

2018-10

Functional diversity mediates macroecological variation in planthummingbird interaction networks

Maruyama, PK

<http://hdl.handle.net/10026.1/12598>

10.1111/geb.12776

Global Ecology and Biogeography

Wiley

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

1 **Running title:** Functional diversity and network structure

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

4 **Authors:** Pietro Kiyoshi Maruyama^{1,2}, Jesper Sonne², Jeferson Vizentin-Bugoni^{3,4}, Ana M.
5 Martín González², Thais B. Zanata^{2,5}, Stefan Abrahamczyk⁶, Ruben Alarcón⁷, Andréa C.
6 Araujo⁸, Francielle P. Araújo⁹, Andrea C. Baquero², Edgar Chávez-González¹⁰, Aline G.
7 Coelho¹¹, Peter A. Cotton¹², D. Matthias Dehling^{13,14}, Erich Fischer⁸, Glauco Kohler¹⁵, Carlos
8 Lara¹⁶, Flor Maria G. Las-Casas¹⁷, Adriana O. Machado¹⁸, Caio G. Machado¹¹, María A.
9 Maglianesi^{13,19}, Tiago S. Malucelli⁵, Oscar Humberto Marín-Gómez²⁰, Paulo E. Oliveira¹⁸,
10 Juan Francisco Ornelas²¹, Raul Ortiz-Pulido²², Mónica B. Ramírez-Burbano²³, Márcia A.
11 Rocca²⁴, Licléia C. Rodrigues²⁵, Liliana Rosero-Lasprilla²⁶, Ana M. Rui²⁷, Brody Sandel²⁸,
12 Jens-Christian Svenning^{29,30}, Boris A. Tinoco³¹, Isabela G. Varassin⁵, Stella Watts³², Carsten
13 Rahbek^{2,33}, Marlies Sazima¹, Matthias Schleuning¹³, Bo Dalsgaard²

14 **Affiliations:**

15 1. Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de
16 Campinas (Unicamp), Cx. Postal 6109, CEP:13083-970 Campinas, SP, Brasil. (PKM:
17 pietrokiyoshi@gmail.com, MSA: msazima@unicamp.br)

18 2. Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark,
19 University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. (JS:
20 jesper2904@hotmail.com, AMMG: ana.maria.martingonzalez@gmail.com, ACB:
21 baquero.andrea@gmail.com, CR: crahbek@snm.ku.dk, BD: bo.dalsgaard@snm.ku.dk)

22 3. Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas (Unicamp),
23 Cx. Postal 6109, CEP: 13083-970, Campinas, SP, Brasil. (jbugoni@yahoo.com.br)

24 4. Natural Resources and Environmental Science Department, University of Illinois at
25 Champaign-Urbana, 61820, IL, USA

26 5. Laboratório de Ecologia Vegetal, Departamento de Botânica, Centro Politécnico,
27 Universidade Federal do Paraná, Cx. 19031, 81531-980, Curitiba, PR, Brasil (TBZ:
28 thaisbzanaata@gmail.com, TSM: malucelli.ts@gmail.com, IGV: isagalarda@gmail.com)

- 29 6. Nees Institute for Biodiversity of Plants, Meckenheimer Allee 170, Bonn 53115, Germany
30 (sabraham@uni-bonn.de)
- 31 7. Biology Program, California State University Channel Islands, Camarillo, CA 23012, USA
32 (ruben.alarcon@csuci.edu)
- 33 8. Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, 79070-900, Campo
34 Grande, MS, Brasil (ACA: andrea.araujo@ufms.br, EF: erich.fischer@ufms.br)
- 35 9. Universidade Estadual do Rio Grande do Sul, São Francisco de Paula, RS, Brasil.
36 (franciaralp@yahoo.com.br)
- 37 10. Red de Ecoetología, Instituto de Ecología, AC, Xalapa, Veracruz, 91070, Mexico
38 (edgar.chavez.gonzalez.18@gmail.com)
- 39 11. Laboratório de Ornitologia, Departamento de Ciências Biológicas, Universidade Estadual
40 de Feira de Santana, Feira de Santana, BA, 44036-900, Brasil (AGC:
41 alinegcoelho@yahoo.com.br, CGM: gracom@uol.com.br)
- 42 12. Marine Biology & Ecology Research Centre, University of Plymouth, Plymouth PL4
43 8AA, UK. (p.cotton@plymouth.ac.uk)
- 44 13. Senckenberg Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25,
45 60325 Frankfurt (Main), Germany. (DMD: dmdehling@gmail.com, MAM:
46 mmaglianesi@uned.ac.cr, MSc: matthias.schleuning@senckenberg.de)
- 47 14. School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch
48 8140, New Zealand.
- 49 15. Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Petrópolis, 69080-
50 971, Manaus, AM, Brasil (certhiaxis@gmail.com)
- 51 16. Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, Km
52 10.5 Autopista Tlaxcala-San Martín Texmelucan, San Felipe Ixtacuixtla, Tlaxcala 90120,
53 Mexico. (laracar@posgradouatx.com.mx)
- 54 17. Laboratory of Ecology, Systematics and Evolution of Birds, Federal University of
55 Pernambuco, 50670-420, Recife, PE, Brasil. (flormarialc@hotmail.com)
- 56 18. Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, MG, Brasil.
57 (AOM: adrianaoliveiramachado@yahoo.com.br, PEO: poliveiragm@gmail.com)
- 58 19. Vicerrectoría de Investigación, Universidad Estatal a Distancia, de la Rotonda la Betania
59 500m al este, Carretera a Sabanilla, Mercedes de Montes de Oca, 474-2050 San José, Costa
60 Rica.
- 61 20. Instituto de Ecología, A.C, Xalapa, Veracruz, 91070 Mexico. (oschumar@gmail.com)

- 62 21. Departamento de Biología Evolutiva, Instituto de Ecología, AC, Xalapa, Veracruz, 91070,
63 Mexico. (francisco.ornelas@inecol.mx)
- 64 22. Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería,
65 Universidad Autónoma del Estado de Hidalgo, Km 4.5, Carretera Pachuca–Tulancingo,
66 Mineral de la Reforma, C.P. 42184 Pachuca, Hidalgo, Mexico. (raulortizpulido@yahoo.com)
- 67 23. Programa de doctorado en Ciencias-Biología, Facultad de Ciencias Naturales y Exactas,
68 Departamento de Biología, Universidad del Valle, Cali, Colombia
69 (monicab.ramirez@gmail.com)
- 70 24. Departamento de Ecologia, Centro de Ciências Biológicas e da Saúde, Universidade
71 Federal de Sergipe, Avenida Marechal Rondon, s/n, Jardim Rosa Elze, CEP: 49100000 - São
72 Cristóvão, SE, Brasil. (roccamarcia@yahoo.com.br)
- 73 25. Laboratório de Ornitologia, Departamento de Zoologia, ICB, Universidade Federal de
74 Minas Gerais. Caixa Postal 486, 31270-901, Belo Horizonte, MG, Brasil.
75 (licleia@yahoo.com.br)
- 76 26. Escuela de Ciencias Biológicas, Grupo de Investigación Biología para la Conservación,
77 Universidad Pedagógica y Tecnológica de Colombia, Tunja, Boyacá, Colombia.
78 (lilianaroslasprilla@gmail.com)
- 79 27. Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade
80 Federal de Pelotas, Pelotas, RS, Brasil. (ana.rui@ufpel.edu.br)
- 81 28. Department of Biology, Santa Clara University. 500 El Camino Real, Santa Clara CA
82 95057, USA. (bsandel@scu.edu)
- 83 29. Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus
84 University, Ny Munkegade 114, Aarhus C 8000, Denmark. (svenning@bios.au.dk)
- 85 30. Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Aarhus
86 University, Ny Munkegade 114, Aarhus C 8000, Denmark.
- 87 31. Escuela de Biología, Ecología y Gestión, Universidad del Azuay, Cuenca, Ecuador.
88 (btinoco@uazuay.edu.ec)
- 89 32. Landscape and Biodiversity Research Group, Department of Environmental and
90 Geographical Sciences, University of Northampton, Avenue Campus, St George's Avenue,
91 Northampton NN2 6JD, UK. (hummingbird_pe@yahoo.com)
- 92 33. Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5
93 7PY, UK.

94

Correspondence: Pietro Kiyoshi Maruyama, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas (Unicamp), Cx. Postal 6109, CEP:13083-970 Campinas, SP, Brasil. **e-mail:** pietrokiyoshi@gmail.com; **phone:** +55 19 98261-6145

Number of words in the Abstract: **294**

Number of words in main body of the paper: **4919**

Number of references: **70**

ACKNOWLEDGMENTS

Financial support was provided by São Paulo Research Foundation through a Postdoctoral grant to PKM (FAPESP grant #2015/21457-4). PKM, JS, TBZ, CR and BD acknowledge the Danish National Research Foundation for funding for the Center for Macroecology, Evolution and Climate, grant no. DNRF96. Funding was also provided by CAPES to JVB (Ph.D. scholarship and PDSE proc. 8012/2014-08), TBZ (PDSE proc. 8105/2014-6), LCR (proc. 2725/2011) and ACA; by CNPq to IGV and TBZ (proc. 445405/2014-7), MSa (proc. 303084/2011-1) and EF (proc. 307016/2015-3); by CONACyT to ROP (project 258364); VILLUM FONDEN to JCS (VILLUM Investigator project, grant 16549). We thank museum curators Paul Sweet (AMNH), John Bates (FMNH), Juliana Paulo da Silva (MBML), Marcos Raposo (MNRJ), Alexandre Aleixo (MPEG), Robert Prys-Jones and Mark Adams (NHMT), Gerald Mayr (SMF), Gary Graves (USNM), Till Töpfer and Karl-Ludwig Schuchmann (ZFMK) and Jon Fjeldså (ZMSNM) for allowing the hummingbirds measurements in the museums and Louis Hansen for help in gathering hummingbird weight data.

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

139 hummingbird functional diversity. Plant functional diversity, however, was unrelated to
140 hummingbird functional diversity and network structure.

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

147

148 **KEYWORDS**

149 functional dispersion, insularity, modularity, network structure, niche partitioning, plant-
150 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 & Tscharntke, 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 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 (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; López-Segoviano, 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 co-

occurring 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, Vizentin-Bugoni, Dalsgaard, Sazima & Sazima, 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 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; 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 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

366 (estimated as the standard deviation across monthly temperatures; TS), and precipitation
367 seasonality (estimated as the coefficient of variation for monthly precipitation means; PS). To
368 determine the topographical variation (Topography) at each study site, we also used the
369 WorldClim digital elevation model (DEM). This combines the SRTM gap-filled 30 arc
370 second DEM (CGIAR - <http://srtm.csi.cgiar.org/>), covering from 60N to 60S with the
371 GTOPO30 DEM (<https://lta.cr.usgs.gov/GTOPO30>) for other parts of the world. Topography
372 was represented by the standard deviation of elevation within a 10 km radius around each
373 study site. We described paleoclimate stability using the change in temperature and
374 precipitation from the Last Glacial Maximum (LGM) to the present, as estimated using two
375 different models, CCSM3 (Collins et al., 2006; Otto-Bleisner et al., 2006) and MIROC 3.2
376 (K-1 model developers, 2004). For each site, we calculated the change in temperature and
377 precipitation from the LGM to the present (Anomaly), and its spatial rate of displacement
378 (Velocity) as complementary measures of past to present climate variability (Loarie et al.,
379 2009). As our data cover a large geographical extent, we assumed that the regionally
380 downscaled climate estimates are good indicators of the variation of local climate among
381 communities. In addition to data on past and current climate and topography, we included
382 insularity as a dummy variable (1 - island, 0 - mainland). To meet statistical assumptions of
383 normality, MAP was square root transformed and TS was log-transformed prior to further
384 analyses. All variables were scaled to zero mean and unit variance. As velocity and anomaly
385 both describe historical climate change, and are derived from the same model projection, we
386 built one model for each of the two measures of historical climate change. As velocity
387 includes topographical heterogeneity in the calculations (Loarie et al., 2009), we did not
388 include velocity and topography in the same models. In the main text, we report the results
389 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 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 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., Σw_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 auto correlation 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 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 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 (Vizentin-Bugoni 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, plant-pollinator 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 plant-hummingbird 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.

REFERENCES

Bartomeus, I., Gravel, D., Tylianakis, J. M., Aizen, M. A., Dickie, I. A., & Bernard-Verdier, M. (2016). A common framework for identifying linkage rules across different types of interactions. *Functional Ecology*, 30, 1894–1903.

604 Barton, K. (2014). MuMIn: Multi-model inference. *R package version 1.10.5*.

605 Bergamo, P. J., Wolowski, M., Maruyama, P. K., Vizentin-Bugoni, J., Carvalheiro, L. G., &
606 Sazima, M. (2017). The potential indirect effects among plants via shared
607 hummingbird pollinators are structured by phenotypic similarity. *Ecology*, 98, 1849–
608 1858.

609 Bjornstad, O. N. (2016) ncf: spatial nonparametric covariance functions. *R package version*
610 *1.1–7*

611 Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: a
612 critique and an ecologist's guide. *Basic and Applied Ecology*, 11, 185–195.

613 Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species
614 interaction networks. *BMC Ecology*, 6, 9.

615 Brosi, B. J., & Briggs, H. M. (2013). Single pollinator species losses reduce floral fidelity and
616 plant reproductive function. *Proceedings of the National Academy of Sciences USA*,
617 110, 13044–13048.

618 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference*. 2nd
619 edn. Springer-Verlag, New York, USA.

620 Bivand, R., & Piras, G. (2015). Comparing implementations of estimation methods for spatial
621 econometrics. *Journal of Statistical Software*, 63, 1–36.

622 Collins, W. D., Bitz, C. M., Blackmon, M. L., Bonan, G. B., Bretherton, C. S., Carton, J. A.,
623 ...Smith, R. D. (2006). The community climate system model version 3 (CCSM3).
624 *Journal of Climate*, 19, 2122–2143.

625 Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular
626 context. *Journal of Experimental Botany*, 59, 715–727.

627 Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A.,
628 Andersen, L. H., & Tossas, A. G. (2009). Plant–hummingbird interactions in the West
629 Indies: floral specialisation gradients associated with environment and hummingbird
630 size. *Oecologia*, 159, 757–766.

631 Dalsgaard, B., Magård, E., Fjeldså, J., Martín González, A. M., Rahbek, C., Olesen, J. M., ...
632 Svenning, J. C. (2011). Specialization in plant-hummingbird networks is associated
633 with species richness, contemporary precipitation and Quaternary climate-change
634 velocity. *PLoS ONE*, 6, e25891.

635 Dalsgaard, B., Schleuning, M., Maruyama, P. K., Dehling, D. M., Sonne, J., Vizentin-Bugoni,
636 J., ... Rahbek, C. (2017). Opposed latitudinal patterns of network-derived and dietary
637 specialization in avian plant-frugivore interaction systems. *Ecography*, 40, 1395–
638 1401.

639 Dormann, C.F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite
640 networks. *Methods in Ecology and Evolution*, 5, 90–98.

641 Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2008). Indices, graphs and null
642 models: analyzing bipartite ecological networks. *Open Ecology Journal*, 2, 7–24.

643 Feinsinger, P., & Colwell R. K. (1978). Community organization among Neotropical nectar-
644 feeding birds. *American Zoologist*, 18, 779–795.

645 Fontaine, C., