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Behavioural and morphological traits influence sex-specific floral resource use by hummingbirds

María A. Maglianesi[1] | **Pietro K. Maruyama**[2] | **Ethan J. Temeles**[3] |
Matthias Schleuning[4] | **Thais B. Zanata**[5] | **Marlies Sazima**[6] |
Aquiles Gutiérrez-Zamora[7] | **Oscar H. Marín-Gómez**[8,9] | **Liliana Rosero-Lasprilla**[10] |
Mónica B. Ramírez-Burbano[11] | **Alejandra E. Ruffini**[12] | **J. Ricardo Salamanca-Reyes**[13] |
Ivan Sazima[14] | **Laura E. Nuñez-Rosas**[15] | **María del Coro Arizmendi**[15] |
Carsten Rahbek[16,17,18,19] | **Bo Dalsgaard**[16,19]

[1]Vicerrectoría de Investigación, Universidad Estatal a Distancia, San José, Costa Rica; [2]Departamento de Genética, Ecologia e Evolução, ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil; [3]Department of Biology, Amherst College, Amherst, MA, USA; [4]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt (Main), Germany; [5]Departamento de Botânica e Ecologia, Instituto de Biociências, Universidade Federal de Mato Grosso, Cuiabá, Brazil; [6]Departamento de Biologia Vegetal, Instituto de Biología, Universidade Estadual de Campinas, Campinas, Brazil; [7]Department of Biology, University of Nariño, Pasto, Colombia; [8]Grupo de Investigación y Asesoría en Estadística, Universidad del Quindío, Armenia, Colombia; [9]Programa de Biología, Grupo de Investigación y Asesoría en Estadística, Universidad del Quindío, Armenia, Colombia; [10]Grupo de Investigación Biología para la Conservación, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia; [11]Grupo Ecología y Diversidad Vegetal, Departamento de Biología, Facultad de Ciencias Naturales, Universidad del Valle, Cali, Colombia; [12]Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Bariloche, Argentina; [13]Escuela de Biología, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia; [14]Museu de Biodiversidade Biológica, Instituto de Biología, Universidade Estadual de Campinas, Campinas, Brazil; [15]Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico; [16]Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen Ø, Denmark; [17]Institute of Ecology, Peking University, Beijing, China; [18]Danish Institute for Advanced Study, University of Southern Denmark, Odense, Denmark and [19]Section for Molecular Ecology and Evolution, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

Correspondence
María A. Maglianesi
Email: mmaglianesi@uned.ac.cr

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Abstract

1. Research on resource partitioning in plant–pollinator mutualistic systems is mainly concentrated at the levels of species and communities, whereas differences between males and females are typically ignored. Nevertheless, pollinators often show large sexual differences in behaviour and morphology, which may lead to sex-specific patterns of resource use with the potential to differentially affect plant reproduction and diversification.

2. We investigated variation in behavioural and morphological traits between sexes of hummingbird species as potential mechanisms underlying sex-specific flower resource use in ecological communities. To do so, we compiled a dataset of plant–hummingbird interactions based on pollen loads for 31 hummingbird species from 13 localities across the Americas, complemented by data on territorial behaviour (territorial or non-territorial) and morphological traits (bill length, bill curvature, wing length and body mass).

3. We assessed the extent of intersexual differences in niche breadth and niche overlap in floral resource use across hummingbird species. Then, we tested whether floral niche breadth and overlap between sexes are associated with

sexual dimorphism in behavioural or morphological traits of hummingbird species while accounting for evolutionary relatedness among the species.

4. We found striking differences in patterns of floral resource use between sex. Females had a broader floral niche breadth and were more dissimilar in the plant species visited with respect to males of the same species, resulting in a high level of resource partitioning between sexes. We found that both territoriality and morphological traits were related to sex-specific resource use by hummingbird species. Notably, niche overlap between sexes was greater for territorial than non-territorial species, and moreover, niche overlap was negatively associated with sexual dimorphism in bill curvature across hummingbird species.

5. These results reveal the importance of behavioural and morphological traits of hummingbird species in sex-specific resource use and that resource partitioning by sex is likely to be an important mechanism to reduce intersexual competition in hummingbirds. These findings highlight the need for better understanding the putative role of intersexual variation in shaping patterns of interactions and plant reproduction in ecological communities.

KEYWORDS

behaviour, hummingbirds, morphological traits, niche breadth, niche overlap, pollen loads, resource similarity, sex differences

1 | INTRODUCTION

Niche theory predicts that coexisting species will partition food resources to limit the effects of interspecific competition, where species with narrow food niches use a reduced diversity of food resources in the community (Carscadden et al., 2020; Chesson, 2000). In addition to different patterns of resource use among species, variation within species is more common than previously thought (Maglianesi et al., 2015; Smith et al., 2019; Temeles et al., 2010). In pollination systems, intraspecific variation in the foraging niche of pollinator species can drive mutualistic interactions and ecosystem processes (Bolnick et al., 2003; Temeles & Kress, 2003). Notably, male and female pollinators can exhibit considerably different patterns of food resource use (Ritchie et al., 2016; Roswell et al., 2019). These differences may include variation in niche breadth, with one sex using more diverse food resources than the other, and niche segregation, with different plant species used by the sexes (Smith et al., 2019). In this context, sexual dimorphism and associated differences in feeding ecology may reduce food niche overlap between the sexes of a given species and, hence, reduce the level of intraspecific competition (Temeles et al., 2010).

Sex differences in use of plant resources across pollinator species have been largely unexplored, despite the important implications such differences might have for plant reproduction and the structure and dynamics of ecological communities (Leimberger et al., 2022). Complementary plant species use between the sexes may represent a mechanism by which a pollinator species could benefit if a given resource is crucial for the fitness of one sex (Roswell et al., 2019). As the vast majority of plant species rely on animal pollen vectors for their reproductive success (Ollerton et al., 2011; Rech et al., 2016; Rodger et al., 2021), sex differences in resource use by pollinators also have the potential to induce large consequences for plant fitness and diversification (e.g. Temeles & Kress, 2003). Moreover, sex-specific resource use by pollinators might benefit a visited plant species due to a higher pollination effectiveness (Temeles et al., 2013, 2019). Therefore, studies on variation in resource use between sexes of pollinators are essential for a thorough understanding of plant–pollinator interactions.

