

Running title: Functional diversity and network structure

Title: Functional diversity mediates macroecological variation in plant-hummingbird interaction networks

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Abstract (up to 300 words)

Aim: Species interaction networks are known to vary in structure over large spatial scales. We investigated the hypothesis that environmental factors affect interaction network structure by influencing the functional diversity of ecological communities. Notably, we expect more functionally diverse communities to form interaction networks with a higher degree of niche partitioning.

Location: Americas.

Time period: Current.

Major taxa studied: Hummingbirds and their nectar plants.

Methods: We used a large dataset comprising 74 quantitative plant-hummingbird interaction networks distributed across the Americas, along with morphological trait data for 158 hummingbird species. First, we used a model selection approach to evaluate associations between environment (climate, topography and insularity), species richness, and hummingbird functional diversity as predictors of network structure (niche partitioning, i.e., complementary specialization and modularity). Second, we used Structural Equation Models (SEMs) to ask whether environmental predictors and species richness affect network structure directly and/or indirectly through their influence on hummingbird functional diversity. For a subset of 28 networks, we additionally evaluated whether plant functional diversity was associated with hummingbird functional diversity and network structure.

Results: Precipitation, insularity and plant richness, together with hummingbird functional diversity (specifically functional dispersion), were consistently strong predictors of niche partitioning in plant-hummingbird networks. Moreover, SEMs showed that environmental

predictors and species richness affected network structure indirectly through their effects on hummingbird functional diversity. Plant functional diversity, however, was unrelated to hummingbird functional diversity and network structure.

Main conclusions: We reveal the importance of hummingbird functional diversity for niche partitioning in plant-hummingbird interaction networks. The lack of support for similar effects for plant functional diversity potentially indicate that consumer functional diversity may be more important for structuring interaction networks than resource functional diversity. Changes in pollinator functional diversity are therefore likely to alter the structure of interaction networks and associated ecosystem functions.

KEYWORDS

functional dispersion, insularity, modularity, network structure, niche partitioning, plantpollinator interactions, pollination networks, specialization, trait diversity

1 INTRODUCTION

Species' traits influence niche partitioning between pairs of species, and thus should affect the structuring of entire networks of interacting organisms (Fründ, Dormann, Holzschuh & Tschardtke, 2013; Junker et al., 2013; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira & Dalsgaard, 2014; Maglianesi, Böhning-Gaese & Schleuning, 2015). We may therefore expect a correspondence between community trait composition (i.e., functional diversity) and interaction network structure, such that communities in which species differ strongly in traits related to their ecological interactions should exhibit a high resource partitioning. Despite the potential importance for community stability and ecosystem functioning (Fontaine, Dajoz,

Meriguet & Loreau, 2005; Fründ et al., 2013; Mouillot, Graham, Villéger, Mason & Bellwood, 2013; Schleuning, Fründ & Garcia, 2015), the relationship between functional diversity and the structure of species interaction networks remains untested at large geographical scales (Kissling & Schleuning, 2015; Gravel, Albouy & Thuiller, 2016).

Several recent studies have used mutualistic networks to examine how large-scale variation in environmental factors, notably climate, relate to network structure (e.g., Dalsgaard et al., 2011; Schleuning et al., 2012, 2014; Trøjelsgaard & Olesen, 2013; Martín González et al., 2015). Likewise, studies have reported relationships between environment and functional diversity of assemblages, for both plants and pollinators (Swenson et al., 2012; Grass, Berens & Farwig, 2014; Rader, Bartomeus, Tylianakis & Laliberté, 2014; Ordonez & Svenning, 2017). However, apart from a few local and regional studies on a small number of networks (e.g., Junker, Blüthgen & Keller 2015; Maglianesi, Blüthgen, Böhning-Gaese & Schleuning 2015), the way in which functional diversity influences species interaction networks is poorly understood. In addition, despite the reported relationships between environmental factors and network structure, the mechanisms behind such relationships remain speculative (reviewed in Trøjelsgaard & Olesen, 2016 and Tylianakis & Morris, 2017).

One plausible way environmental factors may affect interaction network structure is through effects on the distribution of species and, hence, community composition (Dalsgaard et al., 2011; Bartomeus et al., 2016; Sonne et al., 2016, Tylianakis & Morris, 2017). Environmental factors have been shown to affect the distribution of species traits, e.g., body size (Olson et al., 2009), as well as plant richness (Kreft & Jetz, 2007). Moreover, high species richness has been linked to an increase in competition, which should promote greater trait differentiation within plant and pollinator communities (MacArthur & Levins, 1967; Inouye, 1978; Vamosi et al., 2006; Fründ et al., 2013). For example, traits linked to pollinators' body size and shapes have

been shown to determine interaction partitioning within plant-pollinator interactions (e.g., Inouye, 1978; Vizentin-Bugoni, Maruyama & Sazima, 2014). Thus, one hypothesis is that environmental factors influence species and functional diversity in communities (Kreft & Jetz, 2007, Olson et al., 2009, Ordonez & Svenning, 2017), which then mediate effects on network structure (Fründ et al., 2013; Mouillot et al., 2013; Bartomeus et al., 2016, Tylianakis & Morris, 2017). Specifically, a higher functional diversity in communities should lead to networks with a greater partitioning of interactions (Inouye, 1978; Junker et al., 2013, 2015; Maruyama et al., 2014; Maglianesi, Blüthgen et al., 2015).

We investigate this hypothesis using a large dataset of 74 quantitative planthummingbird mutualistic interaction networks distributed widely across the Americas. Hummingbirds, a species-rich family of nectar-feeding birds, are important pollinators in the New World, showing specialized interactions with the plants they pollinate (Stiles, 1981; Cronk & Ojeda, 2008; Zanata et al., 2017). Due to their high diversity and strong specialization for nectarivory, hummingbirds have frequently been used as a model system to study the evolutionary, historical and ecological factors structuring the assembly of species into communities (Snow & Snow, 1972; Stiles, 1981; Graham Parra, Tinoco, Stiles & McGuire, 2012; Vizentin-Bugoni et al., 2014; Maglianesi, Böhning-Gaese et al., 2015; Martín González et al., 2015; Sonne et al., 2016). We here evaluate the relationships between environmental factors, species richness, functional trait diversity, and network structure. Our aim is to elucidate whether functional trait diversity mediates the effects of environmental factors on network structure at a macroecological scale. We focused on hummingbird body mass, bill length and shape, as these traits are known to influence their interactions with their nectar-plants (Feinsinger & Colwell, 1978; Dalsgaard et al., 2009; Maglianesi, Blüthgen, Böhning-Gaese & Schleuning, 2014; Maglianesi, Böhning-Gaese, et al., 2015;

