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Title:

Ecological mechanisms explaining interactions within plant-hummingbird networks

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Abstract

In mutualistic networks, interactions between species are constrained by an array of ecological mechanisms, such as morphological matching, phenological overlap and species' abundances. It remains poorly understood how these mechanisms change in ability to explain interaction frequencies across environmental gradients. Consequently, there is also limited knowledge on how the mechanisms affect geographical patterns in network structure, such as resource specialization. Here, we investigated the degree to which morphological matching, phenological overlap and species' abundances explain interactions between hummingbirds and plants. For 24 quantitative networks sampled across the Americas, we found an increased tendency for species to interact with morphologically matching partners towards low latitudes and areas with low temperature seasonality. Moreover, species' morphologies and phenologies generally performed better than abundance at explaining interaction frequencies. However, only the tendency for species to interact with morphological matching partners correlated positively with network structure, i.e. resource specialization. These findings reveal insights into the ecological mechanisms that underlie geographical patterns in network structure. Our results suggest that morphological constraints on interactions could be an important explanation for increasing resource specialization towards tropical regions.

Keywords: resource specialization, modularity, morphological matching, phenology, abundances, pollination.

Introduction

Understanding the mechanisms that underlie the structure of interaction networks is a growing topic in community ecology [1-3]. For mutualistic networks, these mechanisms mainly comprise species' morphologies, phenologies and abundances, which all may constrain the likelihood for partners to interact [1, 2, 4-8]. Knowledge about which mechanisms determine interaction frequencies in different environmental contexts has implications for how we interpret patterns of resource specialization, measured as the partitioning of interspecific interactions [9-12]. However, to date, only studies on single networks have addressed the relevance of ecological mechanisms, such as morphologies, phenologies and abundances, for explaining interaction frequencies between mutualistic partners [6, 13-17]. Consequently, we still lack knowledge about how the ecological mechanisms may affect network structure under different environmental conditions.

Morphological matching is a frequently discussed constraint to mutualistic interactions [1, 5, 14, 17, 18]. In plant-pollinator communities, morphological matching may comprise the similarity in length and shape between the flower's corolla and the pollinator's feeding apparatus [4, 19, 20]. Matching between these traits may lead to specialized network structures by making resources accessible or energetically favorable to only a subset of the community [ESM1a; modified from 1]. Phenological overlap between species is another mechanism, which constraints the available time for species to interact [2, 21]. Seasonal turnover in community composition may result in some species having none or limited seasonal co-occurrence (ESM1b), and could make some interactions impossible [2, 21, 22]. As for morphological matching, the constraints on species interactions imposed by phenological mismatch could manifest as resource specialization by partitioning of interactions between partners with limited seasonal co-occurrence. Lastly, the local variation in species abundances may influence the random chance for partners to interact [2, 3, 23, 24]. Specifically, under random partner encounters, the likelihood of interactions would be highest between abundant partners [ESM1c; 1, 5]. Interaction frequencies reflecting abundances should imply high overlap between the species' resource use, and thus, result in low degree of network specialization [16, 18, 23].

The ability of morphological matching, phenological overlap and abundance to explain interaction frequencies may depend on the environmental setting. The classical literature on diversity gradients suggests that the benignity and predictability of tropical climates make natural selection more influenced by biotic interactions in comparison to temperate regions [25-28]. In turn, this could lead to greater variety of morphological (co)adaptations and greater resource specialization towards the equator [10, 25-28]. In accordance with this expectation, studies have found plant-hummingbird networks to become increasingly specialized towards tropical climates [10], and coincide with greater diversity of hummingbird functional traits [8]. On this basis, one may hypothesize that the increase in resource specialization towards tropical regions result from morphological matching becoming a stronger constraint to species' interaction frequencies (ESM2).

Opposite to morphological matching, to the best of our knowledge, there exist 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 non-seasonal regions [29]. The synchronized phenologies between plant species in seasonal environments could reduce the chance of phenological mismatching with potential pollinators. In that case, we would expect phenological overlap to impose fewer constrains on interactions in seasonal environments than in non-seasonal environments. Finally, we expect abundances to be the dominating constraint on interactions when there is high overlap between the species' foraging niches, i.e. when the network structure is less specialized [3, 24].

