species to exploit flowers with longer corolla and more nectar than short-corolla flowers fitting their bills.

Floral corolla length was on average also longer than hummingbird bill length across all mainland regions, but not in the Caribbean islands where floral corolla length was shorter than on the mainland (Figure 3A). This result is consistent with reports that the Caribbean hummingbirds often feed on shorter insect-syndrome flowers (Dalsgaard et al., 2009; Lehmann et al., 2019) and have a more generalized feeding behaviour than mainland hummingbirds, both in terms of floral niche overlap and niche breadth (Figure 3B–C). Although the majority of the plants visited by Caribbean hummingbirds are either endemic or native to the region (~33% endemic and ~55% native in our dataset), their opportunism also makes Caribbean hummingbirds more likely to incorporate introduced plants into their feeding niche (~12% in our dataset; Maruyama et al., 2016). As all except one of the Caribbean hummingbirds are endemic to the region (Dalsgaard et al., 2018), these Caribbean versus mainland patterns are in agreement with the idea that many plants and pollinators on oceanic islands have evolved towards generalism (Olesen et al., 2002; Olesen & Valido, 2003; Traveset et al., 2015), but may also reflect the more recent colonization history and limited trait evolution among Caribbean hummingbirds (Dalsgaard et al., 2018). Taken together, despite the distribution of plant families and hummingbird clades differ significantly across regions (Figure 1), functional traits and the degree of resource specialization were similar across mainland regions, but the Caribbean islands had both shorter flowers and hummingbirds with more generalized niches (Figure 3). Traits and resource specialization (niche overlap d') also largely co-varied between hummingbird clades (Figure 2), illustrating the influence of biogeographical and evolutionary histories in both functional traits and floral specificity.

Despite the generally consistent trait-matching and associated level of resource specialization observed between clades, and between mainland versus islands (Figures 2 and 3), trait-matching did not generally translate into trait-mediated resource specialization for individual species, as bill length and bill curvature were only weak predictors of resource specialization (Figure 4C–F; Table 1; Table S1). While the diversity of hummingbird traits within a community influences overall community-level specialization and partitioning of interactions (Maruyama et al., 2018), additional mechanisms appear to operate at the species-level (Simmons et al., 2019; Tinoco et al., 2017). Notably, while functional traits may constrain species into their fundamental niche of possible pairwise interactions (Junker et al., 2013), a hierarchy of multiple mechanisms determines the realized niche, that is, which of the possible pairwise interactions are realized (Junker et al., 2013). In hummingbird–plant communities, trait-matching determines which interactions are possible (Sonne et al., 2020), but other mechanisms – such as hummingbird

abundance and local conditions related to resource availability and competition with other floral visitors – determine how often these interactions are realized (Dalsgaard et al., 2018; Simmons et al., 2019; Tinoco et al., 2017). Thus, there is no general relationship between bill morphology and level of resource specialization (Figure 4C–F; Table 1; Table S1), illustrating that morphological and ecological specialization can be disassociated (Armbruster, 2017; Ollerton et al., 2007). The only exceptions to this trend are the weak associations we found between bill length and resource specialization within the Brilliants and within Lowland South America and the Andes. Here, hummingbirds and plants have had the longest co-evolutionary history (McGuire et al., 2014) and have experienced more benign conditions during the Quaternary to evolve more specialized associations (Dalsgaard et al., 2011; Sonne et al., 2016). A prime example of this is the association between the Andean species of *Passiflora* and the Sword-billed Hummingbird *Ensifera ensifera*, an iconic long-billed species within the Brilliants (Abrahamczyk et al., 2014). The Sword-billed Hummingbird has by far the longest bill of any hummingbird species, uses very long-corolla flowers, and tends to be ecologically specialized (Figure 4; Figures S1 and S2). In line with that, long-tubed *Passiflora*, and other plants specialized on hummingbird pollination, tend to have evolved longer corolla flowers when compared to related plants pollinated by most other groups of pollinators (Abrahamczyk et al., 2014; Pauw, 2019). Nevertheless, even these specialized systems with tightly matching traits may have been dynamic over evolutionary time (Abrahamczyk et al., 2017) and generally long-billed and short-billed hummingbirds show similar degrees of resource specialization (Figure 4C–F).

In conclusion, we demonstrate the influence of biogeographical and evolutionary histories on recurrent patterns of trait-matching in hummingbird–plant associations, and weak effects of functional traits on resource specialization. These findings indicate that morphological traits can be used to predict resource utilization, not only at the level of resource type (e.g. nectarivore, frugivore, granivore and others; Pigot et al., 2020), but even at the level of specific species or functional groups of resources. Thus, our macroecological study reveals that trait-matching rules are generally good predictors of interaction partners across trophic levels, whereas the degree of resource specialization is less predictable by morphological traits but is highly dependent on the biogeographical, ecological and evolutionary context. These findings reveal that functional traits have great potential, but also key limitations, as a toolkit for understanding trophic interactions in ecological communities.

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AUTHORS' CONTRIBUTIONS

B.D., P.K.M., J.S., K.H., C.R., M.Sc. and A.M.M.G. conceived the study; B.D., P.K.M., J.S., T.B.Z., S.A., R.A., A.C.A., F.P.A., S.B., E.C.-G., A.G.C., P.A.C., R.D.-V., M.F.D., P.L.E., M.M.D.F., E.F., G.K., C.L., F.M.G.L.-C., L.R.L., A.O.M., C.G.M., M.A.M., T.S.M., O.H.M.-G., V.M.-G., S.M.A.-J., E.N.S.N., P.E.O., J.F.O., R.O.-P., R.P.-L., B.I.P.-G., S.N.P.Q., M.B.R.-B., A.R.R., M.A.R., L.C.R., A.M.R., I.S., M.Sa., B.A.T., I.G.V., M.F.V., J.V.-B., S.W. and A.M.M.G. collected the data; B.D., P.K.M., K.H., T.B.Z., J.V.-B. and A.M.M.G. compiled and checked the database; J.S. (with help from B.D., P.K.M., J.D.K., M.Sc.) analysed the data; B.D. wrote the first draft of the manuscript with inputs from P.K.M., J.S., K.H., B.I.S., M.Sc., A.M.M.G. All authors contributed to the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd7n> (Dalsgaard et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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