LópezSegoviano, Bribiesca & Arizmendi, 2018). Because hummingbirds depend on floral nectar for energy intake and partition floral resources according to their morphology, we expected that hummingbird communities with higher degree of functional diversity should form specialized interaction networks with higher degree of niche partitioning (MacArthur & Levins, 1967; Feinsinger & Colwell, 1978; Inouye, 1978; Stiles, 1981; Maglianesi, Blüthgen, et al., 2015). We similarly expected a positive relationship between plant functional diversity and the degree of interaction niche partitioning as plant traits have been shown to constrain plant-hummingbird interactions (Maglianesi et al., 2014; Vizentin-Bugoni et al., 2014). Moreover, we expected that predictors linked to productivity, such as temperature and precipitation, are positively associated with both functional diversity (e.g., Ordonez & Svenning, 2017) and network specialization (Dalsgaard et al., 2011; Trøjelsgaard & Olesen, 2013; Martín González et al., 2015), whereas past climate instability should decrease specialization (Dalsgaard et al., 2011; Ordonez & Svenning, 2017). Climatic seasonality, on the other hand, may increase both the functional diversity (Swenson et al., 2012) and interaction partitioning (Schleuning et al., 2014) by causing regular species turnover related to predictable environment variability. In addition to climatic effects, we expected that topographical heterogeneity has a positive effect on both functional diversity and network specialization by generating habitat heterogeneity and enabling species to track changing climates more easily (Sonne et al., 2016; Ordonez & Svenning, 2017), while insularity is expected to have a negative effect due to ecological release and increased generalization on islands (Traveset, Olesen, et al., 2015). We tested these hypotheses by examining how environmental predictors affect network structure both directly and indirectly through their influence on functional diversity.

2 METHODS

2.1 Plant-hummingbird networks

We used a dataset of 74 quantitative plant-hummingbird interaction networks distributed across the Americas (Figure 1), from 38°58' North to 31°48' South (updated from Martín González et al., 2015; see Appendix S1 in Supporting Information). Each network describes interactions among plant and hummingbird species for a given community, with interactions summarized as a quantitative bipartite matrix having plants as rows and hummingbirds as columns, and each cell filled with the observed frequency of pairwise interactions. We focused on mutualistic interactions among plants and hummingbirds, and thus excluded instances of nectar robbery or theft, as they characterize other interaction types (Maruyama, Vizentin-Bugoni, Dalsgaard, Sazima & Sazima, 2015). Species names and classification followed The Plant List (www.theplantlist.org) and the International Ornithological Committee World Bird List (IOC, www.worldbirdnames.org), respectively. In total, our dataset comprised 158 species of hummingbirds (~46% of the 345 species in the IOC Bird List, Appendix S2) and 984 species of plants from 85 families (Appendix S3).

2.2. Hummingbird morphological traits and functional diversity

For all hummingbird species, we compiled information on three morphological traits that influence their interactions with flowers as well as interspecific competition for nectar: bill length, bill curvature and body mass (Snow & Snow, 1972; Feinsinger & Colwell, 1978; Stiles, 1981; Dalsgaard et al., 2009; Maruyama et al., 2014; Vizentin-Bugoni et al., 2014; Maglianesi et al., 2014, Maglianesi, Blüthgen, et al. 2015; López-Segoviano et al., 2018). Bill length and curvature were measured by inspecting an average of 10 adult specimens, both males and females, deposited at museums (see details in Appendix S6); body mass data were gathered

from the literature (Appendix S2). For all three traits, we used the mean trait values per species, as interspecific trait variation is larger than intra-specific variation and plays a larger role in determining the division of floral resources among coexisting hummingbird species (Graham et al., 2012; Tinoco, Graham, Aguilar & Schleuning, 2017). In our data, the intraspecific coefficient of variation across all hummingbird species averaged 6.2% for bill length and 8.3% for bill curvature, while interspecific variation amounted to 42.4% and 246.9%, respectively (see also Appendix S2).

To calculate hummingbird FD metrics, we computed the pairwise Euclidean distances between hummingbird species based on their traits. These distances were projected into a functional trait space using a Principal Coordinate Analysis (Villéger, Mason & Mouillot, 2008; Figure 2). Traits were standardized to zero mean and unit variance prior to the calculation of Euclidean distances. We used two measures to quantify distinct facets of FD in hummingbird communities. First, we calculated from the multivariate trait space the sum of the branch length of the Minimum Spanning Tree (MST) connecting all hummingbirds cooccurring in a community. This measure estimates the total trait variability within each community and is similar to functional richness (Villéger et al., 2008), but has the advantage that it can be calculated for communities comprising only two co-existing species (as was the case for some communities in North America and the Caribbean islands). Large MST values indicate the occurrence of species with distinct traits, but do not consider species abundance in its calculations. Second, we calculated the Functional Dispersion (FDis) of each community by computing the mean distance of all species in a community to its centroid in functional trait space (Laliberté & Legendre, 2010). FDis accounts for differences in species' frequencies in the community, by weighting the mean distance and the position of the community centroid with species' abundances. In this study, we approximated hummingbird species abundance by

using the sum of interactions for each hummingbird species in the interaction matrices (see details in Appendix S7, S8). High values of hummingbird FDis indicate the co-occurrence of hummingbird species with distinct trait combinations (Laliberté & Legendre, 2010).

Calculation of FDis was performed with the function *dbFD* in the R package ‘FD’ (Laliberté & Legendre, 2010). The two functional indices analyzed in this study

(MST and FDis) represent complementary aspects of FD and are only moderately correlated (Pearson's $r = 0.57$, $P < 0.05$, $n = 74$ networks). If FDis is calculated without weighting by species abundance, this correlation becomes higher ($r = 0.80$, $P < 0.05$). Moreover, MST showed a stronger correlation with hummingbird species richness (Pearson's $r = 0.76$, $P < 0.05$) than did weighted FDis ($r = 0.43$, $P < 0.05$).