In this study, we address the relevance of different ecological mechanisms for explaining plant-pollinator interactions. As ecological mechanisms, we focus on species' morphological matching, phenological overlap and abundance, as these have previously been shown to explain plant-pollinator interaction frequencies [2, 5, 6, 14, 16]. First, we investigate how these mechanisms may influence network-derived measures of resource specialization, and second, how they change in ability to explain interaction frequencies across environmental gradients. To do so, we analyzed a unique dataset consisting of 24 plant-hummingbird interaction networks distributed from Central Mexico to Southern Brazil (20ºN-30ºS). For each hummingbird and plant species in these networks we have additional information on phenologies, morphologies and relative abundances. We expected morphological matching and phenological overlap to impose more constraints on interactions frequencies towards the equator. Thus, we expected to find morphological matching and phenological overlap 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]. Because specialized co-adaptations have been proposed to increase in tropical mountains due to the suitable preconditions for species to track changing climates [11, 31, 32], we also expected morphological matching and phenological overlap to impose more constraints on interactions in topographical complex areas. On the other hand, variability in species' abundance should show opposing patterns and best explain interactions in generalized networks where species have overlapping resource niches [24]. Thus, we expected a decreased influence of abundance on interactions frequencies in specialized networks sampled in areas with topographical range, mean annual temperature, mean annual precipitation and low climate seasonality [16, 18]. Finally, we combine the results to discuss how ecological constraints on interactions may shape patterns in resource specialization across large-scale environmental gradients.

Methods

(a) Networks, abundance, phenology and species traits.

We compiled data on 24 quantitative interaction networks collected throughout the Americas, in areas mostly or completely covered with native vegetation [Table ESM3; 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; ESM4a], and 449 plant species belonging to 57 plant families (ESM4b, see ESM5a for additional details on sampling).

The relative 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 relative abundance of hummingbirds within sites was measured in the field by counting the number of visual and aural detections of individuals across transects (n=13 networks) or point counts (n=4 networks), or the number of individuals captured by mist netting (n=7; ESM5a). Differences in the methodology to estimate relative abundances are unlikely to influence our results because (i) there is no significant latitudinal bias in which sampling method that has been used (ESM5b) and (ii) abundance data is not compared between networks but used for modelling interaction frequencies within networks.

Flower morphology was characterized by the effective corolla length [sensu 34], 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 legitimately access the nectar. For each species in each network, seasonal flowering phenology was determined as the presence-absence of open flowers at each period of sampling (usually months).

Bill morphology was measured mainly as the length of the exposed culmen from captured hummingbird individuals (ESM5c). As for the plants, hummingbird phenology was determined as the presence-absence of species per sampling period (usually months).

(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 [35; v 2.0; http://www.worldclim.org]. We included mean annual temperature (MAT) and precipitation (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 90m DEM Version 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 within the 10 km buffer zone.

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

We used the model for morphological matching recently presented in by Sonne *et al.* [36], 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 calculated the Euclidean distance between species pairs ($\boldsymbol{M_{ijk}}$; see ESM6a for details).

In the phenological overlap model, pairwise interaction frequencies within each network were assumed to be proportional to the number of sampling periods (usually months) in which hummingbird *i* and flowering plant species *j* co-occurred over the study period [$\boldsymbol{P_{ijk}}$; 2]. Within a network, 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 ($\boldsymbol{A}_{ijk}$). According to this model, networks should be dominated by interactions between the most common species.

(d) Linking ecological mechanisms with species' interaction frequencies

We used morphological matching ($\boldsymbol{M}$), phenological overlap ($\boldsymbol{P}$) and species' abundances ($\boldsymbol{A}$) to model interaction frequencies individually for each hummingbird and plant species. The modelling procedure was modified from Weinstein & Graham [37] as our data does not allow the estimation of interaction detectability. The following model is described for hummingbirds, but the same method was applied to the plants.

