

RESEARCH ARTICLE

The role of insularity: Plants have few ornithophilous traits but are visited by morphologically more distinct hummingbirds in the Caribbean islands

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Abstract

1. Functional traits determine interactions between plants and pollinators, and to increase pollination efficiency, many plants have evolved traits to attract specific pollinator groups. However, biogeographical setting may influence trait evolution and biotic interactions. For instance, plants pollinated by hummingbirds often have ornithophilous traits, that is, flowers with elongated corollas, dilute nectar and red colours, but—due to colonization history, depauperate biotas and unstable environmental conditions—it might be disadvantageous for species to rely on mutualistic partners with specific functional traits on oceanic islands. Hummingbird-visited plants on islands are thus expected to have fewer ornithophilous traits and be functionally less diverse in their interactions with hummingbirds.

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2. We compiled an extensive dataset of plant–hummingbird interactions (1030 plant and 181 hummingbird species) and associated functional traits. We divided the data into four biogeographical regions across the American mainland and the Caribbean islands and then tested whether biogeographical regions differed in the proportion of ornithophilous floral traits and functional diversity of plant–hummingbird interactions.
3. We found that hummingbird-visited plant communities of the Caribbean islands displayed the lowest proportion of traits typically associated with a functional adaptation towards bird-mediated pollination, with on average the shortest corollas, the highest nectar concentrations and the largest proportion of non-ornithophilous colours. Contrary to our expectations, plants in the Caribbean interacted with hummingbirds that were morphologically more distinct than the plants of mainland regions.
4. Overall, we document a strong imprint of insularity on floral traits and interactions with hummingbirds. While hummingbird-visited plants in the Caribbean displayed floral traits that support island theory, predicting less specific pollination systems on oceanic islands, the functional diversity of plant–hummingbird interactions in the Caribbean communities was higher than on the mainland, possibly driven by competition over resources. These results highlight the influence of insularity on functional traits and plant–pollinator interactions.

KEYWORDS

angiosperms, bird-mediated pollination, functional diversity, mutualistic interactions

1 | INTRODUCTION

Mutualistic interactions between flowering plants and pollinating animals are prime examples of close co-evolutionary histories where functional traits influence interactions between organisms of different trophic levels (Thompson, 2005). The size and shape of a flower's corolla, for instance, often match the size and shape of the pollinator's feeding apparatus (Dalsgaard et al., 2021; Nilsson, 1988; Sonne et al., 2020; Temeles & Kress, 2003). Globally, about 87% of angiosperms rely on animal-mediated pollination, increasing to around 94% in tropical systems (Ollerton et al., 2011; Rech et al., 2016). A high specificity of flower–pollinator interactions may result in greater pollination effectiveness (Montgomerie et al., 1984) and trait-mediated specialization is indeed observed in plant–pollinator interactions (Maruyama et al., 2018; Sonne et al., 2020). Hence, because traits are important in shaping effective plant–pollinator interactions, convergent evolution should cause the traits of flowers and visiting pollinators to repeatedly exhibit functional similarities across different plant families (Faegri & van der Pijl, 1979).

For plants, the concept of pollination syndromes elucidates the evolution of such convergent floral traits in distantly related species (Faegri & van der Pijl, 1979; Fenster et al., 2004; van der Pijl, 1960). It provides a mechanistic explanation for floral diversity as an adaptation to specific pollinator groups (Fenster et al., 2004;

Rosas-Guerrero et al., 2014) and may allow one to predict the pollinator in the absence of direct observations (Faegri & van der Pijl, 1979). While the pollination syndrome concept is debated, as it may not always reliably predict the pollinators for a given plant species (Ollerton et al., 2009), certain ornithophilous traits are described as being strongly associated with bird-mediated pollination (Dalsgaard et al., 2009; Faegri & van der Pijl, 1979). For instance, compared to such flowers that are more adapted towards attracting insects, ornithophilous flowers that are adapted to attract birds comprise elongated and tubular corollas containing nectar with comparatively lower sugar concentrations and exhibit showy, orange-red colours (Cronk & Ojeda, 2008; Faegri & van der Pijl, 1979; Johnson & Nicolson, 2008; Ornelas et al., 2007; Stiles & Freeman, 1993; Temeles & Kress, 2003).

Among vertebrates, hummingbirds are some of the most iconic and well-documented pollinators (Leimberger et al., 2022). While they occasionally supplement their diet with arthropods, hummingbirds are primarily specialized nectar feeders (Smith et al., 2011) and, thus, adapted to access and extract nectar from flowers (Leimberger et al., 2022). This high level of dietary specialization can result in tight plant–pollinator interactions, especially in areas where other pollinators may be scarce (Cruden & Toledo, 1977; Dalsgaard et al., 2009). In fact, the mutualistic interactions between plants and hummingbirds constitute the most specialized bird pollination system on the planet (Zanata et al., 2017). This high

degree of specialization in plant–hummingbird interactions is also reflected in functional traits being adapted between species pairs, for example, the length of a plant's corolla matches the length of the hummingbird's bill (Maglianesi et al., 2014; Temeles et al., 2000; Weinstein & Graham, 2017). Hence, in accordance with the concept of pollination syndromes, in hummingbird-rich areas, a proportion of the animal-pollinated flowers should display floral traits that are adapted to attract hummingbirds (Abrahamczyk & Kessler, 2014), while hummingbird-depauperate regions, such as oceanic islands, should have proportionally fewer ornithophilous traits in their floral displays.

Comparing communities across large spatial scales and between distant biogeographical regions may allow testing for generalities of co-evolutionary processes, such as the evolution of specific, adapted traits in species of different trophic levels and the resulting interactions. For instance, it is hypothesized that the biogeographical setting may drive the extent to which traits matter for plant–pollinator associations (Maruyama et al., 2018; Sonne et al., 2020). Specifically, species with more specialized interactions and stronger co-adaptation of functional traits would be expected in biogeographical regions where species have co-existed for a long time (Dalsgaard et al., 2011; Sonne et al., 2016). In contrast, on oceanic islands, interactions between plants and their pollinators are hypothesized to be less specific, due to their shorter co-evolutionary history and the potential advantages of being a generalist during colonization (Olesen et al., 2002). In addition, since oceanic islands often have depauperate pollinator communities compared to mainland ecosystems (Olesen & Jordano, 2002), and notably insect pollinators are underrepresented, vertebrate pollinators may evolve more generalized feeding niches on oceanic islands (Dalsgaard et al., 2021; Olesen & Valido, 2003; Traveset et al., 2015). If species interactions are indeed more generalized, without specific functional traits being particularly dominant, one would expect to find these interactions grouped around the average functional trait composition of a given community—that is, the community centroid—as all traits would be involved in interactions to similar degrees. Such patterns of generalized interactions and species' functional traits have been demonstrated before in different systems (Maruyama et al., 2018; Pigot et al., 2020; Ricklefs, 2012; Sayol et al., 2023). In contrast, if species were to interact predominantly with specific species, for example, because certain functional traits were particularly important in segregating interactions, one would expect to find such interactions to be more distant from the community centroid. This would reflect a higher functional diversity in interactions.

