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Ecological mechanisms explaining interactions within plant–hummingbird networks: morphological matching increases towards lower latitudes

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Interactions between species are influenced by different ecological mechanisms, such as morphological matching, phenological overlap and species abundances. How these mechanisms explain interaction frequencies across environmental gradients remains poorly understood. Consequently, we also know little about the mechanisms that drive the geographical patterns in network structure, such as complementary specialization and modularity. Here, we use data on morphologies, phenologies and abundances to explain interaction frequencies between hummingbirds and plants at a large geographical scale. For 24 quantitative networks sampled throughout the Americas, we found that the tendency of species to interact with morphologically matching partners contributed to specialized and modular network structures. Morphological matching best explained interaction frequencies in networks found closer to the equator and in areas with low-temperature seasonality. When comparing the three ecological mechanisms within networks, we found that both morphological matching and phenological overlap generally outperformed abundances in the explanation of interaction frequencies. Together, these findings provide insights into the ecological mechanisms that underlie geographical patterns in resource specialization. Notably, our results highlight morphological constraints on interactions as a potential explanation for increasing resource specialization towards lower latitudes.

1. Introduction

The mechanisms that underlie the structure of interaction networks are a frequently investigated topic in community ecology [1–3]. For mutualistic networks, these mechanisms often comprise morphologies, phenologies and abundances, which all may influence the likelihood for species to interact [1,2,4–8]. Knowledge about which mechanisms determine interaction frequencies has implications for interpreting the drivers of resource specialization [9–12]. However, to date, only studies of single networks have addressed the relevance of morphologies, phenologies and abundances for explaining interaction frequencies between mutualistic partners [6,13–17]. Consequently, we still lack knowledge about how these ecological mechanisms may cause variability in resource specialization at large geographical scales.

Morphological matching is a frequently discussed determinant of mutualistic interactions [1,5,14,17,18]. In plant–pollinator communities, morphological matching often represents the similarity in length and shape between a flower's corolla and a pollinator's feeding apparatus [4,19,20].

Matching between these traits may lead to specialized network structures by limiting the species' access and preferences to a subset of mutualistic partners. Phenological overlap between interacting species is a mechanism that limits the available time for interactions to occur [2,21]. Seasonal turnover in community composition may result in some mutualists having none or limited co-occurrence, and consequently, few possibilities to interact [2,21,22]. By constraining interaction probabilities, phenological mismatch is expected to increase a network's level of specialization. Lastly, the local variation in species abundances may influence the random chance for partners to interact [2,3,23,24]. Specifically, under random encounters, the likelihood of interactions would be highest between abundant species [1,5]. Interaction frequencies that reflect abundances would thereby predict a high overlap between the resource use of species, resulting in a low degree of network specialization [16,18,23].

The degree to which morphological matching, phenological overlap and abundance explain interaction frequencies may depend on the environmental setting. The classical literature on diversity gradients suggests that the warm, humid and less seasonal climates of the tropics make natural selection more influenced by biotic interactions in comparison to temperate regions [25–28]. In turn, tropical climates could lead to a greater variety of morphological (co)adaptations and greater resource specialization [10,25–28]. Accordingly, studies have found plant–hummingbird networks to become increasingly specialized towards the equator [10] and to coincide with greater diversity of hummingbird functional traits [8]. On this basis, one may hypothesize that the increase in resource specialization towards tropical regions coincides with an increased tendency of species to interact with morphological matching partners.

In contrast with morphological matching, to the best of our knowledge, there are no clear hypotheses on how phenological constraints on interactions vary across environmental gradients. Plant species in seasonal tropical regions usually have synchronized flowering periods during the rainy season, whereas phenologies are more staggered across the year in less seasonal regions [29]. If the phenologies of pollinator species follow the same pattern, mutualistic partners in seasonal environments should generally experience few phenological mismatches. In that case, we would expect phenologies to impose fewer constraints on interaction frequencies in seasonal environments than in less seasonal environments. If both morphological and phenological constraints on interactions are absent, we expect that species would interact randomly according to their relative abundances [18]. Thus, abundance should best explain interaction frequencies in cold, dry and seasonal environments [3,24].