Several factors could lead to sex-specific resource use within the same species of pollinator, such as differences in life history and behaviour between the sexes (Ne'eman et al., 2006). Noticeably, males and females in some hummingbird species (Trochilidae) have been found to forage differently (Carpenter et al., 1991; Temeles & Kress, 2003). Hummingbird territoriality, mate selection and nesting behaviours are strongly associated with foraging strategies and, hence, may promote sexually dimorphic patterns in floral resource use (Rodríguez-Flores & Arizmendi Arriaga, 2016; Schuchmann, 1999). In addition, intraspecific ecological differences in floral resource use are often associated with morphological differences in bill length or bill curvature (Temeles et al., 2010; Temeles & Kress, 2003). Thus, it is likely that a combination of behavioural and morphological traits jointly determines a sex differential resource use of hummingbirds (Leimberger et al., 2022).

Here, we used pollen loads carried by individuals to assess the degree of intraspecific divergence in patterns of resource use by males and females of 31 hummingbird species distributed widely across the Americas. We explored whether floral resource breadth and overlap is related to sexual differences in behaviour and morphology

of these species. We specifically investigated (a) the extent of inter-sexual differences in floral niche breadth across hummingbird species, (b) the degree to which hummingbird species show sex-specific partition or overlap in plant resources, and (c) whether differences in floral resource use within hummingbird species are associated with sexual dimorphism in behavioural or morphological traits while accounting for evolutionary relatedness among species. We evaluated the hypothesis that floral resource partitioning is greater between males and females of the same species than between individuals of the same sex. Moreover, as sex-specific niche partitioning may arise through sexual dimorphism, that is, different morphology in males and females (Leimberger et al., 2022; Selander, 1966; Temeles et al., 2000), we expected that sexual differences in resource use to be positively related to sexual dimorphism in hummingbird morphology. In addition to hummingbird morphology, we expected that a territorial behaviour might influence floral resource use by the sexes, by restricting highly rewarding resources to the sex that aggressively defends a territory (e.g. Temeles & Kress, 2003).

We found strong differences in the pattern of floral resource use between sex across hummingbird species that were associated with both territoriality and dimorphism in bill curvature. These findings show the relevance of behaviour and morphology as factors influencing sex-specific resource use in plant–hummingbird interactions and the need for downscaling plant–pollinator systems from the community and species levels to the intersexual level to obtain an in-depth insight into pollination ecology.

2 | MATERIALS AND METHODS

2.1 | Plant–hummingbird interactions

We compiled a dataset of 3,265 plant–hummingbird interactions based on pollen loads between 484 plant species and 771 individuals of 31 hummingbird species from six of the nine clades of hummingbirds (sensu McGuire et al., 2014), where two of these species were present in two localities (Appendices 1 and 2). Sampling sites were at 13 localities from five countries across the Americas from Mexico in the north to southern Argentina, ranging from tropical to temperate climate zones and from the sea level to highland ecosystems (>3500 m a.s.l.). Data collection overall was conducted along one or more years, that is, encompassing both the breeding and non-breeding season of hummingbird species. In our dataset, visited plant species were identified by examining pollen loads carried by mist-netted hummingbirds using fuchsine-stained gelatine (Beattie, 1971) or transparent adhesive tape (Kearns & Inouye, 1993). Pollen grains were identified under a light microscope by comparison with reference collections taken from plants at the study sites, as well as from the literature (e.g. Roubik & Moreno, 1991). Pollen grains were classified to plant species whenever possible and to morphospecies if pollen from closely related species or genera were indistinguishable. In cases where species, genus or family could not be determined, pollen grains were determined as morphotypes, based on their size,

shape, type and number of apertures, and exine sculptures. Plants identified at the species or morphospecies level was 58%, whereas the remaining 42% of the plants were identified as morphotypes. Hereafter, we will refer to pollen morphotype of either pollen identified to species level or pollen identified to morphospecies or morphotype level, and each morphotype as equivalent to one plant species. In some studies, a few pollen grains could not be identified to any level, but these represented only 0.8% of all interactions and were excluded from analyses. The number of hummingbird individuals carrying pollen of a particular morphotype was used as a measure of the interaction frequency between that hummingbird species and that morphotype (Maglianesi et al., 2015; Ramírez-Burbano et al., 2017). Pollen loads from recaptured individuals were considered only when recaptures occurred at different sampling periods separated for more than 1 month. Although we lack information about specific pollen attachment times, Bosch et al. (2009) identified pollen grains on insects up to 1 month after the last flowering plant of a given species was blooming in the area. Thus, it is likely that more than 1 month between hummingbird recaptures provide independent pollen samples.

The mean number of individuals sampled for pollen loads was 12 females and 10 males from each species (ranging from 10 to 74 individuals per species) with a minimum of five individuals from each sex. We considered that a minimum sample size of 10 individuals is representative of the interactions for the species included in our study since pollen gives robust, spatially broad, cumulative link evidence and also detects interactions between rare species (Bosch et al., 2009; Ramírez-Burbano et al., 2017; Souza et al., 2021). Thus, pollen loads can be a suitable estimator of an individual's foraging patterns (Courtney et al., 1981). Total sampling effort for plant–hummingbird interactions consisted overall of 771 hummingbird individuals of 31 species with pollen. Our dataset for phylogenetic analysis consisted of 713 individuals of 28 hummingbird species that interacted with 479 plant species, given that we excluded three hummingbird species that were missing in the phylogeny (see below). The mean number of pollen morphotypes carried by hummingbird species was not significantly correlated with the number of individuals sampled for pollen across species in either case ($r = -0.11$, $p = 0.389$ for overall dataset; $r = -0.27$, $p = 0.171$ for phylogenetic analyses dataset), indicating that results are not associated with sample size.

2.2 | Morphological and behaviour data

We included four morphological traits of hummingbird species that have been reported to affect their interactions with plant species, that is, bill length and curvature (Dalsgaard et al., 2021; Maglianesi et al., 2014; Temeles et al., 2010), body mass (Dalsgaard et al., 2009) and wing chord length (Stiles, 2004). We used body mass as a measure for body size, as body mass has been identified as the best indicator of overall size in hummingbirds (Stiles, 1996). Given that the body mass of birds is highly variable (i.e. it depends on the condition of individuals), we repeated our analyses using

wing chord length as another measure of body size. Traits were measured from mist-netted individuals in the field and from museum specimens, encompassing a large dataset of morphological measurements consisting of traits from 1,227 hummingbird individuals with an average of 19 males and 21 females per species (range: 5–64 males and 5–170 females per species). These traits correspond only to adult birds as determined from plumage and/or <10% of bill corrugations (Ortiz-Crespo, 1972), since some morphological traits such as bill length may not be fully developed in juveniles. We used data from the literature for three species to complement missing data (Bleiweiss, 1998; Rodrigues et al., 2019; Stiles & Boesman, 2020).