However, only a few large-scale studies have addressed the role of biogeographical history on patterns of functional adaptation between groups of interacting species, for example, by comparing continental and island communities with drastically different co-evolutionary histories (Dalsgaard et al., 2021). Here we expanded a previous dataset consisting of plant–hummingbird interaction networks across mainland America and the Caribbean islands (Dalsgaard et al., 2021). We included extensive interaction data from multiple Caribbean islands, added multiple plant species and added

a further two functional plant traits (nectar concentration and floral colour), thus creating an extensive dataset of floral traits associated with hummingbird pollination (corolla length, nectar concentration and floral colour). We analysed this unprecedented dataset of floral traits along with a dataset of hummingbird functional traits (bill length, bill curvature and body mass, the latter being another new addition to the dataset compared to Dalsgaard et al., 2021). Our dataset on mutualistic plant–hummingbird interactions and functional traits spans four biogeographical regions of mainland America and the Caribbean islands. Using a plant-centered approach, we specifically tested (i) whether floral traits were interrelated and reflected an ornithophilous pollination syndrome, (ii) whether biogeographical regions differed in the proportion of ornithophilous floral traits and (iii) whether functional diversity in plant–hummingbird interactions differed between biogeographical regions. By using a multivariate approach to investigate associations between plants and hummingbird visitors, notably the functional diversity of the hummingbird visitors on flowers, we obtained a significantly more detailed understanding of interaction patterns between species than presented in Dalsgaard et al. (2021).

2 | MATERIALS AND METHODS

2.1 | Data collection

We used a previously published, extensive dataset consisting of 93 plant–hummingbird interaction networks, encompassing a wide range of species from mainland America and the Caribbean islands (Dalsgaard et al., 2021). The dataset considered only mutualistic interactions, that is, hummingbirds engaging in nectar consumption and interacting with the reproductive parts of flowers, thereby serving as potential pollinators. The hummingbird species' names were based on the International Ornithological Committee World List (<https://www.worldbirdnames.org/new/>). As the database that Dalsgaard et al. (2021) originally derived the plant species' names from is now defunct (The Plant List), we updated all species' names based on 'Plants of the World Online "POWO"' (<https://powo.science.kew.org/>). In this process of updating the plant names, some species were lost due to becoming synonyms of other species, thus the revised dataset contains 181 hummingbird and 1249 plant species, some seven plant species fewer than in Dalsgaard et al. (2021). In addition to visitation data, Dalsgaard et al. (2021) reported two primary traits for the observed plant and hummingbird species. For plants, the effective floral corolla length was measured on-site in the same location as the network, with a few exceptions (~1% of species). In cases where plant species were present in more than one network and corolla length was measured at more than one locality (~19% of the plants), species averages were calculated (Dalsgaard et al., 2021). For hummingbirds, bill length and curvature were gathered from museum specimens and averaged across multiple male and female individuals for 180 of the 181 hummingbird species (Dalsgaard et al., 2021).

For this study, we expanded the dataset by gathering more data from the Caribbean islands and by augmenting the data on floral and hummingbird traits across the dataset. We included data from one additional plant-hummingbird network from Hispaniola as well as data from a field expedition to Trinidad and Tobago and 10 oceanic islands in the Lesser Antilles (Grenada, Saint Lucia, Martinique, Dominica, Guadeloupe, Antigua, Nevis, Saint Kitts, Sint Eustatius and Saba). This increased the database to a total of 1275 plant species. For plants, where possible we gathered data on nectar concentration and floral colour, while for hummingbirds, we added body mass for each species. To gather the additional plant functional trait data, we revisited the original publications of the 93 plant-hummingbird networks used in Dalsgaard et al. (2021). Of these publications, 28 had published data on both nectar concentration and floral colour and 11 had published data on one of the floral traits. We contacted the authors of the 54 remaining original studies and obtained data on one or both floral traits for 48 networks. In total, we gathered data on nectar concentration for 665 of the 1275 plant species (~52% of all plant species in the dataset) and data on floral colour for 1122 plant species (~88%). Corolla length was measured for all new plant species added from the Caribbean, leading to 977 species (~76%) in total. Data on hummingbird body mass was added from the literature (Dunning, 2007).

Finally, we assessed the native status of all plants, that is, we assessed if the plants were native to the given network locations in which they were recorded from. This was done using the distribution tool of 'POWO', with a few exceptions where data were unavailable (<5%). For plants not identified to species level (~15%), the distribution of the lowest available level, for example, genus, was used instead. From this assessment, 1185 plants were identified as native, 29 were introduced, while 61 plants were found in areas marked by 'POWO' as neither native nor introduced. For these, an estimation was made whether these species were likely to be introduced or native for the given localities. Given the relative inconsistencies in South American reporting and taxonomy, gaps in the native distributions of plants are relatively common. For especially troublesome species, experts and other sources were consulted for the native status of these species (<1%). Ultimately, 1221 (~95% of species) species were recorded as being native to the network location they were found, while 54 (~4%) were recorded as being introduced. Four (~0.3%) species were found in both native and introduced locations. As the non-native species did not influence the results (Figure S1), we present analyses including both native and introduced species.

2.2 | Floral traits

For plants, we considered effective corolla length, nectar concentration and floral colour. Effective corolla length, that is, the internal distance from the restrictive opening of a flower to the base of the nectar chamber (Wolf et al., 1976), was measured to the nearest 0.1 mm with handheld callipers. Nectar concentration was measured by extracting the nectar with capillary tubes and then using

a handheld refractometer. Nectar was gathered from at least four individuals, with measurements mainly taken during the early hours of the day (08:00–12:00). Floral colour was assessed in the field and categorized as perceived by the human eye, for instance 'white', 'yellow', 'red'. Thereafter, following the traditional pollination syndrome theory (Faegri & van der Pijl, 1979) we assigned distinct colour codes (Dalsgaard et al., 2009; Wilson et al., 2004). Here, we defined the three following codes: (1) 'one/white': non-ornithophilous syndrome colours, represented by a mix of colours including violet, blue, purple, green, yellow and white; (2) 'two/half red': mixed non-ornithophilous and ornithophilous syndrome colours, represented by pink/salmon or multi-coloured flowers, where orange-red is an important component of the floral display; (3) 'three/red': ornithophilous syndrome colours, that is, predominantly orange-red. In plants where the bract (e.g. Bromeliaceae, Heliconiaceae) or stem (e.g. Rubiaceae) represents a major or principal part of the colour display, they were included in the colour categorization (Dalsgaard et al., 2009).