In this study, we use morphological matching, phenological overlap and abundance to explain plant–hummingbird interaction frequencies at a large geographical scale. We focus our investigation on these three mechanisms, as they have previously been shown to influence interaction frequencies within plant–pollinator networks [2,5,6,14,16]. First, we investigate how the mechanisms may influence network-derived measures of resource specialization, and second, how their explanation of interaction frequencies varies across environmental gradients (see electronic supplementary material, S1 for a conceptual overview of our main hypotheses). To do so, we analysed a unique dataset consisting of 24 plant–hummingbird interaction networks distributed from

central Mexico to southern Brazil (20°N–30°S). For each plant and hummingbird species within these networks, we have additional information on phenologies, morphologies and abundances. We expected morphological matching and phenological overlap to be more relevant for explaining interaction frequencies in regions with low annual climate seasonality and high annual mean temperature and precipitation [8,10–12,25,26,30]. It has been proposed that specialized coadaptations increase in tropical mountains due to the suitable preconditions for species to track changing climates [11,31,32]. Thus, we expected that morphological matching and phenological overlap would impose more constraints on interaction frequencies in topographically complex areas in the tropics. Oppositely, we expected abundance to have a decreased influence on interaction frequencies in specialized networks sampled in areas with high topographical complexity, high mean annual temperature (MAT), high mean annual precipitation (MAP) and low climate seasonality [16,18].

2. Methods

(a) Networks, abundance, phenology and species traits

We compiled data on 24 quantitative interaction networks collected throughout the Americas, in areas mostly or entirely covered with native vegetation (electronic supplementary material, table S2; updated dataset from [24]). The networks comprise 106 hummingbird species, 31% of all described hummingbird species in the world according to the IOC World Bird List v. 7.3 [33] (electronic supplementary material, S3) and 450 plant species belonging to 57 plant families (see electronic supplementary material, S4 and S5a for additional details on sampling).

The abundance of plant species was measured as the number of flowers produced per species in each community throughout the entire sampling period. Flowers were counted in plots or transects estimated regularly throughout the sampling period. The abundance of hummingbirds within sites was measured in the field by counting the number of visual and aural detections of individuals across transects ($n = 12$ networks) or point counts ($n = 4$ networks), or the number of individuals captured by mist-netting ($n = 8$ networks; electronic supplementary material, S5a). Because the abundance sampling protocols were not standardized among networks, we treated the data as relative abundance (i.e. for all species, we calculate their abundance as the proportion of the total number of individuals within a given community). Still, we note that mist nets may be especially efficient for surveying elusive understorey species, such as traplining hummingbirds, whereas transects and point counts may be better at surveying species at higher vegetation strata [34]. We recognize that the caveat inherent in using different sampling schemes across networks may influence the outcome of our analyses. However, as we used relative abundances to model interaction frequencies within networks (not between networks), we believe that the different sampling schemes had a minimal influence on our results.

The phenology of each plant and hummingbird species in each network was determined as the presence–absence of, respectively, open flowers and individuals at each sampling period (usually months). Flower morphology was characterized by the effective corolla length (sensu [35]), measured as the distance from the nectary to the corolla opening. The effective corolla length reflects the minimum length of mouthparts required for pollinators to access the nectar legitimately. Hummingbird bill morphology was measured as the length of the exposed culmen from captured hummingbird individuals (see electronic supplementary material, S5b for further details on sampling).

(b) Climate and topography data

All climate variables were extracted as means within a 10 km radius around the location of each network. Climate variables were downloaded from the WorldClim database in 30 arc second resolution (v. 2.0; http://www.worldclim.org) [36]. We included MAT and MAP, as well as seasonality in temperature (annual standard deviation in monthly mean temperature; TS) and precipitation (annual coefficient of variation in monthly precipitation; PS). Topographical data were retrieved from SRTM 90 m DEM v. 4 (http://srtm.csi.cgiar.org). Within a 10 km zone around each network's location, we determined topographical range as the difference between the maximum and minimum elevation.

(c) Defining models for morphological matching, phenological overlap and abundance

We used the model for morphological matching presented in Sonne et al. [37], which assumes pairwise interaction frequencies to decrease proportionally to the standardized difference in length between the hummingbird's bill and the plant's floral corolla. In this framework, a hummingbird with the longest bill has the highest probability of interacting with the longest flowers, while the shortest-billed hummingbirds have the highest probability of interacting with the shortest flowers. We calculated pairwise morphological matching for each hummingbird i and plant j within each network k. We first standardized the hummingbird's bill length and the plant's corolla length to zero mean and unit variance within networks and then calculated the Euclidean distance between each pair of species (M_{ijk}; see electronic supplementary material, S6a for details).