2.3. Plant functional diversity

For a subset of 28 networks, including mainland and island communities and comprising 103 hummingbird and 467 plant species (51.2% and 47.5% of the complete dataset, respectively), we also computed plant functional diversity. We considered three traits that have been associated with hummingbird specialization and partitioning of interactions among flowers: 1) floral corolla length (e.g., Maglianesi et al., 2014; Maruyama et al., 2014); 2) color spectrum visible to human eye of the visited flowers, reflecting different degrees of specialization to ornithophily (Wilson, Castellanos, Hogue, Thomson & Armbruster, 2004; Dalsgaard et al., 2009); and 3) plant life form, reflecting resource availability (Feinsinger & Colwell, 1978) and/or vegetation strata (Jordano, Bascompte & Olesen, 2006; see details on plant trait assessment at Appendix S4-S6). We calculated plant FDis for each network, based on the pairwise Gower distances as suggested for the combination of continuous and categorical trait variables (Laliberté & Legendre, 2010). Weights of individual species in the FDis metric were given by independent measures of local floral abundances (Appendix S6). For this same subset

of communities, we also re-calculated hummingbird FDis to test whether it relates to plant functional diversity. In addition, we estimated plant and hummingbird FDis based only on corolla and bill length, respectively, as we only had the corolla length as a continuous variable for plants. Results from single-trait analyses were qualitatively identical and are therefore not shown.

2.4 Network indices and sampling intensity

To characterize network structure, we calculated two quantitative indices widely used in the literature to quantify the extent to which species partition their interactions, namely complementary specialization (H_2' and d' , Blüthgen, Menzel & Blüthgen, 2006), and quantitative bipartite modularity (Q , Dormann & Strauss, 2014). Although conceptually distinct, these indices characterize a similar ecological pattern from the hummingbird's perspective, namely the partitioning of interactions along a niche dimension represented by the plant species in the network (Blüthgen, 2010). The complementary specialization indices derive from Shannon's entropy and quantify how realized species' interactions differ from those expected in randomly interacting communities relative to partner availability, i.e. reflect the niche partitioning among species (Blüthgen et al., 2006; Blüthgen, 2010). Two variants, the network-wide specialization H_2' and the species level specialization d' are commonly used; a guild level specialization can be estimated as the weighted mean of d' across all species from the same guild $\langle d' \rangle$ (Blüthgen et al., 2006). In our dataset, hummingbird specialization $\langle d' \rangle$ was strongly correlated with network wide specialization H_2' (Pearson's $r = 0.93$, $P < 0.05$). We mostly focused on $\langle d' \rangle$ as we calculated FD based on morphological data for hummingbird species.

A complementary measure of interaction partitioning is modularity Q , which quantifies the prevalence of preferentially interacting subgroups in the networks (Dormann & Strauss,

2014). The formation of such modules of interacting species can be related to a high degree of trait matching between species (Maruyama et al., 2014, Maruyama, VizentinBugoni, Dalsgaard, Sazima & Sazima, 2015). Here, we used the QuanBiMo, a modularitysearching algorithm specifically designed for quantitative bipartite networks (Dormann & Strauss, 2014). Both $\langle d' \rangle$ and Q scale from 0 to 1, with zero indicating low specialization/modularity and 1 high specialization/modularity (Blüthgen et al., 2006;

Dormann & Strauss, 2014). Network analyses were conducted using the ‘bipartite’ package in R (Dormann, Fründ, Blüthgen & Gruber, 2008; R Core Team, 2016).

Intrinsic characteristics of the networks, such as size (i.e., number of interacting species) and sampling effort, may affect network indices (Blüthgen et al., 2006; VizentinBugoni et al., 2016). The quantitative network indices used here take species interaction frequencies into account and are less sensitive to sampling insufficiency than metrics based on binary networks that only report the presence or absence of interactions between species pairs (Blüthgen et al., 2006; Vizentin-Bugoni et al., 2016). Nevertheless, to minimize potential biases due to differences in sampling among networks, we Δ -transformed our metrics (Schleuning et al., 2012, Dalsgaard et al., 2017). In this transformation, the mean value of a metric obtained by multiple randomizations of a null network is subtracted from the observed value (Schleuning et al., 2012, Dalsgaard et al., 2017). Here, we used the Patefield null model, which fixes the network size and the marginal totals, i.e. species richness and species’ total number of interactions, while shuffling interactions randomly (Dormann et al., 2008). The specialization index $\langle d' \rangle$ is already subject to a correction for the marginal totals of the species in the network (Blüthgen et al., 2006), but modularity is not (Dormann &

Strauss, 2014); thus, we report the null model corrected ΔQ values in the main results. Nonetheless, results for both untransformed and Δ -transformed specialization and modularity metrics were similar (see Appendix S9).

In addition to null model corrections, we calculated sampling intensity (SI) and network asymmetry, both of which may affect the degree of specialization (Blüthgen et al., 2006; Schleuning et al., 2012). Sampling intensity is defined as the square root of the number of interaction events divided by the geometric mean of the total species number in the given bipartite network (Schleuning et al., 2012) and network asymmetry is defined as the ratio between hummingbird and plant richness. Since network asymmetry was only weakly related to the calculated metrics ($r = -0.21$, $P = 0.07$ for $\langle d' \rangle$ and $r = -0.09$, $P = 0.42$ for ΔQ), we did not consider it further. However, SI was included in the models (see Table 1).

2.5 Environmental variables

We extracted information on current climate, topography, and long-term climate stability within a 10 km radius around each study site from WorldClim 30 arc-second rasters (Hijmans, Cameron, Parra, Jones & Jarvis, 2005). Current climate was represented by mean annual temperature (MAT), mean annual precipitation (MAP), temperature seasonality (estimated as the standard deviation across monthly temperatures; TS), and precipitation seasonality (estimated as the coefficient of variation for monthly precipitation means; PS). To determine the topographical variation (Topography) at each study site, we also used the WorldClim digital elevation model (DEM). This combines the SRTM gap-filled 30 arc second DEM (CGIAR - <http://srtm.csi.cgiar.org/>), covering from 60N to 60S with the GTOPO30 DEM (<https://lta.cr.usgs.gov/GTOPO30>) for other parts of the world. Topography was represented by the standard deviation of elevation within a 10 km radius around each study site. We described paleoclimate stability using the change in temperature and precipitation from the Last Glacial

Maximum (LGM) to the present, as estimated using two different models, CCSM3 (Collins et al., 2006; Otto-Bleisner et al., 2006) and MIROC 3.2 (K-1 model developers, 2004). For each site, we calculated the change in temperature and precipitation from the LGM to the present (Anomaly), and its spatial rate of displacement (Velocity) as complementary measures of past to present climate variability (Loarie et al., 2009). As our data cover a large geographical extent, we assumed that the regionally downscaled climate estimates are good indicators of the variation of local climate among communities. In addition to data on past and current climate and topography, we included insularity as a dummy variable (1 - island, 0 - mainland). To meet statistical assumptions of normality, MAP was square root transformed and TS was log-transformed prior to further analyses. All variables were scaled to zero mean and unit variance. As velocity and anomaly both describe historical climate change, and are derived from the same model projection, we built one model for each of the two measures of historical climate change. As velocity includes topographical heterogeneity in the calculations (Loarie et al., 2009), we did not include velocity and topography in the same models. In the main text, we report the results regarding anomaly and topography; results regarding velocity as an integrated measure of historical climate variability were qualitatively similar and are reported in the Supplement (Appendix S10).