2.3 | Biogeographical regions

Since a central question of our study was to determine plant adaptations towards hummingbird pollination at macroecological scales, we divided the data into four regions following the historical radiation of hummingbirds (Figure 1, Table 1). This division should reflect the relative timescale plant communities of the respective regions had to adapt to hummingbirds as pollinators. Modern hummingbirds originated in Lowland South America (~22 Mya), then colonized the Andes (~16 Mya) and radiated into Central & North America (~12 Mya). Hummingbirds then only recently colonized the Caribbean islands (~5 Mya), colonizing from Central & North America as well as from Lowland South America (McGuire et al., 2014).

Lowland South America includes all networks ($n=41$) south of the Isthmus of Panamá, excluding the mountain range of the Andes. The continental islands of Trinidad and Tobago, located south of Bond's line (Carstensen et al., 2012), are included in Lowland South America. The biogeographical region of the Andes ($n=21$) includes all networks within the range of the Andean Mountains (Rahbek et al., 2019). We group all other networks of mainland America in the region Central & North America, which consists of all observations situated north of the Isthmus of Panamá ($n=22$). This includes two networks of the continental USA, which had no influence on any of the observed patterns for this region (Figure S2). Finally, the Caribbean includes all data of the oceanic islands in the Caribbean Basin north of the Bond's line ($n=15$).

2.4 | Statistical analysis

To perform independent comparisons accounting for phylogenetic relatedness, we first built the phylogeny of all plant species in our data. For this, we used the accepted names of all fully identified species (1030, ~80% of the raw data). We then used the *phylo.maker()*

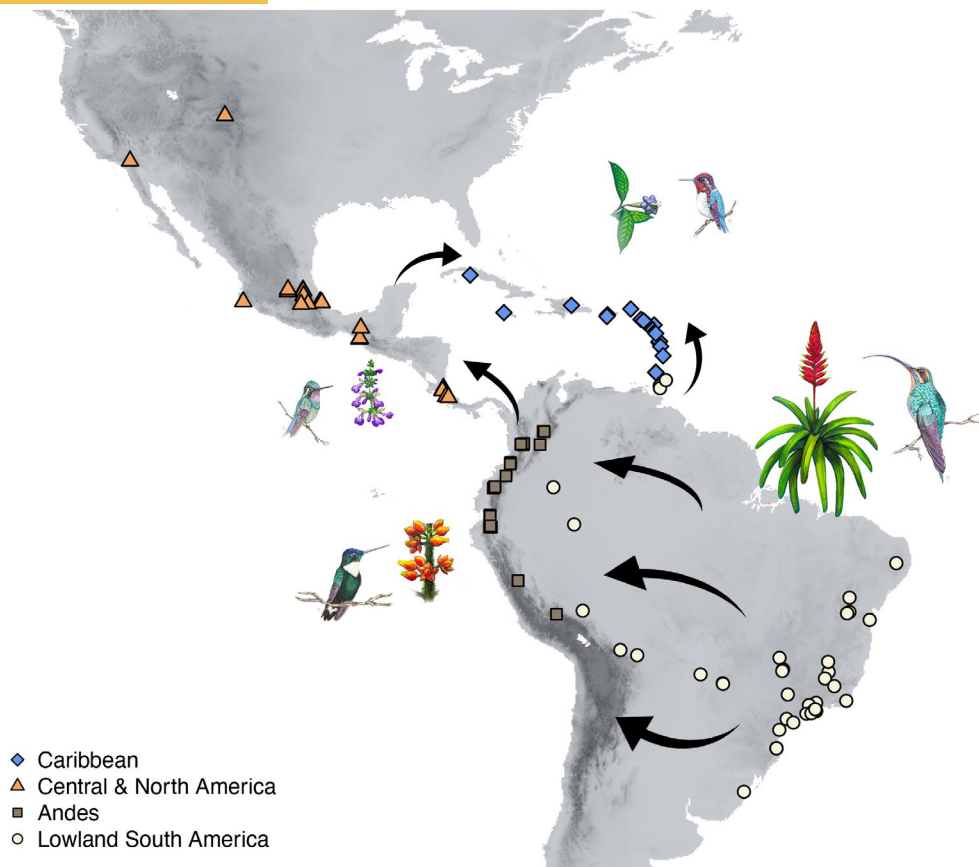


FIGURE 1 Locations of the sampled plant–hummingbird interactions. Hummingbirds first originated in Lowland South America (~22 MYA), then colonized the Andes (~16 MYA) before moving into Central America (~12 MYA). They arrived on the Caribbean islands more recently (~5 MYA). Plants thus had different evolutionary timescales to adapt towards hummingbirds as pollinators and should exhibit ornithophilous plant traits to varying degrees in different regions. Specifically, the Caribbean islands should exhibit the lowest proportion of ornithophilous plant traits because of the shorter co-evolutionary timescale between local plant and hummingbird communities. Furthermore, island theory predicts organisms to be more generalized due to colonization history and depauperate communities on islands, and the Caribbean region is characterized by unstable environmental conditions (e.g. frequent hurricanes), making strong co-evolution less likely. Taken together, the Caribbean islands should thus exhibit the lowest degree of functional adaptation between plants and the local hummingbird visitors. Hummingbird drawings by Katrine Hansen.

function from 'V.PhyloMaker2' (Jin & Qian, 2022), an R package which uses angiosperm megatrees as a phylogenetic backbone (Figure S3).

2.4.1 | Relationships between single plant traits

To test whether plant traits follow the ornithophilous pollination syndrome—that is, for example, flowers with longer corollas should have lower nectar concentration and be more likely to display red colours—we analysed the interrelationships between combinations of the three plant traits.

First, we used the function *pgls()* from the R package 'caper' (Orme et al., 2023), to fit a phylogenetic generalized least-squares model (PGLS) on the relationship between corolla length and nectar concentration. Using a PGLS model controls for phylogenetic relatedness among species; we used a maximum likelihood approach to optimize Pagel's lambda branch length transformation (Freckleton

et al., 2002). Then, we tested for the relationships between corolla length and colour category as well as nectar concentration and colour category, respectively. For this, we used the function *phylANOVA()* from the 'phytools' R package (Revell, 2012), specifying 100,000 simulations. The function is permutation based and performs a phylogenetic ANOVA (Garland et al., 1993) allowing for Bonferroni adjusted post-hoc comparison of group means. In all analyses, we first fitted a model on all data, that is across all regions simultaneously, and later separately fitted the respective model on all regional subsets of the plant community, to test for region specific trends.