In the phenological overlap model, pairwise interaction frequencies increase proportionally to the number of sampling periods (usually months) in which hummingbird i and flowering plant species j co-occurred in network k (P_{ijk}; [2]). Random species encounters should generate pairwise interaction frequencies that are proportional to the partners' relative abundances [2]. Therefore, the pairwise interaction probabilities in network k are calculated by multiplying the relative abundances of hummingbird i and plant j (A_{ijk}). Prior to statistical modelling, M_{ijk}, P_{ijk} and A_{ijk} were scaled to zero mean and unit variance.

(d) Linking ecological mechanisms with species' interaction frequencies

We used morphological matching (M), phenological overlap (P) and species abundances (A) to model interaction frequencies individually for each hummingbird and plant species. The modelling procedure was modified from Weinstein & Graham [38] as our data do not allow the estimation of interaction detectability. While the following model is described for hummingbirds, the same method was also applied to the plants.

The model assumes that the pairwise interaction frequency (Z) for each hummingbird species i in the network k follow a Poisson distribution with mean λ_{ik}, with the log link function of λ_{ik} predicted by the covariates: M_{ijk}, P_{ijk} and A_{ijk}. Model parameters were estimated using Markov chain Monte Carlo. From there, we extracted posterior distributions of the standardized coefficients: β_{ik}^{M}, β_{ik}^{P} and β_{ik}^{A}. As values of M are distances measuring morphological mismatch, a more negative β_{ik}^{M} value indicates greater ability of morphological matching to explain interaction frequencies. Conversely, more positive β_{ik}^{A} and β_{ik}^{P} values indicate better explanations of interaction frequencies by abundances and phenological overlap. These parameters were considered significant if less than 5% of their estimated posterior distribution overlapped with zero [38] (see electronic supplementary material, S6b for details on the model specification).

For each network, we determined the proportion of species with interaction frequencies significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*) and abundance (*Imp.A*). We used these proportions as measures of each mechanisms' ability to explain the hummingbirds' interaction frequencies. We also calculated the *relative* proportion of species by dividing *Imp.M*, *Imp.P* and *Imp.A* by their within-network sum. Each relative proportion represents the degree to which a given ecological mechanism explains interaction frequencies relative to the remaining two mechanisms. We present the relative proportion values for each network as kernel density distributions [39]. Here, the contribution of each network is weighted according to the richness of hummingbirds.

(e) Linking ecological mechanisms with network structure

We investigated whether morphological matching, phenological overlap and abundances influenced two measures of network structure that reflect resource specialization. First, we calculated *complementary specialization* (H_2'), which quantifies the partitioning of interactions relative to their availability (i.e. network marginal sums [40]); it ranges between zero and one, with higher values indicating higher partitioning of interactions between species in the community. Second, we calculated *weighted modularity* (*Q*), which describes a network's tendency to comprise subgroups of interacting species [9]. Modularity is high when species mostly interact with partners from their respective modules. Modularity differs from specialization by quantifying the partitioning of interactions between groups of species rather than between individual species. Modularity was calculated using the DIRTLPA+ algorithm [41]. Due to the stochastic nature of this optimization algorithm, we repeated the analysis 10 times for each network and kept the highest *Q*-value [9].

As empirical networks vary in species richness and sampling intensity, the observed values of network structure, such as specialization and modularity, may not be directly comparable [42]. To overcome this issue, we used null models to calculate the extent to which the observed network metric deviates from a null expectation. To compute the null model, we used Patefield's algorithm [43], and then subtracted the observed values of network structure from the mean values obtained from 1000 randomizations (Δ transformation; see electronic supplementary material, S7 for evaluation of alternative null models). While we report the null model-corrected values for modularity [40,44], we report complementary specialization without the null model correction because this index is already subject to a correction for the marginal totals of the network. Nevertheless, we also ran analyses with the Δ-transformed version as reported in the electronic supplementary material. All network analyses were conducted in R using the 'bipartite' package v. 2.11 [45].