2.6 Macroecological analysis

We divided the macroecological analysis into two steps in order to simplify and reduce the number of predictors in the Structural Equation Models (SEMs). First, we fitted multipredictor linear models for both specialization $\langle d' \rangle$ and modularity ΔQ , considering the two indices for hummingbird FD (MST and FDis), separately, plus hummingbird richness (Hummingbirds).

Besides these predictors, we included the following environmental predictors: temperature (MAT), precipitation (MAP), temperature seasonality (TS), precipitation seasonality (PS),

topography (Topo), temperature anomaly (AnomT), precipitation anomaly (AnomP) and insularity (Insu). Finally, we included plant species richness (Plants) that has been shown to influence resource partitioning in flower-bird networks (Zanata et al., 2017), potentially independent of floral functional diversity (Souza et al., 2018). For the subset of 28 networks with plant FDis measures, we used linear models to test whether plant FDis predicted network level specialization H_2' and ΔQ . The same procedure was repeated with hummingbird FDis within this subset.

We fitted four principal models incorporating the combinations of two measures of FD (MST and FDis) and the two network indices ($\langle d' \rangle$ and ΔQ). The two FD measures were always fitted separately as these were correlated; for comparison, we also fitted a model with unweighted FDis (i.e., without incorporating abundance; Appendix S11). We checked for multicollinearity in the full model by evaluating the condition number ($CN \leq 5$) and the variance inflation factor ($VIF \leq 5$). This led to the exclusion of MAT and Hummingbird richness as predictors (see additional results in Supporting Information). Models considering hummingbird richness instead of FD measures had less statistical support (Appendix S12).

Model performance of all combinations of predictor variables was assessed based on the Akaike Information Criterion with correction for small samples (AIC_C). Model selections were performed with the function *dredge* in the R package ‘MuMIn’ (Barton, 2014), according to their AIC_C . In all cases, multiple models presented ΔAIC_C values ≤ 2.0 in relation to the best model, i.e., no single best model was identified (Burnham & Anderson, 2002). Hence, model averaging was performed across all possible models using the function *model.avg* in ‘MuMIn’ (Barton, 2014). We report the averaged coefficient values and the relative importance of each predictor variable by summing the Akaike weights across the models including the respective variable across all possible models (i.e., $\sum w_i$; Burnham & Anderson, 2002). We did not include

interaction terms between predictors in our models due to the lack of a clear hypothesis justifying their inclusion. Spatial autocorrelation in models' residuals was assessed by computing Moran's I correlograms using the 'ncf' package in R (Bjornstad, 2016), with distance classes of 500 km and a truncation distance of 5000 km. The linear model with specialization $\langle d' \rangle$ showed significant positive spatial autocorrelation. Therefore, we re-ran this model using a simultaneous autoregressive (SAR) model that specifies the autoregressive processes within the error term (Kissling & Carl, 2008). The SAR modeling was conducted using the "spdep" package in R (Bivand & Piras, 2015). The spatial connections between networks were determined as the three nearest neighbors. For the SAR model, no significant spatial autocorrelation remained in the residuals (see also Appendix S6).

The second step of our analysis used SEMs to quantify the extent to which predictors influence network structure directly or indirectly via FD. The advantage of SEMs is that both direct and indirect associations among variables are considered simultaneously, hence allowing a hierarchical model structure (Shipley, 2002). We constructed two sets of SEMs for each of the network metrics: (i) one based on the hypothesis that environmental and species richness predictors affect FD and network metrics in parallel, resulting in covariation between FD and network metrics, and (ii) another based on the hypothesis that FD directly affects network metrics (no covariation between FD and network metrics). *A priori* SEMs were constructed based on results from the previous model selection, which consistently demonstrated that insularity, MAP and plant richness had the greatest importance in determining network structure. All other predictors, except hummingbird FDis, had consistently low importance values, usually with a Σw_i below 0.3, and thus were not included in the SEMs (see Table 1, S9–S12). As MST was found not to influence $\langle d' \rangle$ or ΔQ , only SEMs for FDis were constructed. By including the same set of predictors in each SEM, models were directly comparable,

enabling a direct interpretation of whether environmental factors and plant richness are likely to affect network structure directly or indirectly through the functional composition of morphological traits (Shipley, 2002). Appropriate fits for SEMs were obtained by including error covariance links based on high modification indices and large residual correlations. Model fit was evaluated with a chi-square test, a comparative fit index (CFI), and a Root Mean Square Error of Approximation (RMSA). The chi-square test measures the coincidence between the empirical and the fitted variance-covariance structure in the data. Here, models were accepted if $P > 0.05$. The CFI relates the chi-square of the model, with the chi-square value of an independent model assuming zero correlation among variables while also accounting for sample size (Shipley, 2002). CFI ranges between 0 and 1, and models with $CFI > 0.09$ were considered to have an appropriate fit (Shipley, 2002). Finally, the RMSA index was included due to its sensitivity to the number of fitted parameters. A $RMSA < 0.07$ indicated an appropriate model fit (Shipley, 2002). All SEM analyses were conducted using the ‘lavaan’ package (Rosseel, 2012) in R (R Core Team, 2016).

3 RESULTS

Communities varied considerably in measures of hummingbird functional diversity (coefficient of variation - CV; MST = 55.3%; FDis = 43.4%) and network structure (CV; $\langle d' \rangle$ = 53.1%; Q = 48.5%, Figure 1). No strong latitudinal trend was observed for these variables (linear models with absolute latitude as a predictor; hummingbird FDis: $R^2 = 0.08$, $P = 0.02$; $\langle d' \rangle$: $R^2 = 0.05$, $P = 0.05$; Q : $R^2 = 0.09$, $P < 0.01$), although MST was higher at low latitudes ($R^2 = 0.37$, $P < 0.01$).