2.4.2 | Distribution of plant traits across biogeographical regions

To compare the single plant traits across regions, we applied a phylogenetic ANOVA using '*phylANOVA()*' with 100,000 simulations and Bonferroni adjusted post-hoc comparisons of group means

TABLE 1 Replication statement.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community (plant-hummingbird interaction networks)	Biogeographical region	Four biogeographical regions. Lowland South America (41 networks), Andes (21 networks), Central & North America (22 networks), Caribbean islands (15 networks)
Species (floral traits: corolla length, nectar concentration, floral colour)	Biogeographical region	Four biogeographical regions. Lowland South America (557 species), Andes (250 species), Central & North America (188 species), Caribbean islands (88 species)
Species (hummingbird traits: bill length, bill curvature, body mass)	Biogeographical region	Four biogeographical regions. Lowland South America (55 species), Andes (76 species), Central & North America (54 species), Caribbean islands (12 species)

for corolla length and for nectar concentration. Performing phylogenetic analyses with categorical response variables is however complicated (Ives & Garland, 2014) and the phylogenetic signal for colour was moderate ($\lambda = 0.61$). We thus applied a two-step approach where we first tested whether colour categories were distributed randomly across regions by running a Fisher's Exact test. Then, to test whether plant communities in the Caribbean islands had fewer ornithophilous colours in their floral displays, we specifically tested whether the proportion of non-ornithophilous colours (category 'One') differed between biogeographical regions. For this we used a generalized linear model with binomial distribution through the *glm()* function from the 'stats' R package (R Core Team, 2024) followed by Bonferroni adjusted multiple comparisons. A phylogenetic model using the function *MCMCglmm()* from the 'MCMCglmm' R package (Hadfield, 2010) yielded functionally the same results, but did not converge very well (Figure S4), and we thus present the results from the non-phylogenetic model.

2.4.3 | Functional traits mediating plant–hummingbird interactions

Based on three hummingbird traits, we performed a principal coordinate analysis (PCoA) using Mahalanobis distances between species (Botta-Dukát, 2005). By doing so, we projected all hummingbird species (181 species across four biogeographical regions) into one single three-dimensional space (Bender et al., 2017; Dehling et al., 2016; Villéger et al., 2008). The orthogonal principal coordinates describe the functional differences between species by assigning species-specific coordinates along the different axes. Hence, the resulting PCoA space describes the functional diversity of hummingbird visitors, and by projecting plants (based on their hummingbird visitors) into this trait space, it is possible to quantify whether plants interact

preferentially with specific hummingbird trait configurations or if they are more generalized in terms of being visited by a diverse array of hummingbird traits (Figure S5 for detailed explanation).

To achieve this, we first calculated functional originality for each plant species in each network (Bender et al., 2017; Dehling et al., 2016). To this end, we started by extracting the principal coordinates of the hummingbirds of each biogeographical region, that is, regional space. Then, for each network in each respective region and for every unique plant species in the network, we selected the hummingbirds that visited this plant. The principal coordinates of each of these hummingbird visitors were then weighted by their interaction strength and averaged to calculate the weighted interaction centroid of the respective plant species for the corresponding network (Figure S5). Based on this, we then quantified the functional originality of each plant species by measuring the Euclidian distance to the regional community centroid (Bender et al., 2017; Dehling et al., 2016). The regional community centroid was calculated as the unweighted mean of all plant interaction centroids in each region. Consequently, functional originality quantifies how much a plant is preferentially interacting with specific hummingbird species in relation to all other species of that community. Last, we calculated the mean functional originality per network by averaging across all plants of the network while using interaction strength per plant species as a weight. With this last step, we effectively calculated functional dispersion (FDis) of the plant–hummingbird interactions in the hummingbird functional trait space (Laliberté & Legendre, 2010). High values of FDis correspond to a high diversity of functional traits, in this case meaning that plant communities attract hummingbirds that are functionally distinct from each other, leading to interactions that are on average further away from the community centroid. Low values, in turn, indicate that plant communities attract hummingbirds that are predominantly close to the community centroid, indicating a low functional diversity of the interactions.

As the data were slightly non-normal with modest heteroscedasticity, we applied a Welch Anova followed by Bonferroni adjusted comparisons to test whether regional plant communities differed in the functional diversity of the hummingbird visitors they attracted.

All statistical analyses were performed in R version 4.4.1 (R Core Team, 2024).

3 | RESULTS

Phylogenetic analysis revealed a strong phylogenetic signal for corolla length ($\lambda=0.87$, $p<0.01$) and nectar concentration ($\lambda=0.75$, $p<0.01$), but a weaker phylogenetic signal for floral colour ($\lambda=0.61$, $p<0.01$). Closely related species thus tended to have similar values of corolla length and nectar concentration, but this was less pronounced for floral colour.

3.1 | Relationships between single plant traits—Testing the ornithophilous pollination syndrome

Across all plant species, nectar concentration was negatively associated with corolla length (Figure 2A), but the relationship was very weak ($\beta=-0.04$, $R^2=0.02$, $p<0.01$). When analysing this relationship across the four biogeographical regions separately, the patterns were inconsistent (Figure S6). We confirmed a very weak, negative relationship in the plants of the Caribbean islands ($\beta=-0.10$, $R^2=0.07$, $p<0.05$), but conversely, a very weak positive relationship in the Andes ($\beta=0.04$, $R^2=0.04$, $p<0.05$); and there was no significant relationship in the other regions.

Across all species, plants with non-ornithophilous floral colours had significantly shorter corollas (phyANOVA $F_{2,807}=40.51$, $p<0.01$), while there was no difference between species with flowers displaying ornithophilous colours and species with mixed colours (Figure 2B). When we analysed this relationship within the different regions, we found significant patterns only in the Caribbean (phyANOVA $F_{2,79}=7.92$, $p=0.01$) and in Lowland South America (phyANOVA $F_{2,435}=16.31$, $p<0.01$; Figure S6). In both regions, flowers with non-ornithophilous colours had significantly shorter corollas than flowers with ornithophilous colours. The Andes revealed the same pattern, but this difference was not significant (phyANOVA $F_{2,174}=8.87$, $p=0.05$).

We found no relationship between nectar concentration and floral colour, neither across all species (phyANOVA $F_{2,562}=7.88$, $p=0.24$) nor across region-specific communities (Figure 2C; Figure S6).