The model assumes that the pairwise interaction frequencies (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 $(\boldsymbol{M}, \boldsymbol{A}, \boldsymbol{P})_{ijk}$. Model parameters were estimated using Markov chain Monte Carlo (MCMC). Then, we extracted posterior distributions of the standardized coefficient parameters (β^{M}_{ik}, β^{A}_{ik}, and β^{P}_{ik}). As values of $\boldsymbol{M}$ are distances measuring morphological mismatch; a more negative β^{M}_{ik} value indicates greater ability of morphological matching to explain interaction frequencies. Oppositely, more positive β^{A}_{ik} and β^{P}_{ik} values indicate greater ability of abundances and phenological overlap to explain interaction frequencies. These parameters were considered significant if 95% of their estimated posterior distribution did not overlap with zero [37; see ESM6b 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*), respectively. 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. The relative proportions value represents the degree to which a given ecological mechanism perform in explaining interaction frequencies relative to the remaining two mechanisms. We present relative proportions values for each network as kernel density distributions [38]. 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 were manifested in two measures of network structure reflecting resource specialization: First, *Complementary specialization* (H_2'), which quantifies the partitioning of interactions relative to their availability [i.e. network marginal sums; 39]; 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 the tendency that networks comprise subgroups of interacting species [9]. Modularity is high when species interact frequently with species within their module and less frequently with species outside their module. 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 [40] using $10e^7$ steps. 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 [41]. 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 [42], and using this, we subtracted observed values of network structure from the mean values obtained from 1000 randomizations (Δ-transformation; See ESM8 for evaluation of alternative null models). While we report the null model corrected values for modularity [39, 43], 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 supplementary material. All network analyses were conducted in R using the 'bipartite' package v. 2.11 [44].

We fitted linear models for complementary specialization and ΔWeighted Modularity using the proportion of species within networks having interactions frequencies 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 total richness of hummingbird and plant species, and a measure of sampling intensity, which was calculated as the square root number of interaction events divided by the total richness of hummingbird and plant species [45, 46]. In addition, we tested for the potential confounding effect of spatial autocorrelation in the linear model residuals using the R package *ncf* [47]. 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 (ESM7).

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

Separately for hummingbirds and plants, we fitted logistic models regressing absolute latitude against *Imp.M, Imp.P, Imp.A*. To explore the effect of species richness and sampling, we ran supplementary models including network size (total richness of hummingbird and plant species) and sampling intensity as explanatory variables (ESM9). We noticed that networks were not evenly sampled across the Americas, with the majority of networks occurring either in Central

America/Andes or along the Brazilian Atlantic coast (ESM9). To assess if the latitudinal trend was caused by differences between these two biogeographical 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 environmental variables: Topographic range, mean annual temperature and precipitation, seasonality in temperature and precipitation. 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 ≤ 2.0 between the model with lowest AIC_C and several other models [48]. Therefore, we averaged the estimates from all possible model combinations weighted by Akaike weights (w_i). We additionally present the summed Akaike weights for all models containing each explanatory variable, Σw_i [48]. Model selection and model averaging were conducted using the 'MuMIn' package in R [49]. The goodness of fit for linear models was evaluated by McFadden's R^2 [50].

Results

The tendency for species to interact with morphologically matching partners (*Imp.M*) correlated positively with network structure (both *complementary specialization and modularity;* Figure 1). These correlations remained significant when accounting for the potential confounding influence of sampling intensity and network size (ESM10). Within networks, we found that abundance generally had weaker influence on interactions frequencies than morphological matching and phenological overlap (Figure 2). Uniquely for plants, we found phenological overlap to be slightly better at explaining interaction frequencies than morphological matching.

The tendency in species to interact with morphologically matching partners increased towards tropical latitudes (Figure 3). 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 (ESM 9). Only for hummingbirds, we found phenological overlap to have a stronger influence on interactions towards tropical latitudes (ESM9). For plants, however, phenological overlap was better at explaining interactions within Central America/Andes networks than within networks from the eastern Brazil (ESM9). For hummingbirds, species' abundances were better explaining interaction frequencies towards higher latitudes, when including longitude (Central America/Andes vs. eastern Brazil), network size and sampling intensity as explanatory variables (ESM9).

For both plants and hummingbirds, the morphological matching's ability to explain interaction frequencies 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 was better explaining the hummingbirds' interaction frequencies in areas with low seasonality in temperature and mean annual precipitation (Table 1). Opposite for plants, phenological overlap explained interaction frequencies in areas with high topographic range, mean annual temperature, temperature seasonality, and low species richness (Table 1). For hummingbirds, abundances were better at explaining interaction frequencies in areas with high seasonality in precipitation and low seasonality in precipitation (Table 1). Abundance explained the plants' interactions mostly in areas with high topographic range, mean annual temperature and temperature seasonality (Table 1).

Discussion

The partitioning of interactions within plant-pollinator networks have commonly been used to measure resource specialization [9-12, 43], although the underlying ecological mechanisms have remained poorly understood (ESM2). For plant-hummingbird networks across the Americas, we found that resource specialization associated with species' tendency to interact with morphologically matching partners (Figure 1). This result implies that morphologies vary in ability to explain species' interaction frequencies across networks [7]. Thereby, our results suggest that varying degrees of morphological matching between interacting species may have implications for the geographical patterns in resource specialization.

