

Functional diversity mediates macroecological variation in plant–hummingbird interaction networks

Pietro Kiyoshi Maruyama^{1,2,3}  | Jesper Sonne² | Jeferson Vizontin-Bugoni^{4,5}  | Ana M. Martín González² | Thais B. Zanata^{2,6} | Stefan Abrahamczyk⁷ | Ruben Alarcón⁸ | Andréa C. Araujo⁹ | Francielle P. Araújo¹⁰ | Andrea C. Baquero² | Edgar Chávez-González¹¹ | Aline G. Coelho¹² | Peter A. Cotton¹³ | D. Matthias Dehling^{14,15} | Erich Fischer⁹  | Glauco Kohler¹⁶ | Carlos Lara¹⁷ | Flor Maria G. Las-Casas¹⁸ | Adriana O. Machado³ | Caio G. Machado¹² | María A. Maglianesi^{14,19} | Tiago S. Malucelli⁶ | Oscar Humberto Marín-Gómez²⁰ | Paulo E. Oliveira³ | Juan Francisco Ornelas²¹  | Raul Ortiz-Pulido²² | Mónica B. Ramírez-Burbano²³ | Márcia A. Rocca²⁴ | Licléia C. Rodrigues²⁵ | Liliana Rosero-Lasprilla²⁶ | Ana M. Rui²⁷ | Brody Sandel²⁸ | Jens-Christian Svenning^{29,30} | Boris A. Tinoco³¹ | Isabela G. Varassin⁶  | Stella Watts³² | Carsten Rahbek^{2,33} | Marlies Sazima¹ | Matthias Schleuning¹⁴ | Bo Dalsgaard²

¹Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas (Unicamp), Campinas, Brasil

²Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen Ø, Denmark

³Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Brasil

⁴Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas (Unicamp), Campinas, Brasil

⁵Natural Resources and Environmental Science Department, University of Illinois at Champaign-Urbana, Champaign, Illinois

⁶Laboratório de Ecologia Vegetal, Departamento de Botânica, Centro Politécnico, Universidade Federal do Paraná, Curitiba, Brasil

⁷Nees Institute for Biodiversity of Plants, Bonn, Germany

⁸Biology Program, California State University Channel Islands, Camarillo, California

⁹Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Mato Grosso do Sul, Brasil

¹⁰Universidade Estadual do Rio Grande do Sul, São Francisco de Paula, Rio Grande do Sul, Brasil

¹¹Red de Ecoetología, Instituto de Ecología, AC, Xalapa, Mexico

¹²Laboratório de Ornitologia, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, Brasil

¹³Marine Biology & Ecology Research Centre, University of Plymouth, Plymouth, UK

¹⁴Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany

¹⁵School of Biological Sciences, University of Canterbury, Christchurch, New Zealand

¹⁶Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil

¹⁷Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, San Felipe Ixtacuixtla, Mexico

¹⁸Laboratory of Ecology, Systematics and Evolution of Birds, Federal University of Pernambuco, Recife, Brasil

¹⁹Vicerrectoría de Investigación, Universidad Estatal a Distancia, Carretera a Sabanita, San José, Costa Rica

²⁰Instituto de Ecología, AC, Xalapa, Mexico

²¹Departamento de Biología Evolutiva, Instituto de Ecología, AC, Xalapa, Mexico

²²Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Mineral de la Reforma, Mexico

²³Programa de doctorado en Ciencias-Biología, Facultad de Ciencias Naturales y Exactas, Departamento de Biología, Universidad del Valle, Cali, Colombia

²⁴Departamento de Ecologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de Sergipe, São Cristóvão, Brasil

²⁵Laboratório de Ornitologia, Departamento de Zoologia, ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Brasil

²⁶Escuela de Ciencias Biológicas, Grupo de Investigación Biología para la Conservación, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia

²⁷Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Pelotas, Brasil

²⁸Department of Biology, Santa Clara University, Santa Clara, California

²⁹Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Aarhus C, Denmark

³⁰Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus University, Aarhus C, Denmark

³¹Escuela de Biología, Ecología y Gestión, Universidad del Azuay, Cuenca, Ecuador

³²Landscape and Biodiversity Research Group, Department of Environmental and Geographical Sciences, University of Northampton, Northampton, UK

³³Department of Life Sciences, Imperial College London, Ascot, UK

Correspondence

Pietro Kiyoshi Maruyama, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas (Unicamp), Cx. Postal 6109, CEP: 13083-970 Campinas, São Paulo, Brasil.
Email: pietrokisyoshi@gmail.com

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Abstract

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 the 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 plant richness affected network structure both directly and 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 indicates that consumer functional diversity might 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, plant–pollinator 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, & Tschamntke, 2013; Junker et al., 2013; Maglianesi, Böhning-Gaese, & Schleuning, 2015; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014). 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 (Gravel, Albouy, & Thuiller, 2016; Kissling & Schleuning, 2015).

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; Martín González et al., 2015; Schleuning et al., 2012, 2014; Trøjelsgaard & Olesen, 2013). Likewise, studies have reported relationships between the environment and the functional diversity of assemblages, for both plants (Ordóñez & Svenning, 2017; Swenson et al., 2012) and pollinators (Grass, Berens, & Farwig, 2014; Rader, Bartomeus, Tylianakis, & Laliberté, 2014). 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 influence of functional diversity on 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 by Trøjelsgaard & Olesen, 2016; Tylianakis & Morris, 2017).

One plausible way in which environmental factors might affect interaction network structure is through effects on the distribution of species and, hence, community composition (Bartomeus et al., 2016; Dalsgaard et al., 2011; 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) and species richness (e.g., 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 (Fründ et al., 2013; Inouye, 1978; MacArthur & Levins, 1967; Vamosi et al., 2006). For example, traits linked to the body size and shapes of pollinators 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 richness and functional diversity in communities (Kreft & Jetz, 2007; Olson et al., 2009; Ordóñez & Svenning, 2017), which then mediate effects on network structure (Bartomeus et al., 2016; Fründ et al., 2013; Mouillot et al., 2013;

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; Maglianesi, Blüthgen, et al., 2015; Maruyama et al., 2014).

We investigate this hypothesis using a large dataset of 74 quantitative plant-hummingbird 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 (Cronk & Ojeda, 2008; Stiles, 1981; Zanata et al., 2017). Owing to their high diversity and strong specialization for nectarivory, hummingbirds have been used frequently as a model system to study the evolutionary, historical and ecological factors structuring the assembly of species into communities (Graham, Parra, Tinoco, Stiles, & McGuire, 2012; Maglianesi, Böhning-Gaese, et al., 2015; Martín González et al., 2015; Snow & Snow, 1972; Sonne et al., 2016; Stiles, 1981; Vizentin-Bugoni et al., 2014). In this study, we evaluated the relationships between environmental factors, species richness, functional trait diversity and network structure. Our aim was 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, because these traits are known to influence their interactions with their nectar plants (Dalsgaard et al., 2009; Feinsinger & Colwell, 1978; López-Segoviano, Bribiesca, & Arizmendi, 2018; Maglianesi, Blüthgen, Böhning-Gaese, & Schleuning, 2014; Maglianesi, Böhning-Gaese, et al., 2015). Given that hummingbirds depend on floral nectar for energy intake and partition floral resources according to their morphology, we expected that hummingbird communities with higher degrees of functional diversity should form specialized interaction networks with higher degrees of niche partitioning (Feinsinger & Colwell, 1978; Inouye, 1978; MacArthur & Levins, 1967; Maglianesi, Blüthgen, et al., 2015; Stiles, 1981). Likewise, we 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, would be positively associated with both functional diversity (e.g., Ordóñez & Svenning, 2017) and network specialization (Dalsgaard et al., 2011; Martín González et al., 2015; Trøjelsgaard & Olesen, 2013), whereas past climate instability should decrease specialization (Dalsgaard et al., 2011; Ordóñez & Svenning, 2017). Climatic seasonality, in contrast, 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 would have a positive effect on both functional diversity and network specialization by generating habitat heterogeneity and enabling species to track changing climates more easily (Ordóñez & Svenning, 2017; Sonne et al., 2016). In contrast, insularity is expected to have a negative effect owing to ecological release and increased generalization on islands (Traveset,

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' N to 31°48' S (updated from Martín González et al., 2015; see Supporting Information Appendix S1). 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, because they characterize other types of interactions (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 (c. 46%

of the 345 species in the IOC Bird List; Supporting Information Appendix S2) and 984 species of plants from 85 families (Supporting Information 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 and interspecific competition for nectar: bill length, bill curvature and body mass (Dalsgaard et al., 2009; Feinsinger & Colwell, 1978; López-Segoviano et al., 2018; Maglianesi et al., 2014; Maglianesi, Blüthgen, et al., 2015; Maruyama et al., 2014; Snow & Snow, 1972; Stiles, 1981; Vizentin-Bugoni et al., 2014). Bill length and curvature were measured by inspecting an average of 10 adult specimens, both males and females, deposited in museums (Zanata, Dalsgaard, Rahbek, & Varassin, 2018; see details in Supporting Information Appendix S6); body mass data were gathered from the literature (Supporting Information Appendix S2). For all three traits, we used the mean trait values per species, because interspecific trait variation is larger than intraspecific 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 (CV) across all hummingbird species averaged 6.2% for bill length and 8.3% for bill

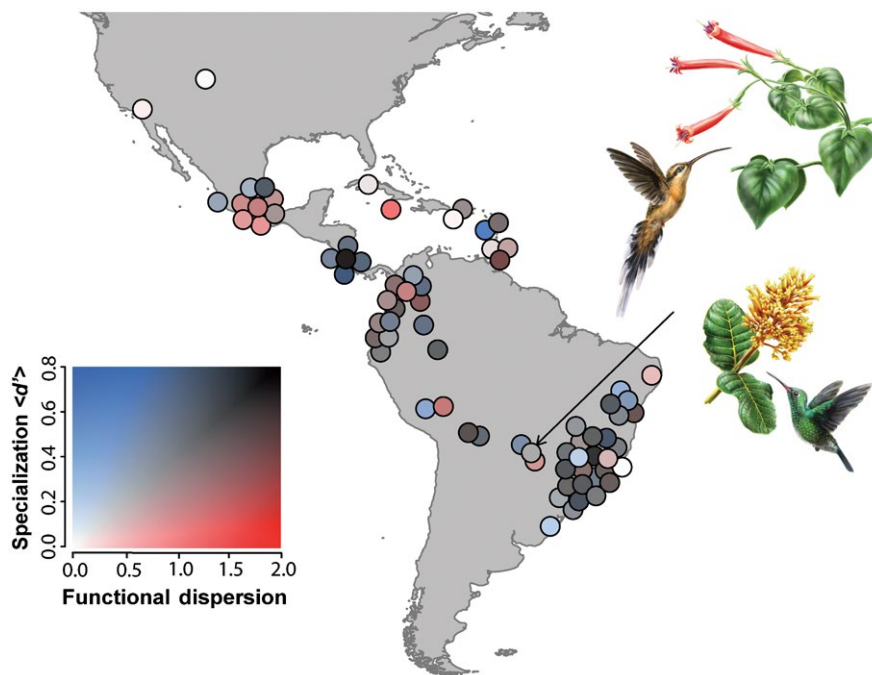


FIGURE 1 The location of the 74 plant-hummingbird networks used in the study, showing the relationship between hummingbird specialization, $\langle d' \rangle$, and functional dispersion. For clarity, circles for some study sites were moved to minimize overlap. The illustration on the right depicts how 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; Credit: Pedro Lorenzo). Points along the white-grey-black gradient indicate communities with better correspondence between functional dispersion and specialization

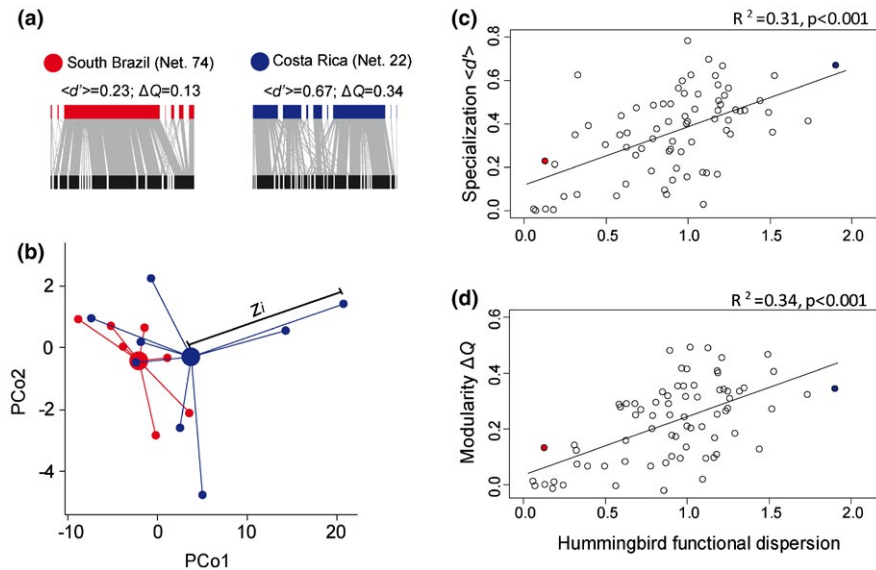


FIGURE 2 The relationship between hummingbird functional dispersion (FDIs) and network structure. (a) An example illustrating two networks with similar number of hummingbird species (Net 74 = 7, Net 22 = 8) but with contrasting FDIs. Networks on top depict the interaction networks, with hummingbird species 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) The FDIs is measured as the mean of the distance (Z_i) of all species (small circles) to its community centroid (large circles) in multivariate trait space generated by a principal coordinates 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). (c,d) 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 colours

curvature, whereas interspecific variation amounted to 42.4% and 246.9%, respectively (see also Supporting Information Appendix S2).

To calculate hummingbird functional diversity (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 coordinates analysis (Villéger, Mason, & Moullot, 2008; Figure 2). Traits were standardized to zero mean and unit variance before 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 co-occurring in a community. This measure estimates the total trait variability within each community. It is equivalent to functional richness (Villéger et al., 2008) and conceptually similar to the FD index of Petchey and Gaston (2002), with the advantage that it can be calculated for communities comprising only two coexisting 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 the 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). The FDIs accounts for differences in the frequencies of species 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 using the

sum of interactions for each hummingbird species in the interaction matrices (see details in Supporting Information Appendices S7 and 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 analysed in this study (MST and FDIs) represent complementary aspects of FD and are only moderately correlated (Pearson’s $r = .57$, $p < .05$, $n = 74$ networks). If FDIs is calculated without weighting by species abundance, this correlation becomes higher ($r = .80$, $p < .05$). Moreover, MST showed a stronger correlation with hummingbird species richness (Pearson’s $r = .76$, $p < .05$) than did weighted FDIs ($r = .43$, $p < .05$).

2.3 | Plant functional diversity

We computed plant functional diversity for a subset of 28 networks, comprising 103 hummingbird and 467 plant species from mainland and island communities (51.2% and 47.5% of the complete dataset, respectively). To do this, we considered three traits that have been associated with hummingbird specialization and partitioning of interactions among flowers: (a) floral corolla length (e.g., Maglianesi et al., 2014; Maruyama et al., 2014); (b) the colour spectrum visible to the human eye, reflecting different degrees of specialization to ornithophily (Dalsgaard et al., 2009; Wilson, Castellanos, Hogue, Thomson, & Armbruster, 2004); and (c) plant life form, reflecting resource availability (e.g., trees having higher floral display

and attracting territorial hummingbirds; Feinsinger & Colwell, 1978) and/or vegetation strata (Jordano, Bascompte, & Olesen, 2006; see details on plant trait assessment in Supporting Information Appendices S4–S6). We calculated plant FDis for each network, based on the pairwise Gower distances as suggested for the combination of continuous (corolla length) and categorical (colour, life form) trait variables (Laliberté & Legendre, 2010). Weighting of individual species in the FDis metric were given by independent measures of local floral abundances (Supporting Information Appendix S6). For this subset of communities, we also recalculated hummingbird FDis to test whether it relates to plant functional diversity. In addition, because corolla length was the only continuous variable available for plants, we also estimated plant and hummingbird FDis based solely on corolla and bill length, respectively. The results from these 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 perspective of the hummingbirds, 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, 2010; Blüthgen et al., 2006). 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 $r = .93$, $p < .05$). We primarily 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, 2015). Here, we used the QuanBiMo, a modularity-searching algorithm specifically designed for quantitative bipartite networks (Dormann & Strauss, 2014). Both $\langle d' \rangle$ and Q scale from zero to one, with zero indicating low specialization/modularity, respectively and one high specialization/modularity, respectively (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; Vizentin-Bugoni 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 report only the presence or absence of interactions between species pairs (Blüthgen et al., 2006; Vizentin-Bugoni et al., 2016). Nevertheless, to minimize potential biases attributable to differences in sampling among networks, we Δ -transformed our metrics (Dalsgaard et al., 2017; Schleuning et al., 2012). In this transformation, the mean value of a metric obtained by multiple randomizations of a null network is subtracted from the observed value (Dalsgaard et al., 2017; Schleuning et al., 2012). Here, we used the Patefield null model, which fixes the network size and the marginal totals, (i.e., species richness and the total number of interactions of the species), 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 but not $\Delta \langle d' \rangle$ in the main results. Nonetheless, results for both untransformed and Δ -transformed specialization and modularity metrics were similar (see Supporting Information 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. Sampling intensity was included in the models (see Table 1), but as network asymmetry was only weakly related to the calculated metrics ($r = -.21$, $p = .07$ for $\langle d' \rangle$ and $r = -.09$, $p = .42$ for ΔQ), we did not consider it further.

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-s rasters (v. 1.4; 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 CV 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-s DEM (CGIAR; <https://srtm.csi.cgiar.org/>), covering from 60 N to 60 S, 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

TABLE 1 Model selection and averaging results of the multi-predictor linear models explaining the variation of hummingbird specialization, $\langle d' \rangle$, and network modularity, ΔQ , corrected by the Patefield null model

	Complementary specialization $\langle d' \rangle$						Modularity ΔQ					
	FDis			MST			FDis			MST		
	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	–
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	–
R^2_{adj}			0.42			0.36			0.48			0.37
AICc			177.3			183.8			168.9			182.7

Notes. We used two functional diversity measures, hummingbird 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 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; and R^2_{adj} = variation explained by the minimum adequate model with the lowest AICc. Acronyms of the predictors: AnomP = precipitation anomaly; AnomT = temperature anomaly; FDis = functional dispersion; MAP = mean annual precipitation; MST = minimum spanning tree; Plants = plant richness; PS = precipitation seasonality; SI = sampling intensity; Topography = topographical variation; TS = temperature seasonality. See Methods for details.

precipitation from the Last Glacial Maximum (LGM) to the present, as estimated using two different models, CCSM3 (Collins et al., 2006; Otto-Bliesner et al., 2006) and MIROC 3.2 (K-2004 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 (one, island; zero, mainland). To meet statistical assumptions of normality, MAP was square root transformed and TS was \log_{10} transformed before 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 the spatial variability of the climatic variable in the calculations (Loarie et al., 2009) and is correlated with topographic heterogeneity, 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 Supporting Information (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 multi-predictor 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 MST and FDis, 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) to the set of predictors. Finally, we included plant species richness (Plants), because this has been shown to influence resource partitioning in flower–bird networks (Zanata et al., 2017) and might potentially act independently 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 and hummingbird FDis predicted network level specialization $\langle d' \rangle$, calculated for plants and hummingbirds separately, and ΔQ .

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 because these were correlated; for comparison, we also fitted a model with unweighted FDis (i.e., without incorporating abundance; Supporting Information 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 (Supporting Information Appendix S12). Model performance of all combinations of predictor variables was assessed based on the Akaike information criterion with correction for small samples (AICc). Model selections were performed with the function *dredge* in the R package “MuMIn” (Barton, 2014), according to their AICc. In all cases, multiple models presented $\Delta AICc$ values ≤ 2.0 in relationship 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 owing to the lack of a clear hypothesis justifying their inclusion. Spatial autocorrelation in model 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 5,000 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 modelling was conducted using the “spdep” package in R (Bivand & Piras, 2015). The spatial connections between networks were determined as the three nearest neighbours. For the SAR model, no significant spatial autocorrelation remained in the residuals (see also Supporting Information 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: (a) 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 (b) another based on the hypothesis that FD directly affects network metrics (i.e., 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 $\sum w_i < 0.3$, and thus were not included in the SEMs (see Table 1; Supporting Information Appendix S9–S12). As MST did not 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 χ^2 test, a comparative fit index (CFI) and a root mean square error of approximation (RMSA). The χ^2 test measures the coincidence between the empirical and the fitted variance-covariance structure in the data. Here, models were accepted if $p > .05$. The CFI relates the χ^2 of the model to the χ^2 value of an independent model assuming zero correlation among variables while also accounting for sample size (Shipley, 2002). The CFI ranges between zero and one, and models with $CFI > .09$ were considered to have an appropriate fit (Shipley, 2002). Finally, the RMSA index was included owing 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 (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: $R^2 = .08$, $p = .02$; $\langle d' \rangle$: $R^2 = .05$, $p = .05$; Q : $R^2 = .09$, $p < .01$), although MST was higher at low latitudes ($R^2 = .37$, $p < .01$).

All best-fitting models explaining network structure included hummingbird FDis as a predictor, showing a positive association with both hummingbird complementary specialization, $\langle d' \rangle$, and network modularity, ΔQ (Table 1; Figure 2). Moreover, hummingbird 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; Supporting Information Appendix S9). On the contrary, MST had a negligible importance in predicting network structure (Table 1), as did unweighted FDis (Supporting Information Appendix S11) and hummingbird richness (Supporting Information Appendix S12). The MAP was positively related to hummingbird specialization, $\langle d' \rangle$ (Table 1), whereas plant richness was positively related 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, plant FDis showed less variation than hummingbird FDis (CV = 24.2% vs. 43.2%, Supporting Information Appendix S5). Plant FDis was unrelated to plant richness ($R^2 = .01$, $p = .51$), hummingbird FDis ($r = .07$, $p = .70$) or network structure (plant $\langle d' \rangle$: $R^2 = .09$, $p = .11$; ΔQ : $R^2 = .04$, $p = .34$). Within this subset of networks, hummingbird FDis was positively associated

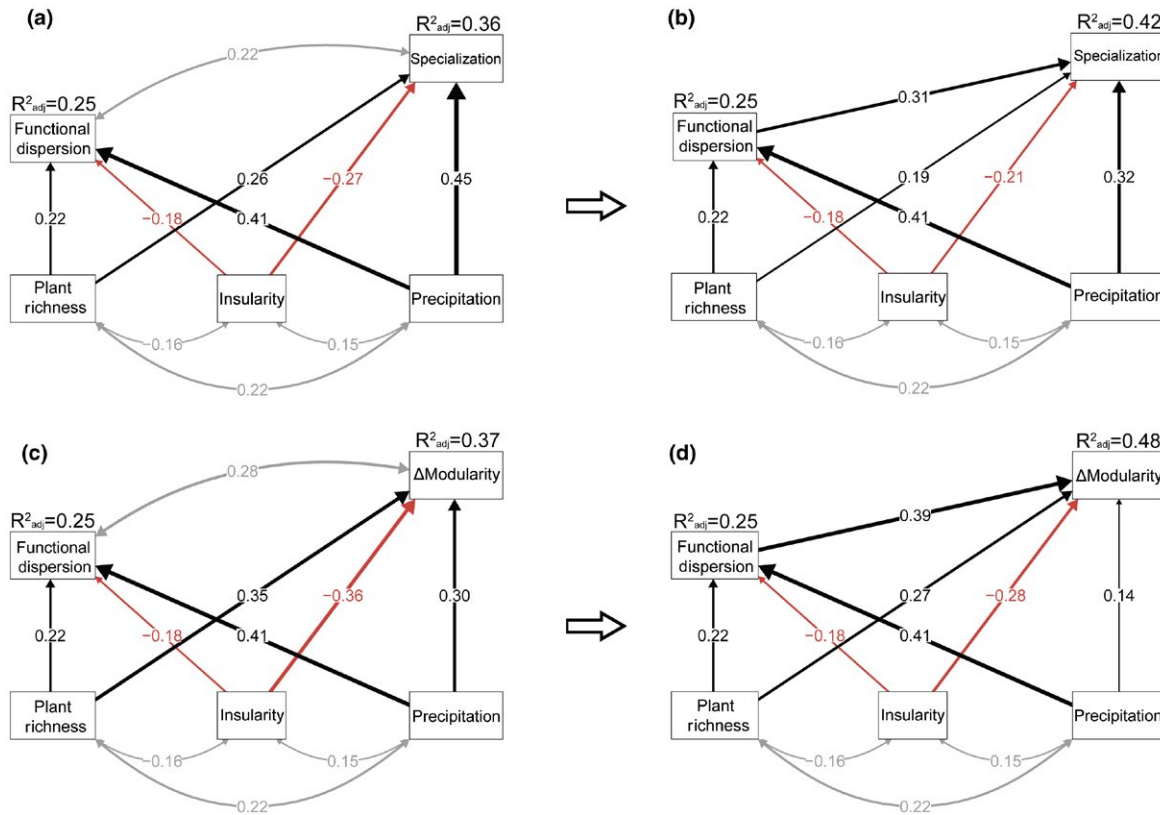


FIGURE 3 Structural equation models (SEMs) showing the direct and indirect associations among environmental and richness predictors, functional dispersion (FDIs) with complementary specialization (d' ; a,b) and modularity (ΔQ ; c,d). Models in (a) and (c) assume a covariation between FDis and network structure, whereas (b) and (d) consider a directional relationship between FDis and network metrics. 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, whereas red arrows indicate negative relationships, with the thickness of each arrow reflecting their standardized path coefficients. Double-headed grey arrows indicate covariance links

with the degree of interaction partitioning (hummingbird $<d'>$: $R^2 = .39$, $p < .01$; ΔQ : $R^2 = .55$, $p < .01$), consistent with the analysis across all networks.

Structural equation models 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 a 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 ($\beta = .32$; Figure 3b) and indirectly through FDis (indirect coefficients are obtained by multiplication of coefficients, i.e., $.41 \times .31 = .13$; Figure 3b). In the case of modularity, the indirect association with precipitation ($.41 \times .39 = .16$; Figure 3d) was similar to the direct one ($\beta = .14$; Figure 3d). Plant species richness (specialization: direct = $.19$, indirect = $.07$; modularity: direct = $.27$, indirect = $.09$; Figure 3b,d) and insularity (specialization: direct = $-.21$, indirect = $-.06$; modularity: direct = $-.28$, indirect = $-.07$; Figure 3b,d) showed stronger direct and weaker indirect associations with network metrics.

4 | DISCUSSION

Functional diversity of hummingbirds correlated with network structure in plant–hummingbird 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 showed that plant species 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 may be related partly to precipitation, because 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), has previously reported a positive relationship between plant richness and network specialization. Interestingly, the association between plant richness and network structure was not mirrored by covariation 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 (Vizentin-Bugoni et al., 2014; Weinstein & Graham, 2017a). For instance, hummingbird-visited plant species with long corollas often have low abundances (Vizentin-Bugoni et al., 2016), thus contributing little to abundance-weighted estimates of plant FDis. However, flowers with long corollas are frequently visited by abundant long-billed hummingbirds, which fosters interaction partitioning (Maglianesi, Böhning-Gaese, et al., 2015; Maruyama et al., 2014; Weinstein & Graham, 2017a). A closer association between network specialization and consumer FD, but not plant FD, may also result from phenological differences between plants and animals. Although many hummingbird species are constantly present in the community, the turnover of flowering plant species is usually high, suggesting that morphologically specialized plant species may be replaced by functionally similar species temporarily (Bergamo et al., 2017; Weinstein & Graham, 2017b). Thus, plant assemblages may have greater species redundancy, 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 is likely to enforce niche partitioning among birds more than among simultaneously flowering plant species. Overall, our results indicate that total resource/niche space, as expressed by plant richness, allows for a finer division of resources and potential occurrences of species with distinct strategies within communities.

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 also detected indirect relationships between network structure and insularity through bird functional diversity. Island communities, especially those from oceanic islands, tend to show a high degree of generalization, consistent with an interaction release and niche expansion in impoverished communities (Traveset, et al., 2015). Consequently, plant-pollinator interaction networks on these islands can be less specialized than those on continents; for example, showing greater pollinator overlap among plants (Traveset et al., 2016). In accordance with this, higher generalization has previously been shown for insular plant-hummingbird networks (Martín González et al., 2015), and our results here indicate that part of this greater 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 (Gravel et al., 2016; Kissling & Schleuning, 2015). 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, because 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 (Brosi & Briggs, 2013; Inouye, 1978). Hence, if pollinator functional diversity is reduced in response to climate change or direct human-induced disturbance (e.g., Grass et al., 2014; Rader et al., 2014), this is likely to result in a reduced resource partitioning among pollinators and lower effectiveness of pollination (Fontaine et al., 2005; Fründ et al., 2013; Schleuning et al., 2015). In this regard, we note that species abundances have an influence in addition to species traits, because unweighted functional diversity metrics (MST and unweighted FDis) were only weakly associated with network structure. Other studies have likewise found that unweighted functional diversity indices were only weakly associated with ecosystem functions delivered by animals (e.g., Gagic et al., 2015). Therefore, functionally distinct species in a community must be sufficiently abundant to fulfil their functional roles in interaction networks and contribute to ecosystem functioning. The apparent asymmetry between plant and bird functional diversity could stem from comparatively low abundance of morphologically specialized plant species, each potentially less important at the community level, compared with functionally specialized hummingbirds with high abundances, fulfilling crucial ecological roles in communities (e.g., large-bodied hermits).

Taken together, our results show how network structure is associated with environmental factors, pollinator functional diversity and plant richness at a continental scale. 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 (Bartomeus et al., 2016; Guimarães et al., 2011). In conclusion, we believe that our results indicating that environmental factors exert indirect effects on interaction niche partitioning, mediated by consumer trait diversity and resource richness, yield a 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.

5 | BIOSKETCH

PIETRO K. MARUYAMA is an ecologist, with a broad interest ranging from natural history to the macroecology of plant-animal mutualistic interactions. This study is part of the HummLab research team (wordpress.hummlab.com), an ongoing research collaboration on plant-hummingbird networks across the Americas involving numerous researchers from a wide range of institutions and countries.

6 | SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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DATA ACCESSIBILITY

All the predictors and network indices used for the macroecological analysis and the hummingbird trait data are supplied as Supporting Information (for bill length and curvature, see also Zanata et al., 2018: <https://doi.org/10.6084/m9.figshare.6151196.v2>).

ORCID

Pietro Kiyoshi Maruyama  <http://orcid.org/0000-0001-5492-2324>

Jeferson Vizentin-Bugoni  <http://orcid.org/0000-0002-6343-3650>

Erich Fischer  <http://orcid.org/0000-0001-8722-9876>

Juan Francisco Ornelas  <http://orcid.org/0000-0002-1124-1163>

Isabela G. Varassin  <http://orcid.org/0000-0001-9189-8765>

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APPENDIX 1

DATA SOURCES AND SUPPORTING REFERENCES

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