We fitted linear models for complementary specialization and Δmodularity using the proportion of species within networks whose interaction frequencies were significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*) and abundance (*Imp.A*). As additional explanatory variables, we included the network size, defined as the total richness of hummingbird and plant species, and a measure of sampling intensity, calculated as the square root number of interaction events divided by the total richness of hummingbird and plant species [46,47]. We also tested for the potential confounding effect of spatial autocorrelation in the linear model residuals using the R package *ncf* [48]. To do this, we fitted Moran's *I* correlograms with 500 km distance classes and a truncation distance of 5000 km. Positive spatial autocorrelation was non-significant in all models, suggesting that spatial autocorrelation had no influence on our results (electronic supplementary material, S8).
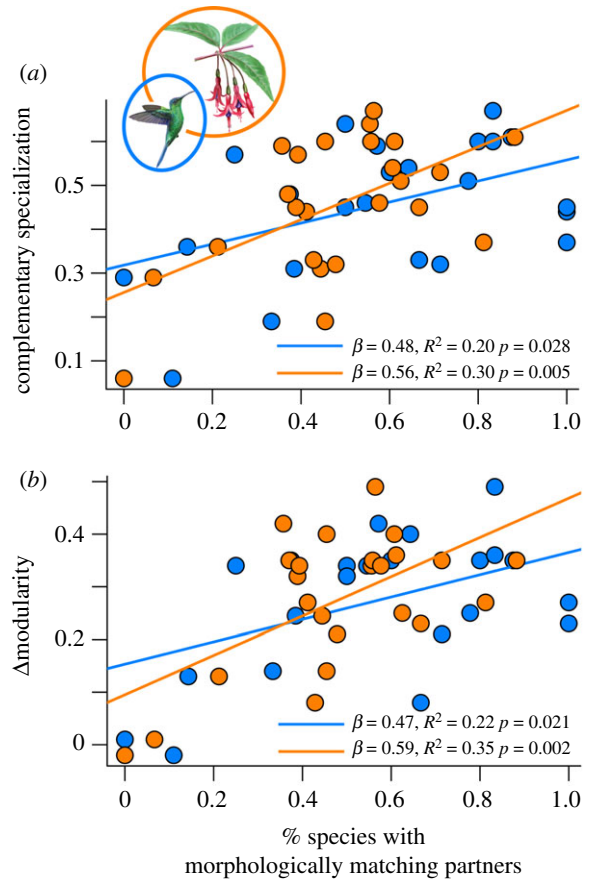

Figure 1. Linear models depicting the relationship between resource specialization and species' morphological matching. Resource specialization was measured as (*a*) complementary specialization and (*b*) Δmodularity. Δ indicates a correction by the *Patefield* null model (see Methods). The *x*-axis shows the proportion of species within networks that exhibited a significant tendency to interact with morphologically matching partners. The linear models were run separately for hummingbirds (blue) and plants (orange). Drawings show *Thalurania glaucopis* and *Fuchsia regia* (credit: Pedro Lorenzo). (Online version in colour.)

(f) Geographical patterns in ecological mechanisms' explanation of interaction frequencies

Separately for hummingbirds and plants, we fitted logistic models that regressed absolute latitude against *Imp.M*, *Imp.P*, *Imp.A*. To explore the effect of species richness and sampling, we ran supplementary models that included network size (total richness of hummingbird and plant species) and sampling intensity as explanatory variables (electronic supplementary material, S9). We noted that networks were not evenly sampled across the Americas, with the majority of networks occurring either in Central America/the Andes or along the Brazilian Atlantic coast (electronic supplementary material, S9). To assess if the latitudinal trend was caused by differences between these two biogeographic regions, we regressed absolute latitude against *Imp.M*, *Imp.P* and *Imp.A* while including a dummy variable stating whether networks were located east or west of 60° longitude (i.e. occurred in Central America/Andes or along the Brazilian Atlantic coast).