For both plants and hummingbirds, morphologies and phenologies were generally better than abundances at explaining interaction frequencies (Figure 2). We interpret this finding as species may interact frequently with rare partners as long as there is long seasonal co-occurrence and a good morphological match. This could suggest that differences in species' ecological niches, i.e. manifested as morphological matching, could be important for maintaining species coexistence in diverse ecological communities. It was recently shown that hummingbird species were more likely generalized in their floral preferences because they were abundant, rather than abundant because they were generalized [24]. Based on our analyses, which focus on explaining pairwise interactions, we interpret that abundant species may be overall generalized in their floral preferences, but the majority of their interactions may not necessarily be with the most abundant partners. We also noticed that phenological matching slightly exceeded morphological matching in ability to explain the plants' interactions (Figure 2) but not the hummingbirds' interactions (ESM11). This could be related to plants generally having short phenologies whereas hummingbird phenologies are more variable in lengths. Thereby, hummingbird phenologies may add more variability to the plants' interaction probabilities than *vice versa*.

The tendency in species to interact with morphologically matching partners increased towards the equator (Figure 3). This result coincides with the idea that tropical environments favor biotic specialization through co-evolutionary adaptations or ecological fitting between species [10, 25, 51, 52]. The expectation that biotic specialization increases towards the tropics has remained debatable as empirical studies have presented idiosyncratic results [10, 45, 46, 53, 54]. Studies on plant-hummingbird networks have documented a latitudinal increase in resource specialization towards tropical regions [10]. Using a larger version of the present network dataset, Maruyama *et al.* [8] showed that geographical patterns in resource specialization were related to environmental conditions as well as hummingbird trait diversity. Our study goes beyond macroecological analyses of network structure [8, 10, 11], and targets the ecological mechanisms that may constrain the likelihood for partners to interact across a large spatial scale.

Morphological matching were better explaining interaction frequencies in areas with low temperature seasonality (Table 1). Annual temperature stability is one of the most important characteristics of tropical climates [55]. The lower seasonality of tropical regions results in the presence of resources throughout the year, which is likely to lay the foundation for plants and pollinators to develop specialized associations [11, 25, 26, 56]. Moreover, theory suggests competition to be a more influential determinant of community structure in the absence of environmental filters, as within the aseasonal tropics [27, 30, 56]. Thus, we speculate that interspecific competition together with diffuse mutualistic coadaptations may explain the high degree of resource specialization within the tropical regions [8, 15, 57, 58]. Similar to morphological matching, phenological overlap had a stronger influence on hummingbird's interactions in areas with low temperature seasonality (Table 1). This result coincides with our hypothesis that synchrony in the plants' flowering periods towards more seasonal environments imply fewer possibilities for phenological mismatches with pollinators. For the plants, however, the same association pointed in opposite direction (Table 1). Such idiosyncratic results could mean that the relationship between environmental conditions and phenological constraints on interactions is differing between guilds. One would therefore need to formulate guild-specific hypotheses on how phenologies distribute in relation to environmental cues and biotic interactions.

In a comparison to other plant-avian pollination systems, hummingbirds and plants have the most specialized morphologies and highest level of resource specialization [20, 59, 60]. Moreover, pollination networks have shown to be more specialized than seed dispersal networks, which is another common mode of plant-bird mutualism [61]. For this reason, we anticipate plant-hummingbird interactions to be particularly suitable for detecting morphological matching. Probably the closest comparable system is plant-hawkmoth networks in which morphological matching has previously been shown to constrain interaction frequencies [62]. The challenging aspect of documenting morphological matching in plant-hummingbird networks is the fact that hummingbirds can extent their tongue to access the flowers' nectar. For this reason, the absolute difference between bill length and flower depth is not a representation of the true morphological mismatch. Our model for morphological matching builds on the assumption that hummingbirds with the relative longest bills should prefer flowers with longest corollas. Thereby, we anticipated morphological matching to have implication for the hummingbird's foraging preferences without making specific assumptions about how far 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 exploiting the flowers with longest corollas [20]. Second, flowers with short corollas typically have less rewarding nectar, which could make them less profitable for long-billed hummingbirds [20, 63]. Therefore, both the competition between hummingbirds and variability in the flowers' nectar reward may explain why morphological matching manifests as high degree of resource specialization [34, 63].