We classified each hummingbird species as territorial or non-territorial based on field observations and previous studies (Appendix 2). Non-territorial species include hummingbirds belonging to the hermit clade, which typically forage using a traplining behaviour, and also those species from other clades that do not defend feeding areas when foraging. Although the same species may change their foraging behaviour according to the availability of resources (Buzato et al., 2000; Justino et al., 2012), we considered all species that are known to exhibit territorial defence in highly rewarding patches as 'territorial' species. This study did not require ethical approval.

2.3 | Statistical analyses

2.3.1 | Patterns in floral resource use

To analyse patterns in floral resource use by males and females of each hummingbird species, we first quantified niche breadth of individual sexes. This was measured as the total number of pollen morphotypes carried by individuals, which represents the number of plant taxa within each pollen load. Hence, a sex that carried many pollen morphotypes indicates broad niche breadth, that is, a high floral resource diversity. To analyse whether males and females within species differed in their niche breadth, we fitted a generalized linear mixed model (GLMM) with Poisson error distribution including the total number of pollen morphotypes as the response variable. In this model, we included sex, species and sex by species interaction as fixed effects, in addition to species and pollen load identity as random effects to control for random variation in pollen samples among individuals. Thus, this model tests whether niche breadth consistently differs between sex for the different hummingbird species. We did not find overdispersion in our GLMM (dispersion ratio = 0.90, $\chi^2 = 630$, $p = 0.982$) after testing with the function *check_overdispersion* in the R package PERFORMANCE (Lüdecke, 2021). We report the statistics of the fixed effects and its interaction from ANOVA performed on the GLMM with chi-squared test.

Next, we assessed niche overlap in floral resource use between sex of each hummingbird species by building separate interaction frequency matrices for each species and location and calculated the Morisita's similarity index (Morisita, 1959) with the *R*-function *niche.*

overlap in the R package SPAA (Zhang, 2016). This index can be estimated more accurately than most other niche overlap indices (Chao et al., 2006). This index ranges from 0 when both sexes do not share any food resource (complete resource partitioning) to 1 when both sexes use identical resources (no resource partitioning, i.e. complete niche overlap). We expected that niche overlap between sexes might be less than niche overlap within sexes. We thus randomly picked two individuals (one male and one female) of a species at a given location and calculated niche overlap. We repeated this procedure 25 times to obtain an estimate of mean and variance of niche overlap between sexes for each species and related these estimates to hummingbird morphology. We then performed two other runs of sampling where we randomly picked individuals of the same sex and estimated the mean and variance of niche overlap within sexes of the same species. Thus, we obtained three measures of niche overlap: between sexes, within males and within females. Random selections in both cases between and within sex were performed with replacement, that is, we replace the individual each time we choose one. To analyse the extent in which hummingbird individuals differ in the plant species they visited according to sex, we compared the between-sex measure of niche overlap separately to within-male and within-female estimates with a paired *t*-test (i.e. we performed the test twice, once for each sex).

2.3.2 | Morphological traits

To examine the underlying causes of dissimilarity in floral resource use between the sexes, we quantified sexual dimorphism (SD) for each hummingbird species. For this, we calculated the mean trait measurements of males and females using the robust ratio on a linear scale proposed by Lovich and Gibbons (1992). This ratio is calculated as: SDI = (L/S−1) × 1 if the female is the larger sex and SDI = (L/S−1) × (−1) if the male is the larger sex, where L is the average size of the larger sex and S is the average size of the smaller sex for that species. The Lovich–Gibbons ratio produces measures of SD that are continuous around zero and directional, easy to interpret and properly scaled across species differing in overall size. To test whether the degree of sexual dimorphism is more pronounced in larger species, which might act as a confounding factor in the interpretation of our results, we performed linear models with sexual dimorphism (Lovich–Gibbons ratio) in a given morphological trait as the response variable and the average body mass for the species as the predictor variable. In none of these models, the association between body mass and sexual dimorphism was significant (Appendix 3).

2.3.3 | Phylogenetic data

The morphological and behavioural traits included here are known to be influenced by evolutionary relatedness between

hummingbirds (Rombaut et al., 2022). Therefore, to control for this in the analyses where we included hummingbird traits (i.e. territoriality or morphology) as predictors, we used different phylogenetic approaches. First, the expected variance–covariance matrix was calculated from the most updated phylogeny of hummingbirds (McGuire et al., 2014). Then, to build this matrix, we pruned the phylogeny selecting only the species present in our study. Among the 31 species compiled here, three were missing in the phylogeny (*Chalcostigma heteropogon*, *Chlorostilbon olivaresi* and *Eriocnemis mirabilis*). Therefore, to arrange our data with the available phylogenetic information, we removed those three species from the analyses.

2.3.4 | Potential mechanisms influencing sex-specific floral resource use

We analysed two factors that may influence variation in pattern of resource use (i.e. niche breadth and niche overlap) between sexes in hummingbird species: morphological and behavioural traits.

Resource use and morphology

To test the relationship between niche breadth and morphological traits in each sex of hummingbird species, we fitted separate Phylogenetic Generalized Least Squares Models (PGLS) with the total number of pollen morphotypes carried by males or females averaged across species as the response variable. In these models, we included mean trait values of each sex (bill length, bill curvature, wing length and body mass) as predictors. Given the strong positive correlation between wing length and body mass ($r = 0.90$, $p < 0.001$), we performed two models including each trait separately. Hence, we performed a total of four models including three predictors each; examples of these models are in Equations 1 and 2, where *p* is the number of pollen morphotypes carried by males:

$$P_m \sim \text{bill length} + \text{bill curvature} + \text{wing length}, \qquad (1)$$

$$P_m \sim \text{bill length} + \text{bill curvature} + \text{body mass}. \qquad (2)$$

To test the relationship between floral similarity and SD of hummingbird species in traits, we fitted two PGLS with mean niche overlap between sexes of hummingbird species (values were square root transformed for residuals normality) as the response variable and sexual dimorphism in bill length, bill curvature and body mass (or wing length) as predictors. The PGLS models were performed with the *pgls* function in the CAPER R package (Orme et al., 2018).