3.2 | Variation of floral traits across biogeographical regions

Floral corolla length differed between biogeographical regions (phyANOVA $F_{3,812}=12.74$, $p=0.04$). Notably, the corolla length of the

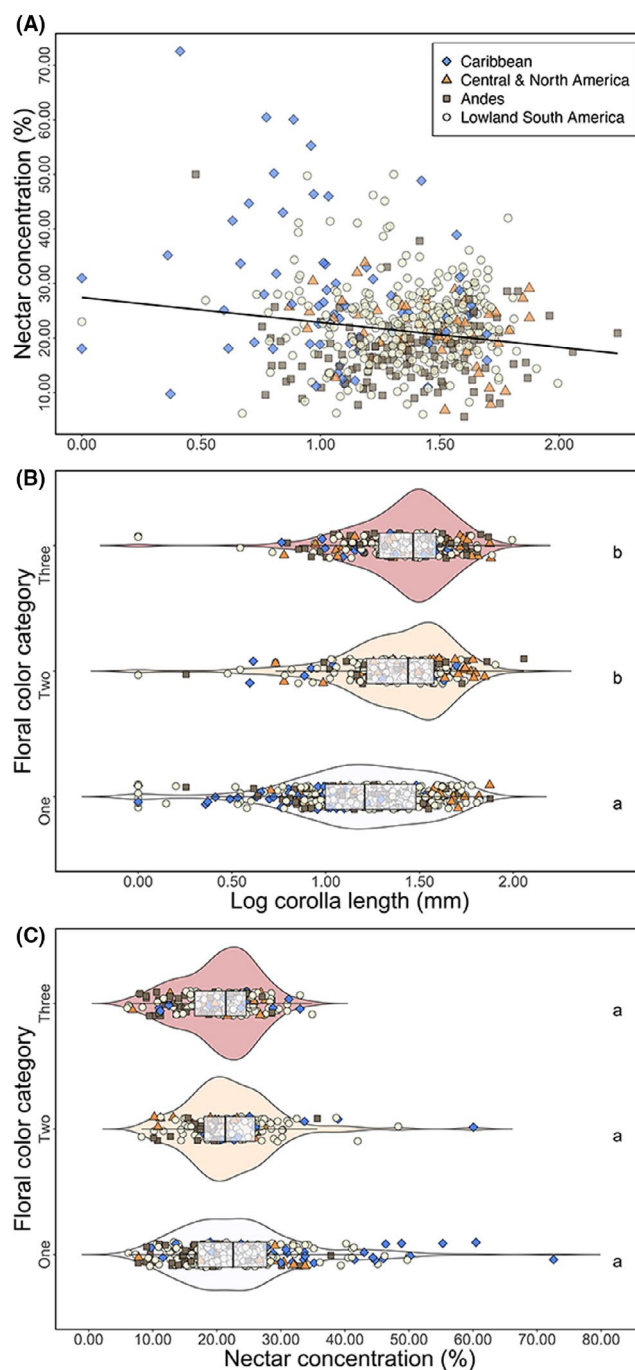


FIGURE 2 Relationships between plant traits. Across all plant species we find a weak, negative relationship between corolla length and nectar concentration (A), indicating that plants with longer corollas also have lower nectar concentrations as indicated by the ornithophilous pollination syndrome. Plants with longer corollas were on average also more likely to display red and reddish colours (B), further fitting the ornithophilous pollination theory. There was no relationship between nectar concentration and floral colour (C).

plants in the Caribbean was on average significantly shorter than that in the mainland regions (Figure 3A), which all had similar average corolla lengths.

Further, nectar concentration differed between biogeographical regions (phyANOVA $F_{3,558} = 26.71$, $p < 0.01$), with the flowers of the Andes and Central & North America having the lowest concentration and the flowers of the Caribbean having the highest nectar concentration (Figure 3B).

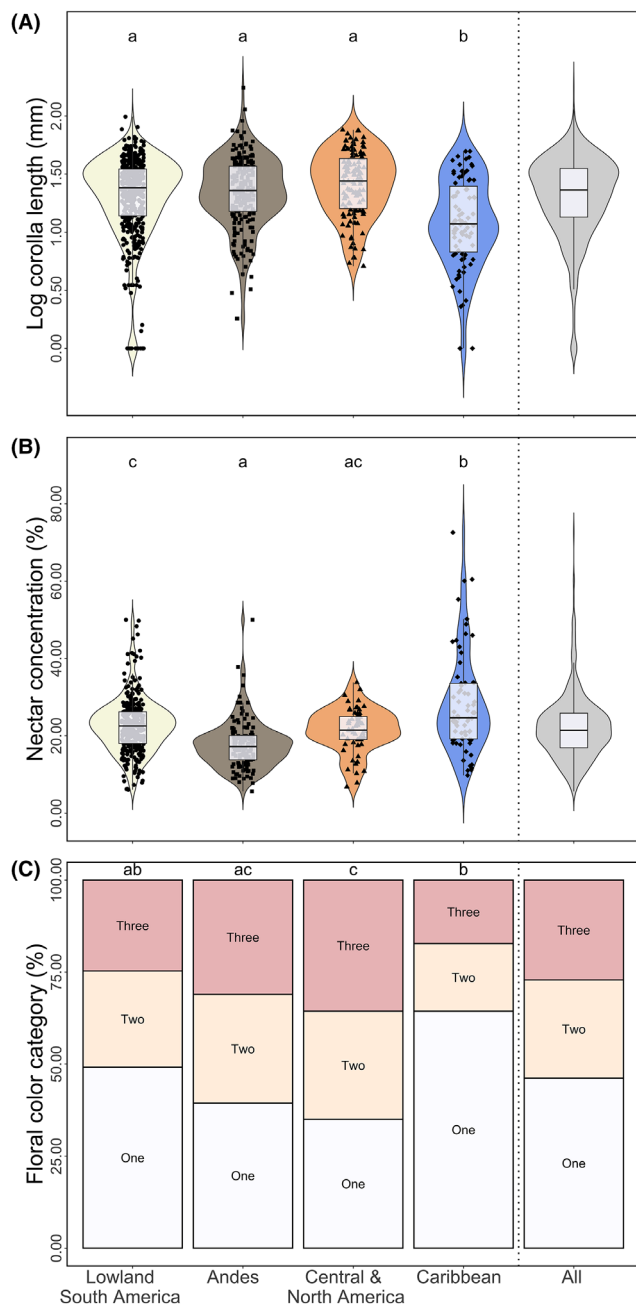


FIGURE 3 Plant floral traits across four biogeographical regions. The plant communities of the Caribbean islands consistently displayed the lowest proportion of traits traditionally associated with an ornithophilous pollination syndrome. Specifically, the plants of the Caribbean had: (A) the on average shortest corollas, (B) on average a significantly higher nectar concentration and (C) had the highest proportion of One/non-ornithophilous colours (i.e. white, purple, blue, green) in their floral displays. See Figure S8 for examples of floral forms in the mainland and the Caribbean islands.