The mechanisms underlying the structure and organization of ecological communities have been studied since the foundation of ecology as a scientific discipline. Using plant-hummingbird networks distributed across the Americas, we have identified morphological matching as a candidate explanation for determining geographical patterns in resource specialization. The tendency in species to have more morphological matching partners closer to the equator suggests that morphological constrains on interactions frequencies varies across environmental gradients. The causal link between environmental variables and morphological matching's constraint on interaction frequencies, however, remains to be determined.

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Tables

Table 1. Model selection and averaging results of logistic models fitted on different ecological mechanisms’ ability to explaining interactions frequencies within networks (n =24). The analyses were repeated individually for hummingbirds and plants. The response variables comprise the proportion of species within networks having interactions frequencies significantly explained by each of the three ecological mechanisms, i.e. 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: max elevation subtracted from min elevation; *MAT*: Mean Annual Temperature; *MAP*: Mean Annual Precipitation; *TS*: Temperature Seasonality; *PS:* Precipitation Seasonality. Goodness of fit is assessed by McFadden's R^2. Σw_i: Sum of ‘Akaike weights’ over 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.

Hummingbirds	***Imp.M***			***Imp.P***			***Imp.A***		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM
Network size	0.20	0.07		0.23	-0.14		0.24	0.17	
Topographic range	0.21	0.08		0.20	0.06		0.35	0.27	
Mean annual temperature	0.26	-0.17		0.33	-0.27		0.25	0.11	
Mean annual precipitation	0.21	0.04		0.73	-0.46	-0.45	0.58	0.38	
Temperature seasonality	1.00	-0.80	-0.83	1.00	-0.79	-0.86	0.69	-0.52	-0.49
Precipitation seasonality	0.24	-0.13		0.29	-0.20		0.97	0.66	0.58
McFadden R^2			0.37			0.55			0.10
Adj. McFadden R^2			0.30			0.40			0.02
N_{MAM}			2			2			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

Figures

Figure 1. Linear models depicting the relationship between network structure and species' morphological matching. Network structure was measured by A. complementary specialization, B. modularity. Δ indicates a correction by the *Patefield* null model (see methods). The x-axis show the

proportion of species within networks, which exhibited a significant tendency to interact with morphologically matching partners. The linear models were repeated individually for hummingbirds (blue) and plants (orange). Drawings by Pedro Lorenzo.