Resource use and behaviour

We tested the influence of feeding strategy on resource similarity between sexes, by using a phylogenetic one-way ANOVA where niche overlap between sex was the response variable and territoriality was the predictor variable. The analysis was done with the *phyloANOVA* function in the R package PHYTOOLS (Revell, 2012).

3 | RESULTS

Hummingbird individuals across the 31 species carried between 1 and 15 pollen morphotypes with a mean of 4.20 ± 0.09 standard error. We found differences in the total number of pollen morphotypes carried by individuals of different sex and species with significant interaction between these terms, where females overall carried more pollen morphotypes than males (Table 1).

Concerning similarity in resource use, we found that niche overlap between individuals of different sexes was low across species with a mean similarity index of 0.30 ± 0.02 (Figure 1), which was, in turn, lower than female–female overlap within the same species (0.34 ± 0.03, $t = -2.09$, $p = 0.045$). Male–male overlap, however, was not different from the male–female overlap across species (0.28 ± 0.03, $t = 0.73$, $p = 0.468$). After controlling for evolutionary relatedness, we found no relationship between niche breadth of each hummingbird sex (i.e. the total number of pollen morphotypes carried by individuals averaged across species) and morphological traits across the species. On the other hand, there was a negative relationship between sexual dimorphism in bill curvature and niche overlap between the sexes across species no matter if including body mass or wing as measure of body size (Table 2; Figure 2a).

We had 14 territorial species out of the 28 species considered in our phylogenetic one-way ANOVA analysis, where territorial species had higher niche overlap between sexes compared to non-territorial species ($F = 5.82$, $p = 0.026$, Figure 2b).

4 | DISCUSSION

From distinct localities and clades across the hummingbird phylogeny, we found sex-related differences in niche breadth and overlap in floral resource use. Our findings show that females had a broader niche breadth than males and differed from males in the visited plant

TABLE 1 Statistics of the analysis of variance on the generalized linear mixed model to test intraspecific variation in the total number of pollen morphotype carried by male and female individuals from 31 hummingbird species across the Americas. Mean number of pollen morphotypes for females was 4.36 ± 0.12, and for males was 4.01 ± 0.13. Sex, species (see Figure 1) and their interaction were considered as fixed effects, whereas species was also included as random effect along with pollen load identity to account for variation among species. Shown are model estimate (Chisq), degree of freedom and *p* value (only those associated to the fixed factors). All three terms in the model were statistically significant ($p < 0.05$); the species × sex interaction indicates that the effect of the sex covariate on the response depends on the hummingbird species.

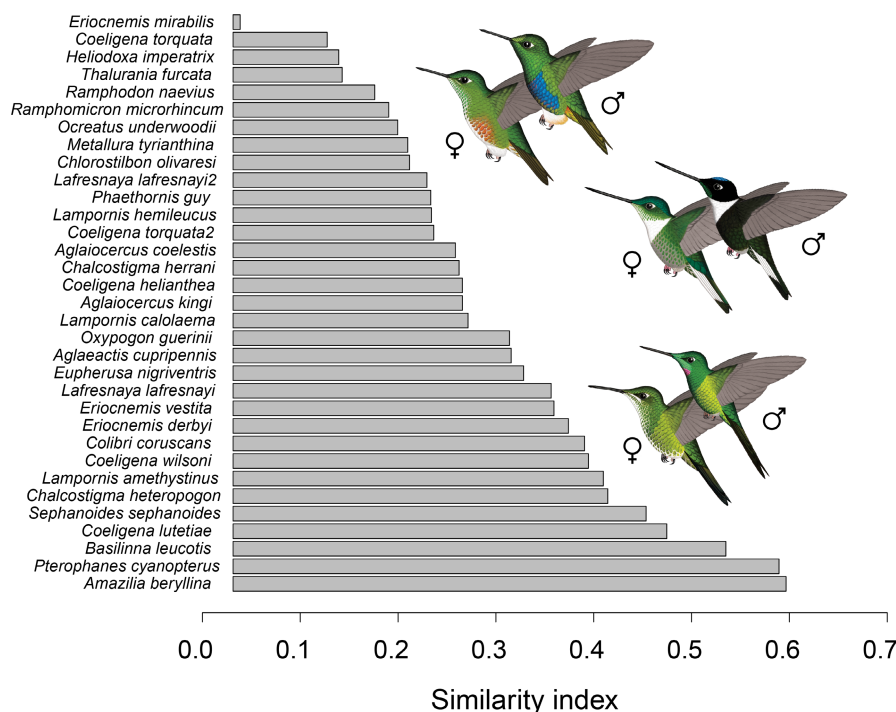| Predictor	Chisq	df	*p*
Sex	6.18	1	0.013
Species	325.46	30	<0.001
Species × sex	44.69	30	0.041

FIGURE 1 Floral resource overlap between males and females of 31 hummingbird species from 13 localities across the Americas quantified by the Morisita's similarity index, where 0 and 1 indicate minimum and maximum floral niche overlap, respectively, that is, maximum and minimum resource partitioning. Two species (*Coeligena torquata* and *Lafresnaya lafresnayi*) occur in two of the studied localities. Illustrations depict female and male of the three species with the most dissimilar resource use between sexes (Morisita's index <0.12): *Eriocnemis mirabilis*, *Coeligena torquata* and (credit: F. Ayerbe-Quiñones, Guía Ilustrada de la Avifauna Colombiana).

TABLE 2 Statistics of the phylogenetic generalized least squares models (PGLS) to test the relationship between niche overlap of male/female individuals and sexual dimorphism (SD) in four morphological traits for 28 hummingbird species across the Americas. Niche overlap is given by the Morisita's similarity index. We show both models including wing chord length and body mass as a body size measurement. Shown are model estimate (β), standard error (*SE*), *t* statistic and *p* value. Statistically significant relationship is highlighted in bold (p<0.05).

Predictor	β	*SE*	*t*	*p*
Model with wing chord length				
Intercept	0.63	0.10	6.32	**<0.001**
SD in bill length	−0.48	0.58	−0.83	0.415
SD in bill curvature	−0.33	0.12	−2.70	**0.012**
SD in wing chord	0.14	0.64	0.22	0.825
Model with body mass				
Intercept	0.68	0.09	7.47	**<0.001**
SD in bill length	−0.75	0.55	−1.36	0.187
SD in bill curvature	−0.30	0.11	−2.64	**0.014**
SD in body mass	0.56	0.29	1.92	0.067

species, which resulted in a high level of resource partitioning between sexes. Furthermore, we found that hummingbird behaviour and morphological traits were related to sex-specific resource use; territorial species and those with less sexual dimorphism in bill curvature showed a higher niche overlap between sexes.