The overall distribution of colour categories across plant species in the respective biogeographical regions was clearly different ($p < 0.01$; Figure 3C). Specifically, the proportion of strictly non-ornithophilous colours (category 'One')—that is, floral displays with predominantly white, yellow and blue hues—was highest in the plant communities of the Caribbean ($\chi^2_{3,939} = 21.42$, $p < 0.01$).

3.3 | Functional traits mediating plant–hummingbird interactions

Across all plant–hummingbird networks, the mean distance of plant–hummingbird interactions from the community centroid (i.e. functional dispersion) differed significantly among biogeographical regions (Welch-ANOVA $F_{3,88} = 41.92$, $p < 0.01$). Strikingly, the networks in the Caribbean islands had a higher functional diversity than those on the mainland, and interactions were thus on average functionally more distinct (Figure 4).

4 | DISCUSSION

Based on a large and comprehensive dataset of plant–hummingbird interactions and associated functional traits, we show that flowers with longer corollas displayed ornithophilous colours more often and had lower nectar concentrations than flowers with shorter corollas (Figure 2), thus fitting the classic ornithophilous pollination syndrome (Faegri & van der Pijl, 1979). In line with our expectations, plants on oceanic islands tended to have traits that are less consistent with the ornithophilous pollination syndrome, exhibiting shorter corollas, higher nectar concentration and proportionally more

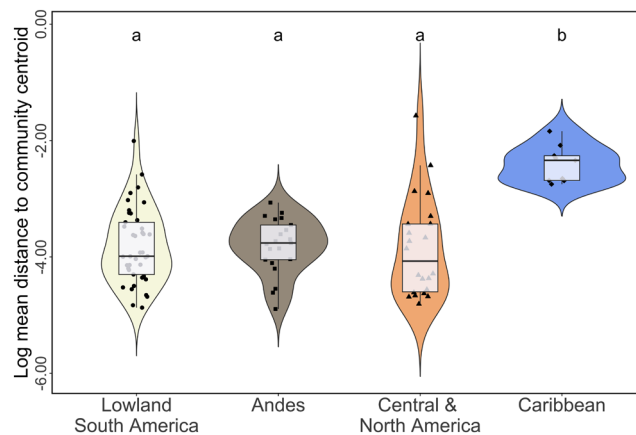


FIGURE 4 Functional dispersion (FDIs) in plant–hummingbird interactions across four biogeographic regions. Functional dispersion measures the mean distance of plant–hummingbird interactions to the community centroid of the respective regional trait space. On average, the interactions between plants and hummingbirds in the communities of the Caribbean islands were functionally more distinct from the community centroid than in other regions. This pattern indicates that Caribbean plant species interacted predominantly with specific types of hummingbirds.

non-ornithophilous colours than plants on the mainland (Figure 3; see Figure S7 for examples of floral forms). Interestingly, however, when we compared the plant–hummingbird interactions among biogeographical regions, we found that plants in the Caribbean islands interacted with morphologically more distinct hummingbirds than the plants in the mainland regions (Figure 4), suggesting predominant interactions with functionally specific hummingbirds. This pattern may possibly be driven by competition over resources in the comparatively depauperate and environmentally unstable conditions (e.g. due to hurricanes) of the Caribbean islands.

4.1 | Variation of functional floral traits across biogeographical regions

We expected the plants of the Caribbean islands to display traits that would be less consistent with the ornithophilous pollination syndrome (Dalsgaard et al., 2021), as it is commonly expected that species in depauperate communities on islands display a more generalized behaviour (Olesen & Jordano, 2002; Traveset et al., 2015). Moreover, frequent hurricanes and other natural disasters in the region inflict periodically recurring disturbances to the local ecosystems, potentially altering the interactions between plants and their hummingbird pollinators (Dalsgaard & Temeles, 2024; Rathcke, 2000; Schröder et al., 2024). Tight plant–pollinator co-evolution, and notably adaptation towards hummingbirds, may thus be a disadvantage and, consequently, rare in the Caribbean islands (but see Temeles et al., 2000 for an example).

When we analysed the distribution of plant traits across the four biogeographical regions, our findings aligned with these theoretical expectations (Dalsgaard et al., 2021; Olesen et al., 2002; Olesen & Valido, 2003; Traveset et al., 2015). The hummingbird-visited plants of the Caribbean islands displayed proportionally the fewest traits typically associated with bird-mediated pollination (Figure 3; see Figure S7 for examples of floral forms). It has previously been suggested that hummingbirds on the Caribbean islands are more likely to feed on flowers displaying traits that are mostly associated with insect pollination (Dalsgaard et al., 2009, 2021; Lehmann et al., 2019), indicating a more generalized pollination system than in the corresponding mainland communities (Martén-Rodríguez et al., 2015). Such altered visitation habits could result from the depauperated insect fauna on the oceanic islands, as hummingbirds may benefit from the lower diversity and abundance and easily fill the niche of insects. This is particularly evident at higher elevations, where temperatures are lower, rainfall is often higher and insect activity consequently declines even further (Dalsgaard et al., 2009; Lehmann et al., 2019). However, while plants may have a clear advantage on islands when they attract mixed groups of pollinators, visitation rates of hummingbirds can be significantly lower (Martén-Rodríguez et al., 2010) which may lead plants to experience pollen limitation and accordingly lower fruit sets (Martén-Rodríguez & Fenster, 2010).

It is thus unclear whether additionally interacting with hummingbirds may be a reproductive advantage for plants in regions such

as oceanic islands, where insect pollinators are typically less abundant (Traveset et al., 2013). In fact, in the Caribbean islands, within the Gesnerieae, autonomous breeding systems have been documented only in hummingbird-pollinated lineages (Martén-Rodríguez et al., 2010). Hence, hummingbirds may not always be reliable pollinators, making reproductive assurance mechanisms necessary (Martén-Rodríguez et al., 2010). Consequently, it remains uncertain if insect-pollinated plants 'actively' seek to attract hummingbirds in the Caribbean islands to compensate for the lack of insects.

Another potential mechanism driving Caribbean hummingbirds to frequently visit plants which hummingbirds would typically rather avoid in mainland regions, might be the low proportion of 'typical' ornithophilous syndrome flowers and the comparatively low nectar quantities in plants adapted to insect pollination (Baker & Baker, 1983). Hence, to make up for the low volume per flower, hummingbirds may be driven to visit more flowers in order to retrieve similar nectar quantities and successfully fuel their metabolism, which is among the most demanding of all vertebrates (Gass et al., 1999). Such substitutional visitation patterns in combination with possibly low pollination efficiency might result in little to no selection pressure exerted by hummingbirds, leading plants to largely maintain or evolve reproductive assurance mechanisms, such as generalization and autogamy.