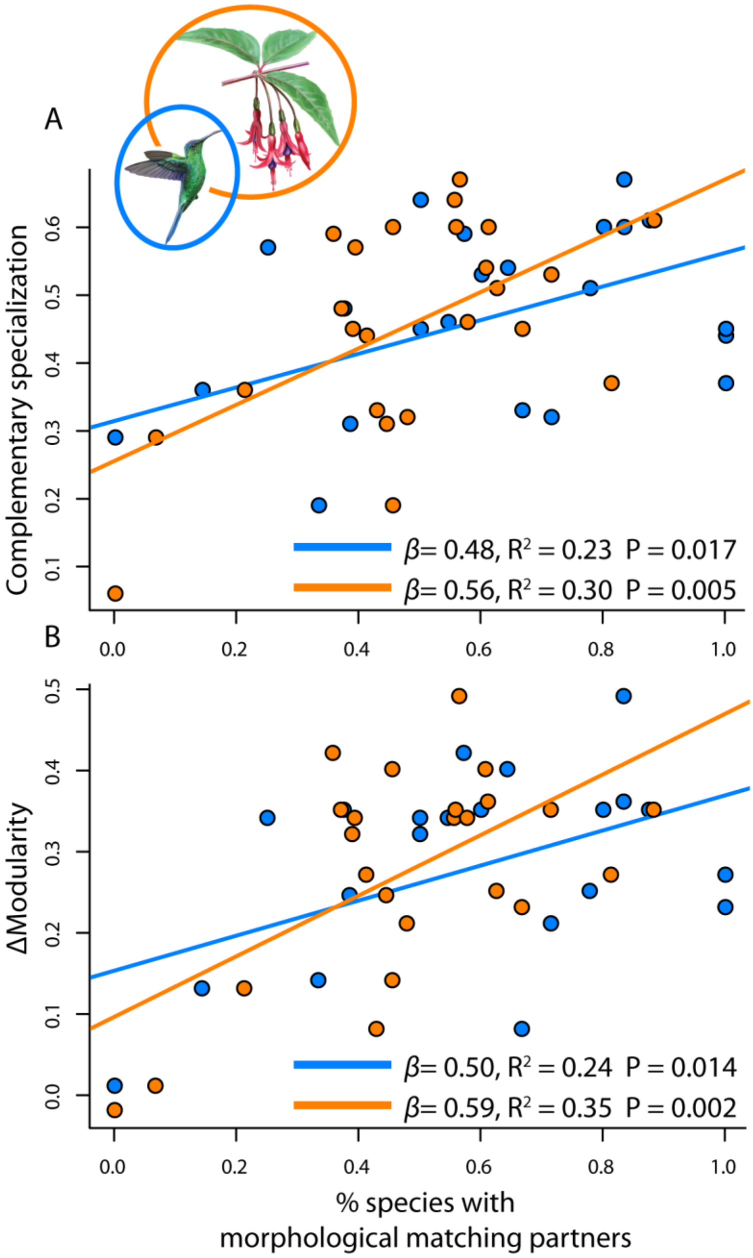


Figure 2. Kernel density distributions depicting the relative contribution of morphological matching, phenological overlap and abundance to the explanation of species' interaction frequencies. The x-axis shows the proportion of hummingbirds (blue) and plants (orange) within

networks having interactions frequencies significantly explained by morphological matching, phenological overlap and abundance respectively. Each of these values were divided by their within-network sum, thereby obtaining a *relative* proportion of species. Relative proportion values higher than 0.50 indicate that a focal ecological mechanism, within a given network, was more effectively explain interaction frequencies than the two remaining ones combined. Drawings by Pedro Lorenzo.