All best-fitting models included hummingbird FDis as a predictor, showing a positive association with both hummingbird complementary specialization $\langle d' \rangle$ and network modularity ΔQ (Table 1; Figures 1–2). Moreover, FDis was the only variable that consistently

had high importance values across different models, with a positive effect on both untransformed and Δ -transformed network indices (Table 1, Appendix S9). On the other hand, MST had a negligible importance in predicting network structure (Table 1), as did unweighted FDis (Appendix S11) and hummingbird richness (Appendix S12). MAP was positively related to hummingbird specialization $\langle d' \rangle$ (Table 1), whereas plant richness was positively and insularity negatively related to modularity ΔQ (Table 1). Other environmental variables were not important in any of our models.

For the subset of 28 networks with plant abundance and trait data, plant FDis showed less variation than hummingbird FDis (Coefficient of Variation = 24.2% vs. CV = 43.2%, Appendix S5). Plant FDis was unrelated to plant richness ($R^2 = 0.01, P = 0.51$) and hummingbird FDis ($r = 0.07, P = 0.70$), and also to network structure (H_2' : $R^2 = 0.01, P = 0.54$; ΔQ : $R^2 = 0.04, P = 0.34$). Within this subset, hummingbird FDis was positively associated with the degree of interaction partitioning (H_2' : $R^2 = 0.36, P < 0.01$; ΔQ : $R^2 = 0.55, P < 0.01$), consistent with the analysis across all networks.

SEMs indicated that the combined influence of precipitation, insularity and plant richness explained a larger amount of the variation in specialization and modularity than in FDis (Figure 3a, c). Notably, including hummingbird FDis as predictor of network structure (Figure 3b, d) increased the overall explanatory power of the models (adjusted R^2 , Figure 3). Environmental predictors affected network structure more strongly through direct links, but also had indirect effects through their influence on functional diversity. Precipitation (MAP) affected specialization both directly ($\beta = 0.32$; Figure 3b) and indirectly through FDis (indirect coefficients are obtained by multiplication of coefficients, i.e., $0.41 \times 0.31 = 0.13$; Figure 3b). In the case of modularity, the indirect association with precipitation ($0.41 \times 0.39 = 0.16$; Figure 3d) was similar to the direct one ($\beta = 0.14$; Figure 3d). Plant species richness

(specialization: direct = 0.19, indirect = 0.07; modularity: direct = 0.27, indirect 0.09; Figure 3b, d) and insularity (specialization: direct = -0.21, indirect = -0.06; modularity: direct = -0.28, indirect -0.07; Figure 3b, d) showed stronger direct and weaker indirect associations with network metrics.

4 DISCUSSION

Functional diversity of hummingbirds was correlated with network structure in planthummingbird communities across the Americas, with hummingbird communities composed of functionally distinct species (i.e., those with a high functional dispersion) forming specialized and modular interaction networks with their nectar plants. In contrast, plant functional diversity was unrelated to network structure. Our result that precipitation was both directly and indirectly related to network structure through its association with hummingbird functional diversity illustrates how the environment, through its effects on community trait composition, may influence the realization of species interactions within local communities (McGill, Enquist, Weiher & Westoby, 2006).

In addition to precipitation, we show that plant richness was positively related to the extent to which hummingbirds partition floral resources, with both direct and indirect effects through hummingbird functional diversity. This association may be driven by the resource diversity for hummingbirds, and partly be related to precipitation since the annual number of days with rainfall – a variable closely related to annual precipitation – is one of the major drivers of global vascular plant richness (Kreft & Jetz, 2007). This notion is reinforced by the importance of plant species richness in our models, and its covariation with precipitation (Table 1, Figure 3). A global analysis of nectarivorous birds, including hummingbirds, honeyeaters and sunbirds (Zanata et al., 2017), had previously reported a positive relationship between plant richness and network specialization. Interestingly, the association between plant richness and

network structure was not mirrored by co-variation between network structure and plant functional diversity (see also Souza et al., 2018). One possible reason for this is that, in contrast to birds, interaction frequencies of plants usually do not reflect their abundances (VizentinBugoni et al., 2014; Weinstein & Graham et al., 2017). For instance, plant species with long corollas often have low abundances (see Vizentin-Bugoni et al., 2016), thus contributing little to abundance-weighted estimates of plant FDis. However, long corolla flowers are frequently visited by abundant long-billed hummingbirds, thus generating interaction partitioning

(Maruyama et al., 2014; Maglianesi, Böhning-Gaese et al., 2015; Weinstein & Graham et al., 2017). This potentially results in a mismatch between the functionally most distinct plant species and those that provide most floral resources, i.e., higher floral abundance. A closer association between consumer FD and network specialization may also result from phenological differences between plants and animals.

While most hummingbirds stay in the community for most of the year, plant species flowering turnover is usually high, meaning that morphologically specialized plant species are temporarily replaced by other functionally similar ones (Bergamo et al., 2017). This means that from the plant side, there is higher redundancy between species and the processes driving niche partitioning may differ between plants and animals. For instance, hummingbirds often compete for floral resources, as exemplified by their frequent aggressive defense of floral resources (Feinsinger & Colwell, 1978), which likely enforces niche partitioning among birds more than among co-flowering plant species. Overall, our results indicate that total resource/niche space, as expressed by plant richness, allows for a finer division of resources (Dalsgaard et al. 2011)

In addition to the positive effect of precipitation and plant richness, insularity had a negative association with functional diversity and network metrics (Figure 3). Although the

direct links between insularity, specialization and modularity were stronger than the indirect effects, we could also detect indirect relationships between network structure and insularity through bird functional diversity. Island communities, especially from oceanic islands, tend to show a high degree of generalization, consistent with an interaction release and niche expansion in improvised communities (Traveset, Olesen, et al., 2015). Consequently, plantpollinator interaction networks on these islands can be less specialized than those on continents, for instance by showing higher pollinator overlap among plants (Traveset, Tur, et al., 2015). In accordance with this, higher generalization has been previously shown for insular planthummingbird networks (Martín González et al., 2015), and our results here indicate that part of this higher generalization is associated with the lower functional diversity of hummingbirds on islands.