4.2 | Functional traits mediating plant–hummingbird interactions

Given the lower proportion of ornithophilous floral traits, the comparatively depauperate communities and the widely hypothesized reduction of interspecific competition on oceanic islands (Olesen et al., 2002; Olesen & Jordano, 2002; Traveset et al., 2015), we would have expected to detect signs of functional generalization in the plant–hummingbird interactions. Additionally, the islands of the Caribbean are environmentally unstable with frequent, devastating natural disasters, notably hurricanes, which alter and re-shape associations between species (Rathcke, 2000; Schröder et al., 2024) and make tight reciprocal adaptation less likely (Dalsgaard & Temeles, 2024). In fact, it has already been shown that plant–hummingbird interactions in the Caribbean islands exhibit greater pollinator overlap than mainland communities (Dalsgaard et al., 2021; Martín González et al., 2015; Maruyama et al., 2018), which would also suggest a lower functional diversity of the interactions in these communities. Interestingly, however, our results show a higher functional diversity in the plant–hummingbird interactions of the Caribbean networks, that is, hummingbird-visited plants interacted predominantly with specific functional subsets of the hummingbird communities (Figure 4).

Hummingbird communities of the Caribbean mostly comprise one large and one small species (Lack, 1973), with few intermediate-sized hummingbirds, which could contribute to the high functional diversity observed in their interactions. However, while the Caribbean hummingbird communities are characterized by a low

taxonomic diversity, their functional diversity (FDIs) did not differ significantly from the mainland regions (Figure S8). It is thus unlikely that the species pool alone would drive the patterns of high functional diversity in the plant–hummingbird interactions of the Caribbean islands. Another potential mechanism contributing to the detected patterns might be the necessity to defend resources in the comparatively depauperate and environmentally unstable oceanic islands. Hummingbirds are well known to compete over resources, particularly when they are scarce (Maglianesi et al., 2015; Pimm et al., 1985; Tinoco et al., 2017). Indeed, one of the best-known examples of very competitive exclusion in plant–hummingbird pollination systems is described from the Caribbean islands. In the Lesser Antilles, *Heliconia caribaea* flowers may be almost completely monopolized by the large-sized Purple-throated Carib *Eulampis jugularis* (Temeles et al., 2000, 2013; Temeles & Kress, 2003).

Consequently, our results might suggest that competition may be a widespread mechanism shaping plant–hummingbird interactions across the Caribbean islands and is likely particularly driven by larger hummingbird species defending the resources they may most efficiently exploit. Recently, it was demonstrated that following a devastating hurricane on the island of Dominica, smaller hummingbird species increased their visitation rates on *Heliconia* flowers which they could previously not access, as a hurricane-induced population crash of the Purple-throated Carib led to a breakdown in the competitive exclusion (Schröder et al., 2024). As this demonstrates, all hummingbirds may visit these flowers in the absence of competition, and our findings thus further corroborate the importance of competition driving the high functional diversity of plant–hummingbird interactions in the Caribbean islands, rather than species pools or functional traits alone.

Interestingly, we found the same pattern in two networks from continental North America, where the functional diversity of the interactions was also high (Figure 4; two uppermost data points of Central & North America). The hummingbird communities in these networks are composed of only two species and similar mechanisms may explain why plants in these communities receive interactions predominantly from functionally distinct hummingbirds. Unstable environmental conditions with seasonal fluctuations and potentially lower abundance of insect pollinators could lead to interactions with hummingbirds which in turn defend specific resources. However, our sample size is too small to reliably test such relationships in continental North America.

In the other biogeographical regions, we found contrasting patterns with plant–hummingbird interactions being closer to the functional community centroid. This could reflect a certain level of ‘functional redundancy’ in the speciose mainland communities, where many similar species may populate a functional space (Pigot et al., 2016). This may in turn reflect either a more fine-grained—but functionally similar—specialization or higher niche overlap between different species with similar traits (Karr & James, 1975; Klopfer & MacArthur, 1961). Increased functional redundancy can be associated with generally higher ecological carrying capacities which facilitates coexistence between species, as typically found in tropical

forests (Hubbell, 2011; MacArthur, 1965). The long co-evolutionary timescales, notably in the communities of Lowland South America, where modern hummingbirds originated ~22 Mya (McGuire et al., 2014), in combination with high species richness and comparatively stable environmental conditions, may thus explain why many hummingbird-visited plants have ornithophilous floral traits but high functional similarity of plant–hummingbird interactions in the mainland communities (Hubbell, 2011; MacArthur, 1965).

5 | CONCLUSIONS

We present a comprehensive analysis of a large, unprecedented dataset of plant–hummingbird interactions and associated functional traits across large spatial gradients. Our results indicate the presence of an ornithophilous pollination syndrome in plants, but show that in the Caribbean islands, hummingbird-visited plants display low proportions of traits typically associated with bird-mediated pollination. Caribbean hummingbirds probably expand their feeding niche to include plants with traits that they tend to avoid in the mainland because the lower diversity and abundance of insect pollinators makes it easier to fill this niche. Interestingly, against our expectations, we find a higher functional diversity in the plant–hummingbird interactions of the Caribbean islands. This contradicts theoretical predictions but could be a response to competition over comparatively scarce resources in the environmentally unstable oceanic islands.