It is not only in hummingbirds that sex influences floral resource use, but also in other animal pollinators. For instance, female bees are often more generalists due to offspring provisioning behaviour, since they need to gather pollen in addition to nectar

(Smith et al., 2019). More diverse pollen loads carried by hawk-moth females may be linked to differences in foraging behaviour, in which males spend more time flying across patches while females spend more time feeding on flowers (Smith et al., 2021). In some hummingbird species, only females engage in parental care, whereas males are segregated on leks, which may contribute to sex differences in resource use (Bleiweiss, 1999; Temeles et al., 2010). In addition, variation in floral niche breadth may also be related to sex-specific foraging behaviour, which is the case of hummingbirds for territorial and social dominance behaviours (Carpenter et al., 1993; Leimberger et al., 2022; Stiles, 1975). Several studies of hummingbirds have found that the defence of flowers is performed mostly or entirely by males in some species, whereas females usually feed at scattered flowers, probably requiring them to forage over larger areas than territorial males (Feinsinger, 1976; Temeles et al., 2000; Wolf et al., 1976). Consequently, foraging activity of males is more restricted in space, which may limit the diversity of plant species they have available within their territories, leading males to have narrower niches than females. Visiting a few, nectar-rich plant species may explain why male hummingbirds had a narrower niche breadth in our study. In contrast, females with wider floral niches may reflect their greater tendency to forage at undefended resources due to their subordinate status relative to males (Carpenter et al., 1993). These results may mirror patterns in resource use at the species level. For example, Borgella Jr. et al. (2001) found that *Phaethornis guy*, a traplining species, had a much greater number of pollen morphotypes than territorial, non-hermit species.

Different patterns of resource use between sexes could be due to local resource competition in communities, similarly as it occurs between species (Chesson, 2000; Noske, 1986). In addition to interference competition among hummingbirds, exploitation
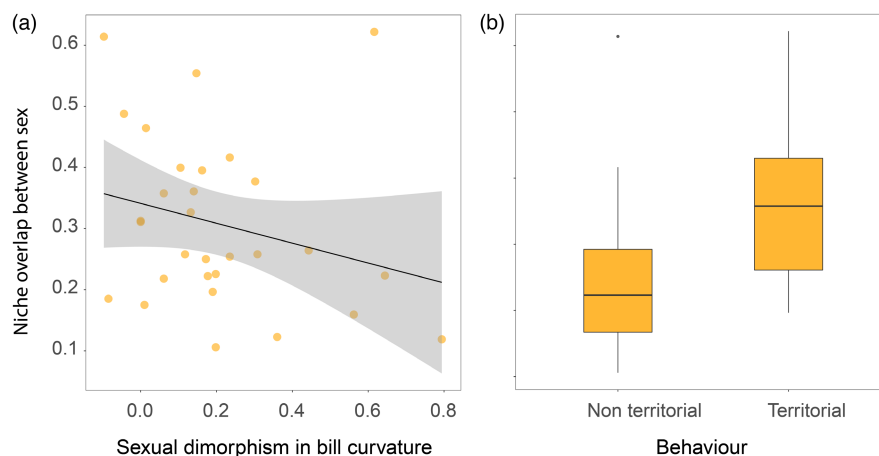
FIGURE 2 Relationship between floral resource use by male/female individuals and (a) morphology and (b) behaviour (territorial vs non-territorial hummingbird species, $n = 14$ each) from 13 localities across the Americas. Similarity was quantified by the Morisita's similarity index, where 0 and 1 indicate minimum and maximum floral niche overlap, respectively, that is, maximum and minimum resource partitioning. Sexual dimorphism was measured with the Lovich–Gibbons ratio where negative values indicate male bias. Each data point represents one hummingbird species at a given locality; two species occurred in two localities. The regression line (with grey 95% confidence intervals) represents the overall fits of the linear mixed-effects model. In the boxplot, the horizontal line represents the median, the boxes indicate the first and third quartiles (Q1 and Q3), the vertical lines indicate the $Q1/Q3 + 1.5$ interquartile ranges of the data, and the black circle indicates an outlier.

competition also can play an important role, especially among non-territorial individuals (Wolf et al., 1976). Through niche partitioning, individuals of different sexes may feed on different plant resources, thus reducing intersexual competition (Shine, 1989; Temeles et al., 2010). We found overall a reduced level of niche overlap between sexes (30% in average across all species) and that females are more dissimilar in the plants visited with respect to males than to other females within species. These findings indicate that resource partitioning by sex is likely to be an important mechanism to reduce intraspecific competition in hummingbird assemblages, especially for females.

Sexual resource partitioning has been associated with sexual dimorphism in some cases (Leimberger et al., 2022; Temeles et al., 2010). Our results reveal that hummingbird species with a high degree of sexual dimorphism in bill curvature had less overlap in the floral resources they used than less dimorphic species. This is consistent with previous work where food resource partitioning has been linked with morphology in some species with sexual dimorphism (e.g. Temeles et al., 2000). Females with more curved bills may be more specific in their resource choice and forage preferably on plant species with corresponding curved flowers, whereas males with less curved bills may forage mostly on plant species with straighter flowers, thereby reducing niche overlap and consequently intersexual competition for floral resources. An alternative interpretation of this observed pattern is that certain morphological differences between the sexes may have evolved as a consequence of sexual selection rather than feeding ecology (Andersson, 1994). For example, in certain hummingbird species, the straighter bill of males compared to that of females has been attributed to the fact that they are used like weapons to compete with other males (Rico-Guevara & Araya-Salas, 2015).

Across species, territorial hummingbirds showed higher resource overlap between sexes than non-territorial ones. This result may reflect that non-territorial hummingbirds meet only infrequently while feeding, and thus show reduced overlap in resource use (Feinsinger, 1976). On the other hand, territorial species associated with resource-rich clumps often comprise dominant territory holders as well as subordinate individuals that act as territorial intruders on the same plant species (Justino et al., 2012; Sazima et al., 1995). Although these behavioural roles are often associated with sexes (Wolf et al., 1976), both sexes are usually linked to the same nectar-rich plant clumps in territorial hummingbird species, which could explain the higher overlap. A narrow niche breadth of males, combined with their territoriality and higher overlap in resource use in territorial species, suggests a more spatially restricted foraging by males nested within the foraging space of females, a pattern which should be investigated in future studies. Moreover, the analyses of other factors that could influence the observed pattern, such as habitat, migratory behaviour and mating display, constitute avenues for new research (Ornelas, 1995).