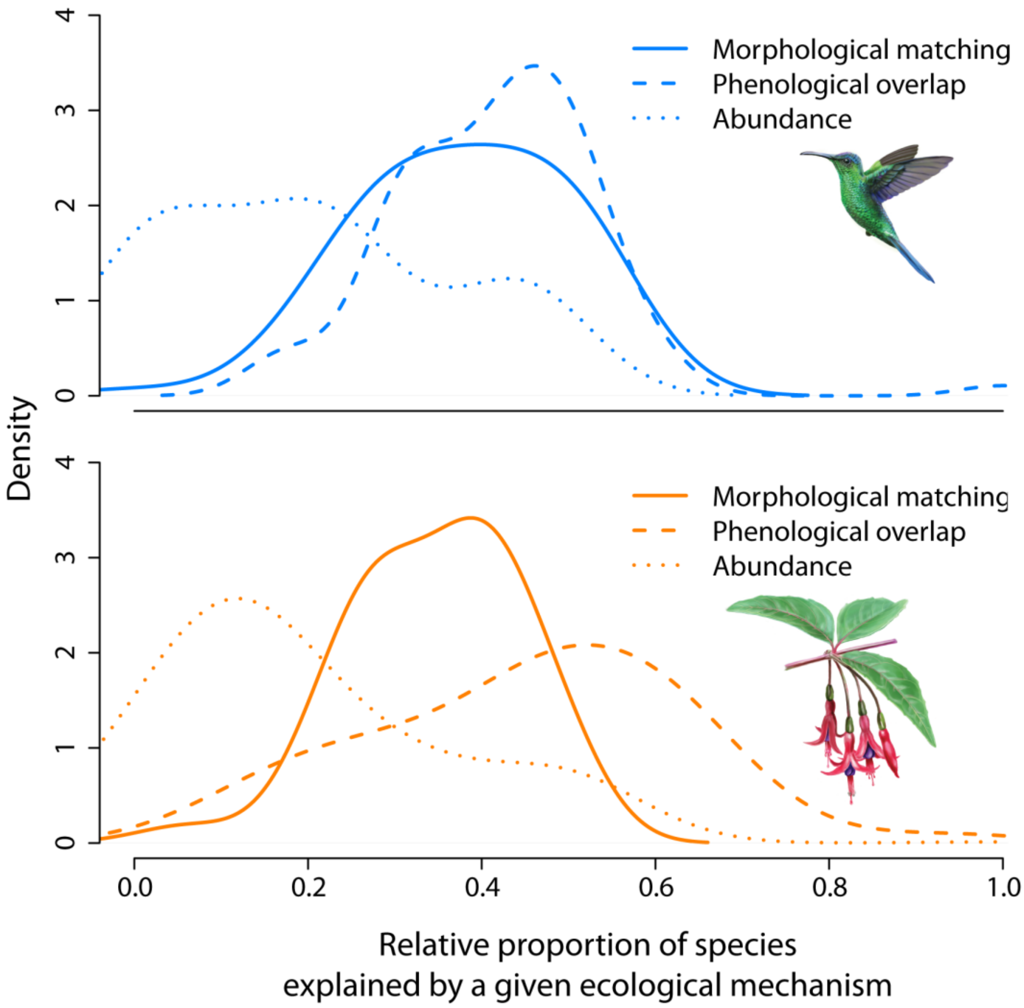
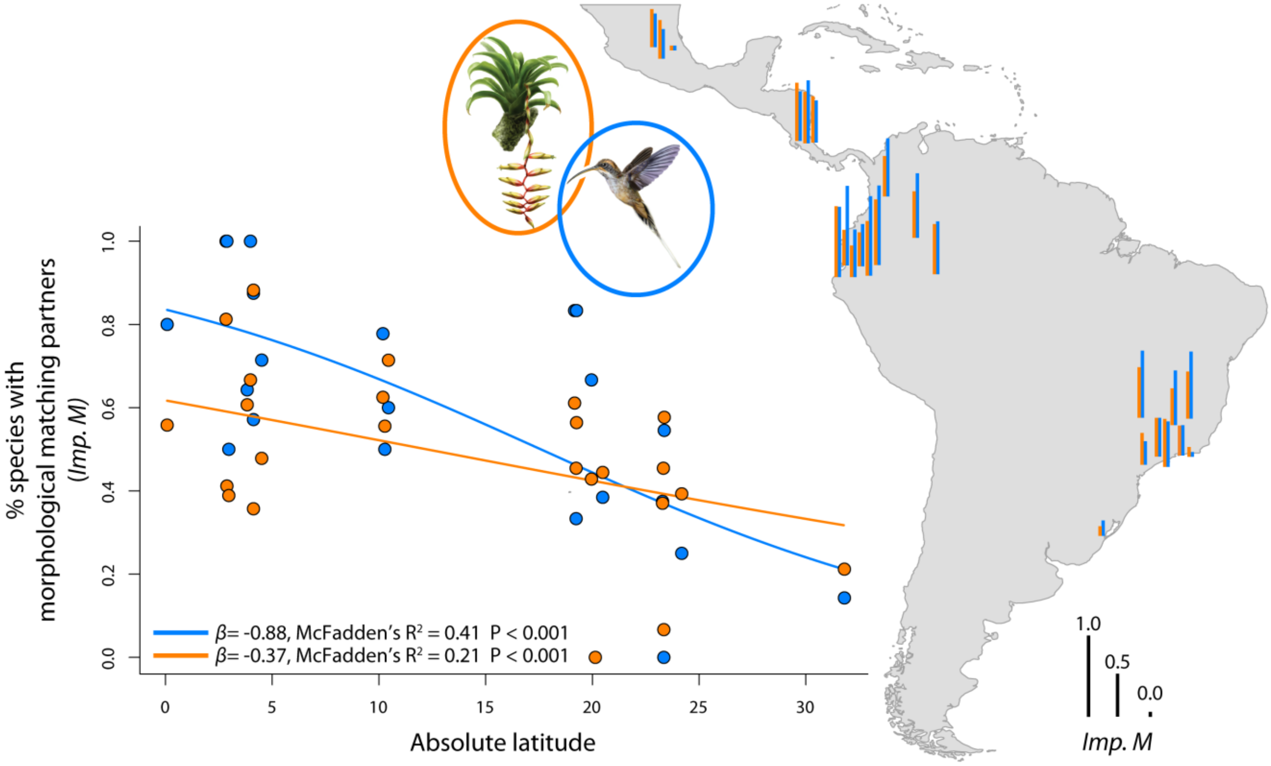


Figure 3. Geographical distribution of the 24 plant-hummingbird networks. Height of the bars on the map shows the proportion of hummingbird species (blue) and plant species (orange) within networks, which exhibited a significant tendency to interact with morphologically matching partners (*Imp. M*). Points on the map have been slightly separated to improve visual clarity. The scatterplot shows the negative correlation between *Imp. M* and absolute latitude, modelled by logistic regression. Drawings by Pedro Lorenzo.



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