AUTHOR CONTRIBUTIONS

Maximilian G. R. Vollstädt, Rasmus D. Jensen and Bo Dalsgaard conceived the study; Rasmus D. Jensen, Maximilian G. R. Vollstädt, Pietro K. Maruyama, Matthias Schleuning, Francielle P. Araújo-Hoffmann, Marlies Sazima, Jesper Sonne, Taia S. O. Schröder, Fredrik Møller-Stranges, Stefan Abrahamczyk, Mónica B. Ramírez-Burbano, Marcelo Ferreira de Vasconcelos, Boris A. Tinoco, María A. Maglianesi, Ruth Partida-Lara, José Raúl Vázquez-Pérez, Paula L. Enríquez, André Rodrigo Rech, Aline G. Coelho, Fernando Gonçalves, Edvaldo Nunes da Silva Neto, Manoel Martins Dias Filho, Matheus Reis, Oscar H. Marín-Gómez, Juan Francisco Ornelas, Peter A. Cotton, Paulo Eugenio Oliveira, Adriana Oliveira Machado, Jeferson Vizentin-Bugoni, Pedro Joaquim Bergamo, Carlos Lara, Márcia Alexandra Rocca, Ivan Sazima, Oscar Gonzalez, Erich Fischer, Andréa C. Araujo, Raúl Ortiz-Pulido, Blanca Patiño, Rubén Pineda López, Stella Watts, Ruben Alarcon, Caio Graco Machado, Flor Maria G. Las-Casas, Benno I. Simmons, Christopher N. Kaiser-Bunbury, Trine Bilde and Bo Dalsgaard collected the data; Rasmus D. Jensen and Maximilian G. R. Vollstädt compiled and checked the database; Maximilian G. R. Vollstädt and Rasmus D. Jensen analysed the data with input from Matthias Schleuning; Maximilian G. R. Vollstädt and Rasmus D. Jensen wrote the first draft of the manuscript with inputs from Pietro K. Maruyama, Peter A. Cotton and Bo Dalsgaard. All authors contributed critically to the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests. Matthias Schleuning is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo Online Repository: <https://doi.org/10.5281/zenodo.15276347> (Vollstädt et al., 2025).

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SUPPORTING INFORMATION

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

Figure S1: All results are functionally the same without the 52 introduced species, indicating that there is no confounding effect of including these species in this analysis (compare with Figures 2, 3 and 4 in the main text).

Figure S2: All results are functionally the same without the networks of North America, indicating that there is no confounding effect of pooling the data with observations from Central America (compare with Figures 2, 3 and 4 in the main text).

Figure S3: Phylogeny for all fully identified plant species and their distribution across biogeographical regions. In each region, we highlight the plant families with the largest respective species numbers.

Figure S4: Diagnostic plot of a MCMCglmm testing the proportion of colour category ‘One’, that is, the strictly non-ornithophilous colours across the four biogeographical regions. The model did not converge well; hence we do not present the results. We note that the outcome of the MCMCglmm model was similar to the glm model we present in the results section of the main text, comparing the distribution of colour categories across biogeographical regions, revealing that the proportion of non-ornithophilous colours was highest in the Caribbean.

Figure S5: Methodological approach for calculating the mean distance of plant–hummingbird interactions to the community centroid in a given functional trait space. (1) We first calculate the functional space of hummingbird visitors for all hummingbird species across all regions. (2) For each region and each network separately, we then pick each single plant species one by one. (3) We then identify the hummingbird visitor(s) for a given plant species in the given network. (4) We then locate the PCoA positions of the(se) hummingbird(s). (5) and (6) Based on interaction strength, we project the plant species into the hummingbird trait space. (7) We repeat this procedure for all plant species per network and calculate the regional interaction centroid (e.g. all interactions of a region, such as the ‘Caribbean’). (8) Lastly, we measure the Euclidian distance of each species in each network to the regional centroid and calculate the mean by weighing each plant species by its interaction strength. Hummingbird drawings by Katrine Hansen.

Figure S6: Regional associations between single plant traits. From left to right: Corolla length vs. nectar concentration; Corolla length per colour category; Nectar concentration per colour category. From top to bottom respectively: Caribbean, Central & North America, Andes, Lowland South America.

Figure S7: Examples of the floral forms of hummingbird-visited plants in mainland Americas and the Caribbean islands. In the mainland Americas, there is a rich flora of hummingbird-visited flowers following the traditional bird pollination syndrome (Upper left; A–H), and fewer hummingbird-visited plant species following traditional insect-syndrome flowers (Lower left; I–L). On the contrary, in the Caribbean islands, few hummingbird-visited plants fit the traditional bird-syndrome flowers (Upper right; M–P), whereas many species

of hummingbird-visited flowers fit the traditional insect-syndrome (Lower right; Q-Y). (A) *Mutisia coccinea*, Campinas, Brazil, Ivan & Marlies Sazima; (B) *Erythrina speciosa*, Campinas, Brazil, Ivan Sazima; (C) *Centropogon conutus*, Brazil, Marlies Sazima; (D) *Sinningia rupicola*, Minas Gerais, Marcelo Ferreira de Vasconcelos; (E) *Sinningia cooperi*, Nucleo Santa Virginia, Brazil, Jeferson Vizontin-Bugoni; (F) *Russelia sarmentosa*, Central America, Stefan Abrahamczyk; (G) *Tillandsia stricta*, Jureia, Brazil, Erich Fischer; (H) *Vriesea ensiformis*, Jureia, Brazil, Erich Fischer; (I) *Centrosema coriaceum*, Minas Gerais, Brazil, Marcelo Ferreira de Vasconcelos; (J) *Paliavana sericiflora*, Minas Gerais, Brazil, Marcelo Ferreira de Vasconcelos; (K) *Abutilon regnellii*, Campos de Jordao, Brazil, Ivan & Marlies Sazima; (L) *Stachytarpheta glabra*, Minas Gerais, Brazil, Marcelo Ferreira de Vasconcelos; (M) *Heliconia caribea*, Saba, Rasmus D. Jensen; (N) *Guzmania berteroniana*, Puerto Rico, Bo Dalsgaard; (O) *Gesneria ventricosa*, St. Kitts, Rasmus D. Jensen; (P) *Heliconia bihai*, Grenada, Allan Timmermann; (Q) *Cordia globosa*, Dominica, Bo Dalsgaard; (R) *Besleria lutea*, Guadeloupe, Rasmus D. Jensen; (S) *Hyptis atrorubens*, Dominica, Bo Dalsgaard; (T) *Lobelia cirsiiifolia*, Grenada, Rasmus D. Jensen; (U) *Petrea volubilis*, Antigua, Rasmus D. Jensen; (V) *Schradera exotica*, Dominica, Bo Dalsgaard; (X) *Renalmia pyramidalis*, Dominica, Rasmus D. Jensen; (Y) *Psychotria urbaniana*, Dominica, Bo Dalsgaard. For land-shapes indicating region and syndrome, *Campylopterus ensipennis* in the outline of South America represents bird-syndrome flowers in the Mainland, *Archaeoprepona demophoon* in the outline of South America represents insect-syndrome flowers in the Mainland,

Orthorhyncus cristatus in the outline of Dominica represents bird-syndrome flowers in the Caribbean Islands and *Anartia amathea* in the outline of Dominica represents insect-syndrome flowers in the Caribbean Islands, photos taken by Rasmus D. Jensen.

Figure S8: Functional diversity of the respective hummingbird communities, measured as functional dispersion (FDis). FDis was highest in the Andean hummingbird communities but did not differ significantly among other regions. Interestingly, the functional diversity of Caribbean hummingbirds did not differ significantly from any other biogeographical region.

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