Finally, we used logistic models to regress *Imp.M*, *Imp.P* and *Imp.A* against network size and the following environmental variables: topographic range, MAT, MAP, temperature seasonality and precipitation seasonality. All possible model combinations were fitted and then evaluated using the Akaike information criterion with correction for small sample sizes (AIC_C). Usually, we found no single best model for the response variables, as ΔAIC_C was less than or equal to 2.0 between the model with the lowest AIC_C and several other models [49]. Therefore, we averaged the estimates from all possible model combinations weighted
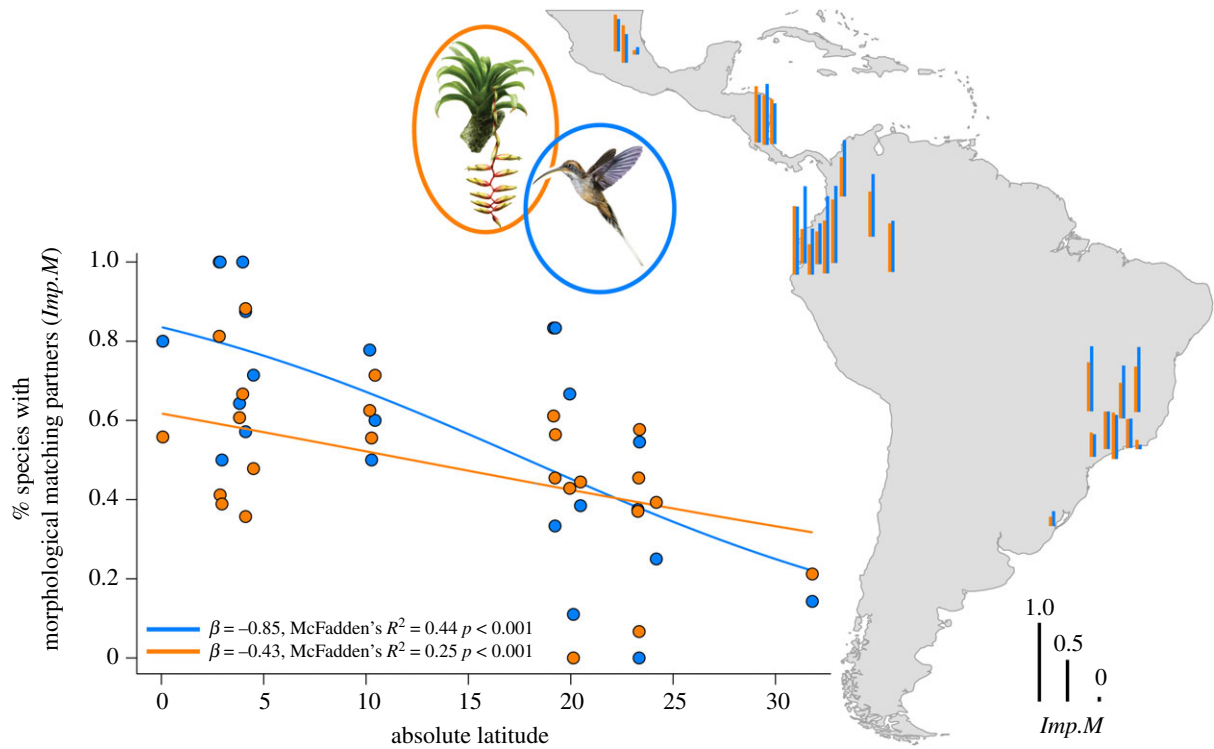
Figure 2. Geographical distribution of the 24 plant–hummingbird networks. The height of the bars reflects the proportion of hummingbird species (blue) and plant species (orange) within networks that showed significant tendencies to interact with morphologically matching partners (*Imp.M*). Some points on the map have been slightly separated to improve visual clarity. The scatterplot shows the negative relationship between *Imp.M* and absolute latitude, modelled by logistic regression. Drawings show *Phaethornis eurynome* and *Vriesea simplex* (credit: Pedro Lorenzo). (Online version in colour.)

by Akaike weights (w_i). Additionally, we present the summed Akaike weights for all models containing each explanatory variable, Σw_i[49]. Model selection and model averaging were conducted using the 'MuMIn' package in R [50]. The goodness of fit for linear models was evaluated by McFadden's R^2 [51].

3. Results

The proportion of species interacting with morphologically matching partners (*Imp.M*) correlated positively with both metrics of resource specialization (*complementary specialization* and *modularity*; figure 1). These correlations remained significant when accounting for the potential confounding influence of sampling intensity and network size (electronic supplementary material, S10).

The tendency of species to interact with morphologically matching partners increased towards tropical latitudes (figure 2). This trend remained after accounting for the clustering in network sampling between the Central America/Andes and Eastern Brazil, and when including network size and sampling intensity as additional explanatory variables (electronic supplementary material, S9). For hummingbirds, we found phenological overlap to have a stronger influence on interaction frequencies towards tropical latitudes, while species' abundances better explained interaction frequencies towards higher latitudes, when including region (i.e. Central America/Andes versus Eastern Brazil), network size and sampling intensity as explanatory variables (electronic supplementary material, S9). For plants, however, phenological overlap better explained interaction frequencies within networks from Central America/Andes than within networks from Eastern Brazil (electronic supplementary material, S9).