The incorporation of functional diversity constitutes an important step towards identifying determinants of network structure at large spatial scales and is particularly promising for scaling up our understanding of natural systems from local to global scales (Kissling & Schleuning, 2015; Gravel et al., 2016). Furthermore, it may allow a better assessment of the association between community structure, ecosystem functioning and responses to disturbance (Fontaine et al., 2005; Fründ et al., 2013; Mouillot et al., 2013; Schleuning et al., 2015; Tylianakis & Morris, 2017). For instance, niche partitioning among morphologically distinct hummingbirds may promote optimal foraging, as trait-matching leads to an increased efficiency in floral resource use (Maglianesi et al., 2014). In addition, an increase in floral niche partitioning among pollinators is likely to increase the quality of pollination services among plants through an increase in conspecific pollen transfer (Inouye, 1978; Brosi & Briggs, 2013). Hence, if pollinator functional diversity is reduced in response to climate change or direct human-induced disturbances (e.g., Grass et al., 2014; Rader et al., 2014), this is likely to result

in a reduced resource partitioning among pollinators and lower pollination effectiveness (Fontaine et al., 2005; Fründ et al., 2013; Schleuning et al., 2015). In this regard, we note that not only species traits, but also species' abundances seem to be relevant, as unweighted functional diversity metrics (MST and unweighted FDis) were only weakly associated with network structure. Other studies have similarly found that unweighted functional diversity indices were only weakly associated with ecosystem functions delivered by animal communities (e.g., Gagic et al., 2015). Therefore, functionally distinct species in a community must be sufficiently abundant to fulfill their functional roles in interactions networks and contribute to ecosystem functioning. The apparent asymmetry between plant and bird functional diversity could stem from generally low floral abundances of morphologically specialized plant species, each playing a minor role at the community level, compared to functionally specialized hummingbirds with high abundances, which fulfill critical ecological roles in many communities.

Taken together, our results show an association between environmental factors, pollinator functional diversity, and network structure at a continental scale, in which environmental and species richness predictors determined network structure both directly and indirectly through functional trait diversity. Moving forward, studies should investigate how interaction networks affect the evolution of the traits of the species embedded in networks (Guimarães, Jordano & Thompson, 2011) and the assembly of interacting species within communities (Bartomeus et al., 2016). For instance, simulation studies may be able to evaluate how present network structure will affect the diversity of species and their functional traits in potential future communities, which in turn should feedback on the structure of interaction networks (Guimarães et al., 2011, Bartomeus et al., 2016). In conclusion, we believe that our results showing that environmental factors exert indirect effects on interaction niche partitioning

mediated by consumer trait diversity yield a first step towards a mechanistic understanding of how the environment influences the structure of species interaction networks. Hence, potential future changes in pollinator functional diversity are expected to alter the structure of interaction networks and associated ecosystem functions such as pollination.

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Data Accessibility statement

All the predictors and network indices used for the macroecological analysis, as well as hummingbird trait data are supplied as supporting information and will be uploaded to Figshare upon acceptance of the manuscript in the journal (Here we will provide the link).

Biosketch

Pietro K. Maruyama is an ecologist, with a broad interest ranging from natural history to macroecology of plant–animal mutualistic interactions. This study is part of the HumLab research team (www.humlab.weebly.com), an ongoing research collaboration on plant–

hummingbird networks across the Americas involving numerous researchers from a wide range of institutions and countries.

TABLE 1 Model selection and averaging results of the multi-predictor linear models explaining the variation of hummingbird specialization

Plants	0.75	0.16	0.19	0.89	0.23	0.26	0.98	0.28	0.28	0.98	0.34	0.35
MAP	0.92	0.30	0.33	0.99	0.44	0.45	0.32	0.03	-	0.70	0.17	0.30
TS	0.32	0.03	-	0.30	0.03	-	0.23	-0.01	-	0.25	0.01	-
PS	0.23	-0.01	-	0.23	0.01	-	0.54	-0.08	-0.16	0.36	-0.04	-
AnomT	0.27	-0.02	-	0.26	-0.02	-	0.26	0.01	-	0.27	0.02	-
AnomP	0.29	-0.02	-	0.25	-0.01	-	0.44	-0.06	-	0.38	-0.05	-
Topography	0.32	0.03	-	0.33	0.03	-	0.27	-0.02	-	0.26	-0.02	-
Insularity	0.77	-0.17	-0.21	0.86	-0.22	-0.27	0.99	-0.31	-0.28	0.97	-0.32	-0.35
SI	0.29	-0.02	-	0.38	-0.05	-	0.52	0.08	-	0.31	0.03	-

R² adj 0.42 0.36 0.48 0.37 $\langle d' \rangle$ and network modularity ΔQ , corrected by the Patefield

null model. We used two functional diversity measures, functional dispersion (FDis) and minimum spanning tree (MST) reflecting different aspects of trait diversity in hummingbird communities. Important predictors in explaining network indices variation ($\Sigma w_i > 0.8$) are highlighted in bold. We also show the AICc: corrected Akaike's information criterion; AVM: standardized coefficients of the averaged model across all models; MAM: standardized coefficients of the minimum adequate model with the lowest AICc value; R² adj: variation explained by the minimum adequate model with the lowest AICc. Acronyms of the predictors - FDis: functional dispersion; MST: minimum spanning tree; Plants: plant richness; MAP: mean annual precipitation; TS: temperature seasonality; PS: precipitation seasonality; AnomT: temperature anomaly; AnomP: precipitation anomaly; Topography: topographical variation; SI: sampling intensity. See Methods for details.

	complementary ecialization			$\langle d' \rangle$			Modularity ΔQ					
				MST			FDis			MST		
	FDis			AVM								
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM
FD index	0.97	0.33	0.31	0.28	0.02	-	1.00	0.43	0.43	0.55	0.12	-