The here documented differential use of resources by males and females may have a direct effect on plant fitness with important implications for plant reproduction (Leimberger et al., 2022; Maruyama et al., 2016; Temeles et al., 2000). If males and females of the same species differ in their patterns of floral resource use because of distinct foraging behaviours or morphology, they may also differ in their effectiveness as pollinators. For instance, territorial males of hummingbird species may contribute less than females in outcross pollination (Justino et al., 2012; Linhart et al., 1987), whereas non-territorial females, flying greater distances, likely transfer more high-quality outcross pollen (Leimberger et al., 2022; Maruyama et al., 2016).

However, the narrower niche breadth of males compared to females may cause males to deposit relatively higher rates of conspecific pollen (Larsson, 2005), with a trade-off in pollination effectiveness (Smith et al., 2019). Lastly, to the extent that sexes of pollinators differ both in the species of plants they pollinate and in trophic morphology, such differences may contribute to floral diversification (Temeles et al., 2016). Further studies of sex differences in resource use by pollinators are clearly warranted to determine the generality of our findings among different pollinator taxa (e.g. bats, bees, moths, butterflies and other taxa of nectar-feeding birds).

5 | CONCLUSIONS

We provide empirical evidence on substantial differences in patterns of resource use between sex in a set of hummingbird species across the Americas. Our results show that these differences are associated with behavioural and morphological traits. Thus, resource partitioning by sex is likely to be an important mechanism that reduces intersexual competition in hummingbird assemblages. Our findings demonstrate the importance of considering pollinators' resource use at the sex level and highlight the need for further understanding the role of intersexual variation in shaping plant–pollinator and other mutualistic interactions in ecological communities.

AUTHORS' CONTRIBUTIONS

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.h18931zp7 (Maglianesi et al., 2022).

ORCID

María A. Maglianesi https://orcid.org/0000-0002-4053-6956
Pietro K. Maruyama https://orcid.org/0000-0001-5492-2324
Ethan J. Temeles https://orcid.org/0000-0002-8059-1474
Matthias Schleuning https://orcid.org/0000-0001-9426-045X
Thais B. Zanata https://orcid.org/0000-0001-9614-4241
Marlies Sazima https://orcid.org/0000-0002-1017-9281
Oscar H. Marín-Gómez https://orcid.org/0000-0002-0743-8350
Liliana Rosero-Lasprilla https://orcid.org/0000-0002-0163-9231
Mónica B. Ramírez-Burbano https://orcid.org/0000-0002-3810-8119
Ivan Sazima https://orcid.org/0000-0002-0362-1756
Laura E. Nuñez-Rosas https://orcid.org/0000-0001-7705-8110
María del Coro Arizmendi https://orcid.org/0000-0003-4838-5432
Bo Dalsgaard https://orcid.org/0000-0003-2867-2805

REFERENCES

Andersson, M. (1994). *Sexual selection*. Princeton University Press. Retrieved from https://press.princeton.edu/books/paperback/9780691000572/sexual-selection

Beattie, A. J. (1971). A technique for the study of insect-borne pollen. *The Pan-Pacific Entomologist*, *47*, 82. Retrieved from https://digitalcommons.usu.edu/bee_lab_ba/8

Bleiweiss, R. (1998). Relative-rate tests and biological causes of molecular evolution in hummingbirds. *Molecular Biology and Evolution*, *15*, 481–491. https://doi.org/10.1093/oxfordjournals.molbev.a025947

Bleiweiss, R. (1999). Joint effects of feeding and breeding behaviour on trophic dimorphism in hummingbirds. *Proceedings of the Royal Society B: Biological Sciences*, *266*, 2491–2497. https://doi.org/10.1098/rspb.1999.0951

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, *161*, 1–28. https://doi.org/10.1086/343878

Borgella, R., Jr., Snow, A. A., & Gavin, T. A. (2001). Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. *Biotropica*, *33*(1), 90–109. Retrieved from https://www.jstor.org/stable/2663768

Bosch, J., González, A. M., & Navarro, R. A. (2009). Plant-pollinator networks: Adding the pollinator's perspective. *Ecology Letters*, *12*, 409–419. https://doi.org/10.1111/j.1461-0248.2009.01296.x

Buzato, S., Sazima, M., & Sazima, I. (2000). Hummingbird-pollinated floras at three Atlantic forest sites. *Biotropica*, *32*(4b), 824–841. https://doi.org/10.1111/j.1744-7429.2000.tb00621.x

Carpenter, F. L., Hixon, M. A., Paton, D. C., Temeles, E. J., & Russell, R. W. (1991). Sexual differences in resource acquisition by migrant hummingbirds. *Acta XX Congressus Internationalis Ornithologici*, *2*, 1156–1165.

Carpenter, F. L., Hixon, M. A., Temeles, E. J., Russell, R. W., & Paton, D. C. (1993). Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds. *Behavioral Ecology and*

Sociobiology, *33*, 305–312. Retrieved from https://www.jstor.org/stable/4600885

Carscadden, K. A., Emery, N. C., Arnillas, C. A., Cadotte, M. W., Afkhami, M. E., Gravel, D., Livingstone, S. W., & Wiens, J. J. (2020). Niche breadth: Causes and consequences for ecology, evolution, and conservation. *Quarterly Review of Biology*, *95*, 179–214. https://doi.org/10.1086/710388

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2006). Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics*, *62*, 361–371. https://doi.org/10.1111/j.1541-0420.2005.00489.x

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Courtney, S. P., Hill, C. J., & Westerman, A. (1981). Pollen carried for long periods by butterflies. *Oikos*, *38*, 260–263. https://doi.org/10.2307/3544030

Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: Floral specialisation gradients associated with environment and hummingbird size. *Oecologia*, *159*, 757–766. https://doi.org/10.1007/s00442-008-1255-z

Dalsgaard, B., Maruyama, P. K., Sonne, J., Hansen, K., Zanata, T. B., Abrahamczyk, S., Alarcón, R., Araujo, A. C., Araújo, F. P., Buzato, S., Chávez-González, E., Coelho, A. G., Cotton, P. A., Díaz-Valenzuela, R., Dufke, M. F., Enríquez, P. L., Dias Filho, M. M., Fischer, E., Kohler, G., … Martín González, A. M. (2021). The influence of biogeographical and evolutionary histories on morphological trait-matching and resource specialization in mutualistic hummingbird-plant networks. *Functional Ecology*, *35*, 1120–1133. https://doi.org/10.1111/1365-2435.13784

Feinsinger, P. (1976). Organization of a tropical guild of nectarivorous birds. *Ecological Monographs*, *46*, 257–291. https://doi.org/10.2307/1942255

Justino, D. G., Maruyama, P. K., & Oliveira, P. E. (2012). Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *Journal of Ornithology*, *153*, 189–197. https://doi.org/10.1007/s10336-011-0726-x

Kearns, C. A., & Inouye, D. W. (1993). *Techniques for pollination biologists*. University Press of Colorado.