For both plants and hummingbirds, the explanation of interaction frequencies by morphological matching correlated

negatively with temperature seasonality, which was the only predictor variable that remained present in all best-fitting models (ΔAICc < 2.0; table 1). Phenological overlap best explained the hummingbirds' interaction frequencies in areas with low-temperature seasonality (table 1). For plants, phenological overlap best explained interaction frequencies in areas with high topographic range, MAT, temperature seasonality and low species richness (table 1). For hummingbirds, abundance best explained interaction frequencies in areas with high seasonality in precipitation and low seasonality in temperature (table 1). Abundance was best explaining the plants' interaction frequencies in areas with high topographic range, MAT and temperature seasonality (table 1).

Overall, we found that abundance generally had a weaker influence on interaction frequencies than morphological matching and phenological overlap (figure 3).

4. Discussion

Across plant–hummingbird networks, we show that resource specialization increases with the tendency of species to interact with morphologically matching partners (figure 1). Moreover, we found that morphological matching is a more prominent driver of species' interaction frequencies when the networks are located closer to the equator (figure 2). Together, these results highlight that the relevance of traits for explaining interaction frequencies is context-dependent [7]. In some communities, traits matter more than in others, and this variability may contribute to the latitudinal pattern in resource specialization. In addition to morphologies, we found phenologies to be important for determining interaction frequencies, more so than the local variability in abundance (figure 3). Based on our findings, we speculate that partitioning of ecological niches, by morphological matching and phenological overlap,

Table 1. Model selection and averaging results of logistic models fitted on different ecological mechanisms' ability to explain interaction frequencies within networks ($n = 24$). The analyses were repeated individually for hummingbirds and plants. The response variables comprised the proportion of species within networks whose interaction frequencies were significantly explained by morphological matching (*Imp.M*), phenological overlap (*Imp.P*) and abundance (*Imp.A*). Explanatory variables include *network size*: total richness of hummingbirds and plants within networks; *topographic range*: maximum elevation subtracted from minimum elevation; *mean annual temperature*; *MAP*; *temperature seasonality*; and *precipitation seasonality*. Goodness of fit is assessed by McFadden's R^2. Σw_i, Sum of 'Akaike weights' from all models including the predictor variable. MAM, standardized coefficients of variables present in all minimum adequate models (ΔAICc < 2). N_{MAM}, number of minimum adequate models. AVM, standardized coefficients of the averaged model across all models including a focal predictor variable.

	Imp.M			*Imp.P*			*Imp.A*		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM
hummingbirds									
network size	0.44	0.28		0.19	0.03		0.24	0.17	
topographic range	0.20	0.08		0.21	0.12		0.35	0.27	
mean annual temperature	0.34	−0.24		0.31	−0.22		0.25	0.11	
mean annual precipitation	0.21	−0.03		0.62	−0.39		0.58	0.38	
temperature seasonality	0.99	−0.82	−0.82	0.99	−0.77	−0.76	0.69	−0.52	−0.49
precipitation seasonality	0.21	−0.07		0.30	−0.20		0.97	0.66	0.58
McFadden R^2			0.40			0.34			0.10
adj. McFadden R^2			0.32			0.25			0.02
N_{MAM}			4			3			3
plants									
network size	0.29	0.09		0.92	−0.27	−0.28	0.99	0.36	0.35
topographic range	0.20	−0.04		1.00	0.80	0.78	1.00	−1.06	−1.07
mean annual temperature	0.25	0.07		0.99	0.57	0.52	0.99	−0.78	−0.78
mean annual precipitation	0.40	0.17		0.28	−0.27		0.17	−0.19	
temperature seasonality	1.00	−0.40	−0.40	0.97	0.37	0.40	0.91	−0.36	−0.40
precipitation seasonality	0.20	0.04		0.15	0.06		0.48	−0.25	
McFadden R^2			0.22			0.24			0.40
adj. McFadden R^2			0.15			0.17			0.31
N_{MAM}			4			1			2

could be important for maintaining coexistence within diverse communities of interacting species.