AICc

177.3

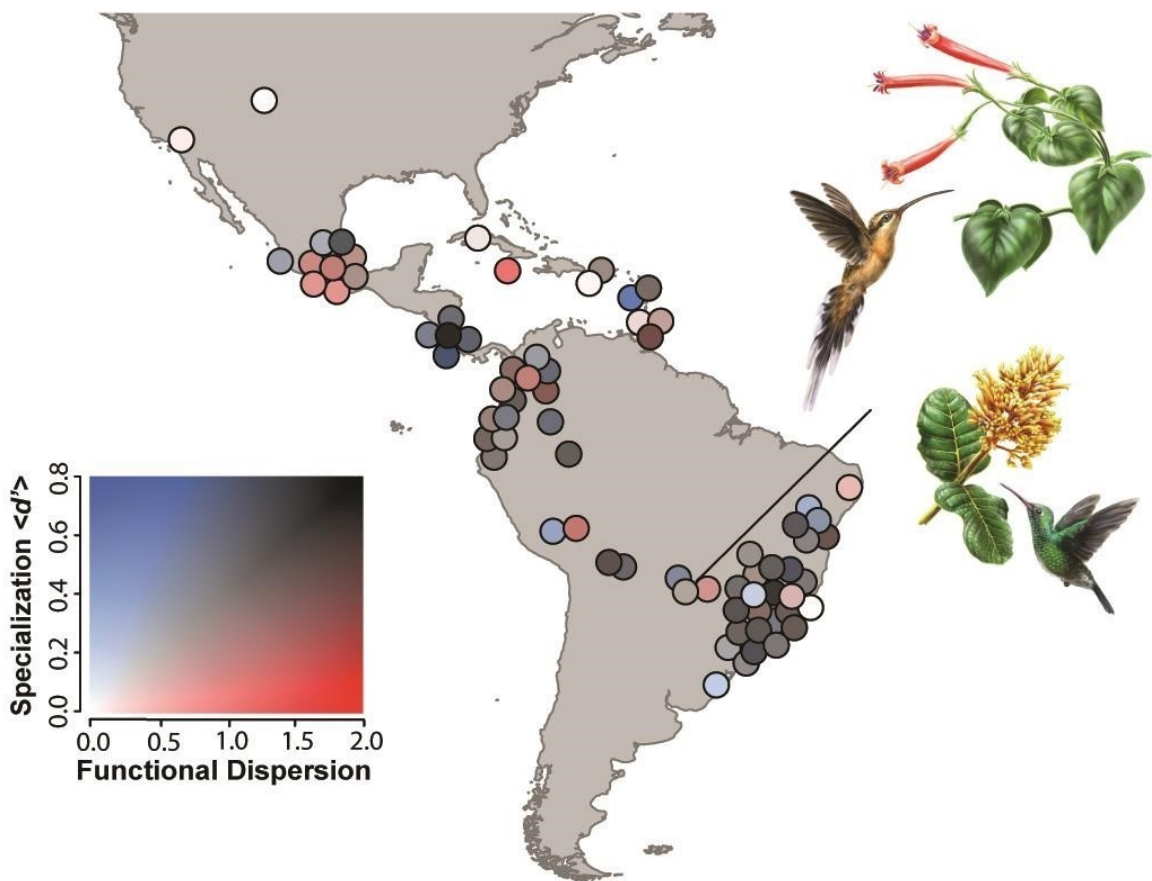
183.8

168.9

182.7

FIGURE

1 The location of the 74 plant-hummingbird networks used in the study, showing the relationship between hummingbird specialization $\langle d' \rangle$ and functional dispersion. For clarity, circles for some study sites were moved slightly to minimize overlap. The illustration on the right depicts how hummingbirds with distinct morphologies partition their interactions by associating with flowers of corresponding morphology (from network ID 52; Top: Planalto Hermit, *Phaethornis pretrei* and *Manettia cordifolia* with long curved corolla; Bottom: Glittering-throated Emerald, *Amazilia fimbriata* and *Palicourea rigida* with a short corolla). Points along the white-grey-black gradient indicate communities with better correspondence between functional dispersion and specialization.

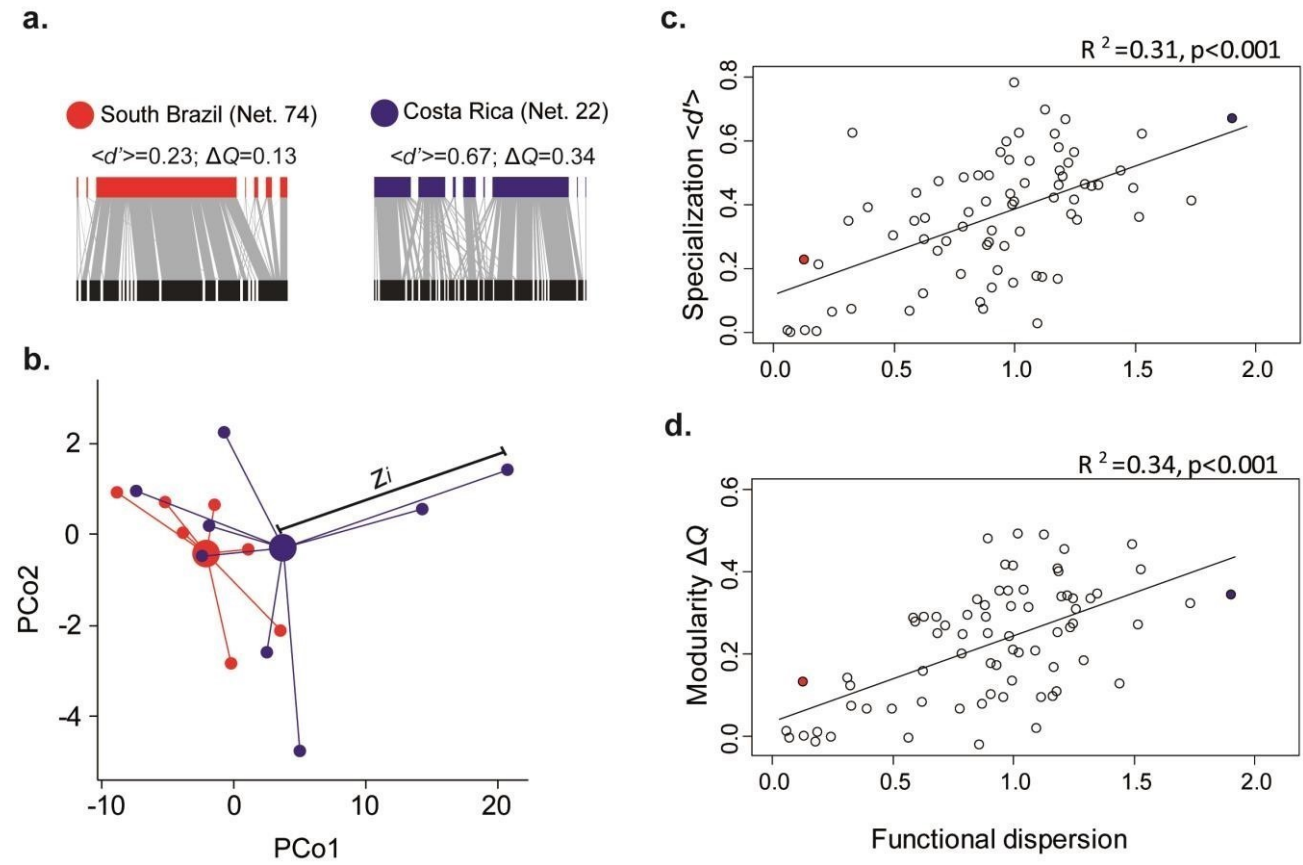


2 The relationship between hummingbird functional dispersion (FDis) and network

FIGURE

structure. (a) An example illustrating two networks with similar number of hummingbird species (Net 74 = 7, Net 22 = 8), but with contrasting FDis. Networks on top depict the interaction networks with hummingbird species indicated by red and blue boxes at the top and plant species indicated by black boxes at the bottom (with the interactions indicated by grey lines). (b) FDis is measured as the mean of the distance (Z_i) of a species (small circles) to its community centroid (large circles) in multivariate trait space generated by a Principal Coordinate Analysis. Notice that the community from Costa Rica (blue/right) includes several species located distantly from the community centroid, in contrast to the community from Southern Brazil (red/left). Linear regressions showing the relationship between hummingbird (c) specialization $\langle d' \rangle$ and (d) modularity ΔQ with FDis. Note that the two networks from (a) are indicated with their respective colors.

FIGURE

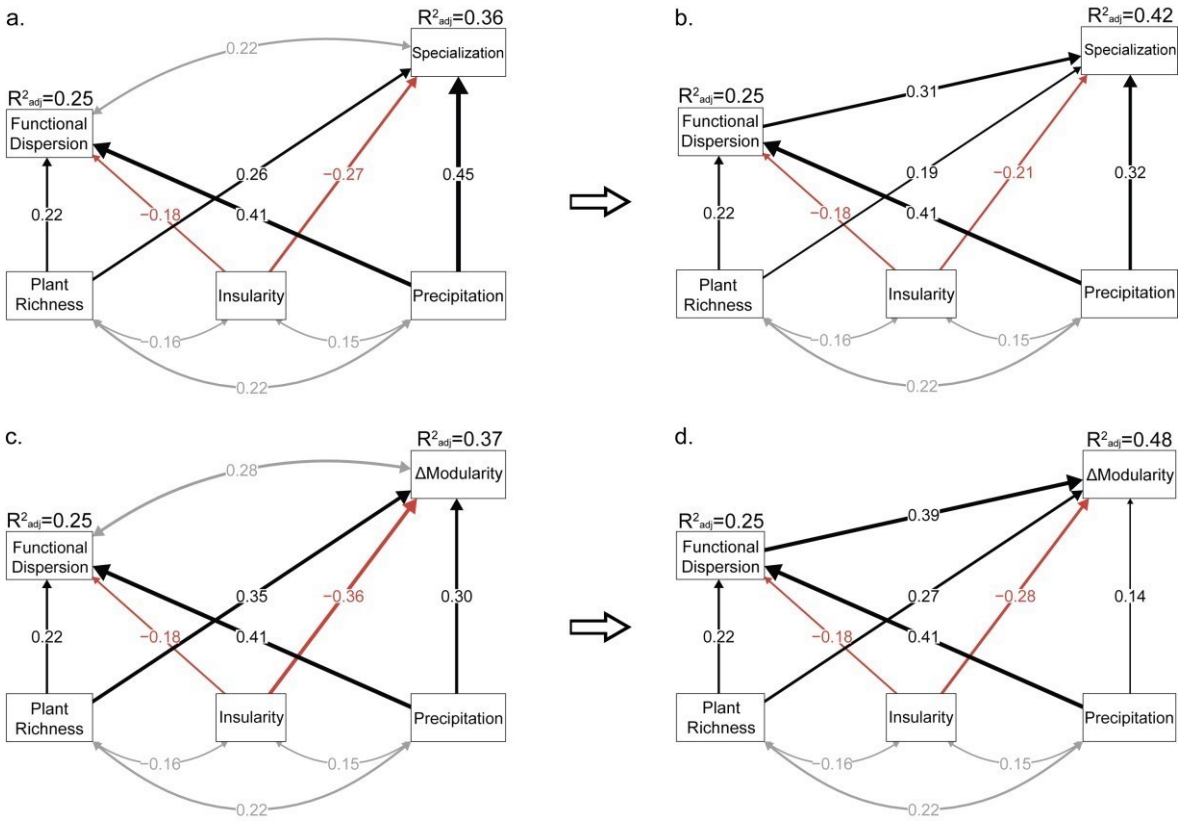


3 Structural equation models (SEMs) showing the direct and indirect associations

among environmental and richness predictors, functional dispersion (FDIs) with complementary specialization ($\langle d' \rangle$; 3a, b) and modularity (ΔQ ; 3c, d). Models in (a) and (c) assume a covariation between FDIs and networks structure, while (b) and (d) consider a directional relationship between FDIs and network structure. In both cases, the value of R^2 is substantially higher in the models that include the direct link between FDIs and network metrics. Black arrows indicate positive relationships while red arrows indicate negative relationships, with the thickness of each arrow reflecting their standardized path coefficients.

Double-headed grey arrows indicate covariance links.

FIGURE



APPENDIX 1: Data sources and supporting references

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Additional Supporting Information:

Appendix S1. Location, details and sources of the plant-hummingbird networks

Appendix S2. List of hummingbirds occurring in the studied networks

Appendix S3. List of plant species occurring in the studied networks

Appendix S4: List of plant species occurring in the subset of 28 networks with data on plant traits and abundances. The same nomenclature as in Appendix 3 is used.

Appendix S5: Details and sources of the subset plant-hummingbird networks.

Appendix S6. Additional details on Methods

Appendix S7. Hummingbird abundance correlations

Appendix S8. A plot showing the relationship between the values of FDis calculated using two measures of hummingbird abundance

Appendix S9. Model selection results for null model corrected specialization and un-corrected modularity

Appendix S10. Model selection results using Velocity, instead of Anomalies as measure of historical climate

Appendix S11. Model selection results using unweighted Functional Dispersion index Appendix

S12. Model selection results using hummingbird richness