Larsson, M. (2005). Higher pollinator effectiveness by specialist than generalist flower-visitors of unspecialized *Knautia arvensis* (Dipsacaceae). *Oecologia*, *146*, 394–403. https://doi.org/10.1007/s00442-005-0217-y

Leimberger, K. G., Dalsgaard, B., Tobias, J. A., Wolf, C., & Betts, M. G. (2022). The evolution, ecology, and conservation of hummingbirds and their interactions with flowering plants. *Biological Reviews*, *97*, 923–959. https://doi.org/10.1111/brv.12828

Linhart, Y. B., Busby, W. H., Beach, J. H., & Feinsinger, P. (1987). Forager behavior, pollen dispersal, and inbreeding in two species of hummingbird-pollinated plants. *Evolution*, *41*, 679–682. https://doi.org/10.2307/2409272

Lovich, J. E., & Gibbons, J. W. (1992). Review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging*, *56*, 269–281.

Lüdecke, D. (2021). *Package 'performance'. Assessment of Regression Models Performance*. Retrieved from https://rdrr.io/cran/performance/

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant–hummingbird networks in the Neotropics. *Ecology*, *95*, 3325–3334. https://doi.org/10.1890/13-2261.1

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2015). Functional structure and specialization in three tropical plant–hummingbird interaction networks across an elevational gradient in Costa Rica. *Ecography*, *38*, 1119–1128. https://doi.org/10.1111/ecog.01538

Maglianesi, M. A., Maruyama, P. K., Temeles, E. J., Schleuning, M., Zanata, T. B., Sazima, M., Gutiérrez-Zamora, A., Marín-Gómez, O. H., Rosero-Lasprilla, L., Ramírez-Burbano, M. B., Ruffini, A. E., Salamanca-Reyes, J. R., Sazima, I., Nuñez-Rosas, L. E., Arizmendi, M. C. Rahbek, C., & Dalsgaard, B. (2022). Data from: Behavioural and morphological traits influence sex-specific floral resource use by hummingbirds. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.h18931zp7

Maruyama, P. K., Justino, D. G., & Oliveira, P. E. (2016). Does intraspecific behavioural variation of pollinator species influence pollination? A quantitative study with hummingbirds and a neotropical shrub. *Plant Biology*, *18*, 913–919. https://doi.org/10.1111/plb.12492

McGuire, J. A., Witt, C. C., Remsen, J. V., Jr., Corl, A., Rabosky, D. L., Altshuler, D. L., & Dudley, R. (2014). Molecular phylogenetics and the diversification of hummingbirds. *Current Biology*, *24*, 910–916. https://doi.org/10.1016/j.cub.2014.03.016

Morisita, M. (1959). Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science, Kyushu University, Series E (Biol.)*, *3*, 65–80. https://doi.org/10.18960/seitai.11.6_252_4

Ne'eman, G., Shavit, O., Shaltiel, L., & Shmida, A. (2006). Foraging by male and female solitary bees with implications for pollination. *Journal of Insect Behavior*, *19*, 383–401. https://doi.org/10.1007/s10905-006-9030-7

Noske, R. A. (1986). Intersexual niche segregation among three bark-foraging birds of eucalypt forests. *Austral Ecology*, *11*, 255–267. https://doi.org/10.1111/j.1442-9993.1986.tb01396.x

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*, 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). *Caper: Comparative analyses of phylogenetics and evolution in R*. R package version 1.0.1. Retrieved from https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf

Ornelas, J. F. (1995). *Radiation in the genus Amazilia: A comparative approach to understanding the diversification of hummingbirds*. A dissertation submitted to the Faculty of the Department of ecology and evolutionary biology. The University of Arizona.

Ortiz-Crespo, F. I. A. (1972). New method to separate immature and adult hummingbirds. *The Auk*, *89*, 851–857. https://doi.org/10.2307/4084114

Ramírez-Burbano, M. B., Stiles, F. G., González, C., Amorim, F. W., Dalsgaard, B., & Maruyama, P. K. (2017). The role of the endemic and critically endangered Colorful Puffleg *Eriocnemis mirabilis* in plant-hummingbird networks of the Colombian Andes. *Biotropica*, *49*, 555–564. https://doi.org/10.1111/btp.12442

Rech, A. R., Dalsgaard, B., Sandel, B., Sonne, J., Svenning, J. C., Holmes, N., & Ollerton, J. (2016). The macroecology of animal versus wind pollination: Ecological factors are more important than historical climate stability. *Plant Ecology and Diversity*, *9*, 253–262. https://doi.org/10.1080/17550874.2016.1207722

Revell, L. J. (2012). phytools: An *R* package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rico-Guevara, A., & Araya-Salas, M. (2015). Bills as daggers? A test for sexually dimorphic weapons in a lekking hummingbird. *Behavioral Ecology*, *26*, 21–29. Retrieved from https://academic.oup.com/beheco/article/26/1/21/2262689

Ritchie, A. D., Ruppel, R., & Jha, S. (2016). Generalist behavior describes pollen foraging for perceived oligolectic and polylectic bees. *Environmental Entomology*, *45*, 909–919. https://doi.org/10.1093/ee/nvw032

Rodger, J. G., Bennett, J. M., Razanajatovo, M., Knight, T. M., van Kleunen, M., Ashman, T.-L., Steets, J. A., Hui, C., Arceo-Gómez, G.,

Burd, M., Burkle, L. A., Burns, J. H., Durka, W., Freitas, L., Kemp, J. E., Li, J., Pauw, A., Vamosi, J. C., Wolowski, M., … Ellis, A. G. (2021). Widespread vulnerability of flowering plant seed production to pollinator declines. *Science Advances*, *7*, eabd3524. https://doi.org/10.1126/sciadv.abd3524

Rodrigues, R. C., Hasui, É., Camara Assis, J., Castro Pena, J. C., Muylaert, R. L., Rodrigues Tonetti, V., Martello, F., Regolin, A. L., Vieira da Costa, T. V., Pichorim, M., Carrano, E., Esteves Lopes, E., Ferreira de Vasconcelos, M., Suertegaray Fontana, C., Langeloh Roos, A., Gonçalves, F., Banks-Leite, C., Cavarzere, V., Amorim Efe, M., … Ribeiro, M. C. (2019). Atlantic bird traits: A data set of bird morphological traits from the Atlantic forests of South America. *Ecology*, *100*, e02647. https://doi.org/10.1002/ecy.2647

Rodríguez-Flores, C. I., & Arizmendi Arriaga, M. C. (2016). The dynamics of hummingbird dominance and foraging strategies during the winter season in a highland community in Western Mexico. *Journal of Zoology*, *299*, 262–274. https://doi.org/10.1111/jzo.12360

Rombaut, L. M., Capp, E. J., Hughes, E. C., Varley, Z. K., Beckerman, A. P., Cooper, N., & Thomas, G. H. (2022). The evolution of the traplining pollinator role in hummingbirds: Specialization is not an evolutionary dead end. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1967), 20212484. https://doi.org/10.1098/rspb.2021.2484

Roswell, M., Dushoff, J., & Winfree, R. (2019). Male and female bees show large differences in floral preference. *PLoS ONE*, *14*(4), e0214909. https://doi.org/10.1371/journal.pone.0214909

Roubik, D. W., & Moreno, J. E. (1991). *Pollen and spores of Barro Colorado Island*. Missouri Botanical Garden Press.

Sazima, I., Buzato, S., & Sazima, M. (1995). The saw-billed hermit, *Ramphodon naevius*, and its flowers in southeastern Brazil. *Journal für Ornithologie*, *136*(2), 195–206. https://doi.org/10.1007/BF01651241

Schuchmann K.-L. (1999). Family Trochilidae. In J. del Hoyo, A. Elliott, & J. Sargatal (Eds.), *Handbook of the birds of the world, vol. 5. Barn owls to hummingbirds, vol 5. Barn owls to hummingbirds* (pp. 468–680), Lynx. Retrieved from https://academic.oup.com/auk/article/117/2/532/5561620

Selander, R. K. (1966). Sexual dimorphism and differential niche utilization in birds. *Condor*, *68*, 113–151. https://doi.org/10.2307/1365712

Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *The Quarterly Review of Biology*, *64*, 419–461. https://doi.org/10.1086/416458

Smith, G. P., Bronstein, J. L., & Papaj, D. R. (2019). Sex differences in pollinator behavior: Patterns across species and consequences for the mutualism. *Journal of Animal Ecology*, *88*, 971–985. https://doi.org/10.1111/1365-2656.12988

Smith, G. P., Davidowitz, G., Alarcón, R., Papaj, D. R., & Bronstein, J. L. (2021). Sex differences in the foraging behavior of a generalist hawkmoth. *Insect Science*, *29*, 304–314. https://doi.org/10.1111/1744-7917.12926

Souza, C. S., Maruyama, P. K., Santos, K. C., Varassin, I. G., Gross, C. L., & Araujo, A. C. (2021). Plant-centred sampling estimates higher beta diversity of interactions than pollinator-based sampling across habitats. *New Phytologist*, *230*, 2501–2512. https://doi.org/10.1111/nph.17334

Stiles, F. G. (1975). Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology*, *56*, 285–301. https://doi.org/10.2307/1934961

Stiles, F. G. (1996). A new species of Emerald hummingbird (Trochilidae, *Chlorostilbon*) from the Sierra de Chiribiquete, Southeastern Colombia, with a review of the *C. mellisugus* complex. *Wilson Bulletin*, *108*, 1–27. Retrieved from https://www.jstor.org/stable/4163634

Stiles, F. G. (2004). Phylogenetic constraints upon morphological and ecological adaptation in hummingbirds (Trochilidae): Why are there no hermits in the paramo? *Ornitología Neotropical*, *15*, 191–198. Retrieved from https://sora.unm.edu/sites/default/files/journals/on/v015s/p0191-p0198.pdf

Stiles, F. G., & Boesman, P. (2020). Empress brilliant (*Heliodoxa imperatrix*). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & E. de Juana (Eds.), *Handbook of the birds of the world alive*. Lynx Edicions. https://doi.org/10.2173/bow.empbri1.01

Temeles, E. J., & Kress, W. J. (2003). Adaptation in a plant-hummingbird association. *Science*, *300*, 630–633. https://doi.org/10.1126/science.1080003

Temeles, E. J., Liang, J., Levey, M. C., & Fan, Y.-L. (2019). Floral isolation and pollination in two hummingbird-pollinated plants: The roles of exploitation barriers and pollinator competition. *Evolutionary Ecology*, *33*, 481–497. https://doi.org/10.1007/s10682-019-09992-1

Temeles, E. J., Miller, J. S., & Rifkin, J. L. (2010). Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): A role for ecological causation. *Philosophical Transactions of the Royal Society*, *365*, 1053–1063. https://doi.org/10.1098/rstb.2009.0284

Temeles, E. J., Newman, J. T., Newman, J. H., Cho, S. Y., Mazzotta, A. R., & Kress, W. J. (2016). Pollinator competition as a driver of floral divergence: An experimental test. *PLoS ONE*, *11*(1), e0146431. https://doi.org/10.1371/journal.pone.0146431

Temeles, E. J., Pan, I. L., Brennan, J. L., & Horwitt, J. N. (2000). Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, *289*, 441–443. https://doi.org/10.1126/science.289.5478.441

Temeles, E. J., Rah, Y. J., Andicoechea, J., Byanova, K. L., Giller, G. S., Stolk, S. B., & Kress, W. J. (2013). Pollinator-mediated selection in a specialized hummingbird–*Heliconia* system in the Eastern Caribbean. *Journal of Evolutionary Biology*, *26*(2), 347–356. https://doi.org/10.1111/jeb.12053

Wolf, L. L., Stiles, F. G., & Hainsworth, F. R. (1976). Ecological organization of a tropical, highland hummingbird community. *Journal of Animal Ecology*, *45*, 349–379. https://doi.org/10.2307/3879

Zhang, J. (2016). Package 'spaa'. Version 0.2.2, Species association analysis. Retrieved from https://cran.r-project.org/web/packages/spaa/spaa.pdf

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