The fact that morphological matching best explained interaction frequencies closer to the equator is consistent with the classical view of tropical environments as favourable to biotic specialization, either through coevolutionary adaptations or ecological fitting [10,25,52,53]. Still, the idea that biotic specialization increases towards the tropics has remained a subject of debate, as empirical studies have presented idiosyncratic results [10,46,47,54,55]. Previous work on our hummingbird–plant networks showed that network-derived resource specialization increases towards tropical latitudes [10], and coincides with high diversity of hummingbird traits [8]. Our study goes beyond previous macroecological analyses of network structure [8,10,11] and targets some potential ecological mechanisms that may constrain the likelihood for partners to interact. We recognize the caveat inherent to the geographical distribution of our sampling localities (figure 2), and that expanding the sampling to cover a wider latitudinal gradient would be important to strengthen our conclusions. Yet, the results presented here bring us closer to a mechanistic understanding of how morphological traits may influence the variability in resource specialization across environmental gradients.

Beyond the latitudinal patterns, we also found that morphological matching best explained interaction frequencies in areas with low-temperature seasonality (table 1). Annual temperature stability is one of the most important characteristics of tropical climates [56]. The lower seasonality of tropical regions causes resources to be present throughout the year, which may lay a foundation for plants and pollinators to develop specialized associations [11,25,26,57]. Moreover, theory suggests competition to be more influential on community structure in the absence of environmental filters, as within the tropics [27,30,57]. Thus, we speculate that interspecific competition within guilds together with diffuse mutualistic coadaptations may contribute to the high degree of resource specialization within the tropical regions [8,15,58,59]. Similar to morphological matching, phenological overlap had a stronger influence on hummingbird's interactions in areas with low-temperature seasonality (table 1). This result supports our hypothesis that seasonal climates cause more synchronized flowering periods among plant species in comparison to aseasonal climates. When plants synchronize their flowering, each pollinator species may overall experience fewer phenological mismatches with their mutualistic partners. For the plants, however, the same association pointed in the opposite direction:
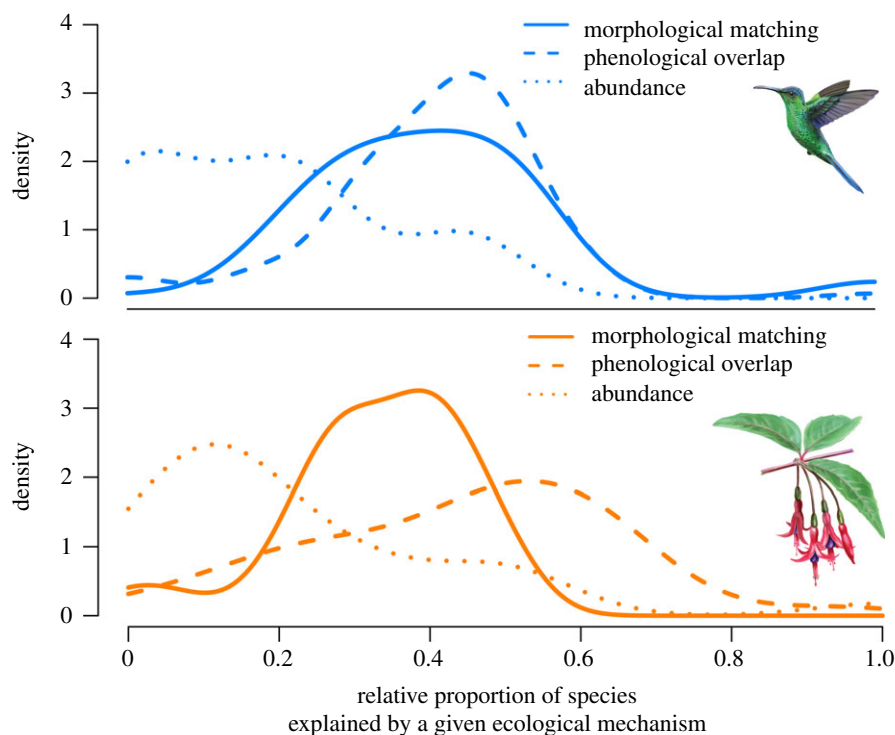
Figure 3. Kernel density distributions depicting the relative contribution of morphological matching, phenological overlap and abundance to the explanation of species' interaction frequencies. The x-axis shows the proportion of hummingbirds (blue) and plants (orange) within networks whose interaction frequencies are significantly explained by morphological matching, phenological overlap and abundance, respectively. Each of these values was divided by their within-network sum, thereby obtaining a *relative* proportion of species. Relative proportion values higher than 0.50 indicate that a particular ecological mechanism was more effective at explaining interaction frequencies than the two remaining mechanisms combined within a given network. Drawings by Pedro Lorenzo. (Online version in colour.)

phenological overlap had a stronger influence on interactions in areas with a high temperature seasonality (table 1). This result may be driven by hummingbirds with migratory behaviour, which are more common in seasonal regions. Hummingbird migrations could impose higher seasonal turnover in species composition, thereby causing higher phenological constraints to the plants' interactions. Regardless of the underlying explanation, the idiosyncratic results between hummingbirds and plants highlight that the environmental conditions that cause seasonal species turnover may depend on the ecological guild. Contrarily to morphological matching and phenological overlap, our results do not support the idea that abundance is a general explanation for why some interactions occur more frequently than others. Thus, although abundant hummingbirds may be more generalized in their floral preferences [24], our result suggests that abundant species do not necessarily have the most frequent interactions with abundant partners. Taken together, although abundance matters to a lesser extent, we have identified phenologies and morphological matching as key determinants of species' interaction frequencies.

The most challenging aspect of documenting morphological matching in plant–hummingbird networks is the fact that hummingbirds can extend their tongue to access the flowers' nectar. As such, the absolute difference between bill length and flower depth is not an accurate representation of the actual morphological mismatch. Our model for morphological matching builds on the assumption that hummingbirds with the relatively longest bills should prefer flowers with the longest corollas. Thereby, the model anticipates morphological matching to affect the hummingbirds' floral preferences without making specific assumptions about how much their tongues can be extended. The model also implies that long-

billed hummingbirds should interact less with short flowers [13]. The ecological explanation for this may be twofold. First, long-billed hummingbirds could minimize competition with short-billed species by preferentially using the flowers with the longest corollas [20]. Second, flowers with short corollas typically have low nectar volume, which could make them unprofitable for long-billed hummingbird [20,60]. Therefore, both interspecific competition between hummingbirds and variability in the flowers' nectar reward may also explain why morphological matching contributes to a high degree of resource specialization [35,60].

When compared with other avian pollination systems, hummingbirds and plants have the most specialized morphologies and the highest level of resource specialization [20,61,62]. Moreover, pollination networks are usually more specialized than seed dispersal networks, which is another common form of plant–bird mutualism [63]. In plant–frugivorous bird communities, network-derived specialization has previously been shown to increase towards temperate latitudes [47], but dietary specialization (i.e. the proportion of obligate frugivores) increases towards tropical latitudes [46]. As such, one may obtain opposing results depending on the scale at which resource specialization is measured. While only some fruit-eating birds are specialized frugivores, all hummingbirds rely mostly on nectar as a food resource. Hence, plant–hummingbird networks should be a suitable system to investigate morphological matching. Although many orders of insect pollinators have specialized adaptations to nectar extraction, they are also found collecting other floral resources [64]. In bees, for instance, tongue-lengths may affect floral preferences during nectar-gathering, but flowers with inaccessible nectar may still receive visits when bees are collecting pollen [64]. Plants and hawkmoths exhibit some

highly specialized coadaptations, and this is probably the closest analogue to a system in which morphological matching is crucial for determining interaction frequencies [65].

The mechanisms underlying the structure and organization of ecological communities have remained poorly understood at the large geographical scale. Using plant–hummingbird networks distributed across the Americas, we have identified morphological matching as a potential key driver of geographical patterns in resource specialization. Notably, closer to the equator, species tended to show stronger preferences for mutualistic partners with morphologically matching traits. Thus, our findings support the hypothesis that trait-mediated resource specialization increases towards lower latitudes.

Data accessibility. Field data from study sites (i.e. species interactions, morphologies, phenologies and abundances) are archived at the Dryad Digital Repository: https://doi.org/10.5061/dryad.dncjsxkw2 [66].

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collected the data. J.V.-B., P.K.M., J.S., B.I.S., A.M.M.G. and B.D. jointly compiled the data. J.V.-B., J.S., B.O., B.I.S. and P.K.M. performed the analyses. B.O. and M.Sc. advertised on the analyses. J.V.-B., J.S., P.K.M., M.Sa., M.Sc. and B.D. wrote the manuscript. All authors contributed to the final version of the manuscript.

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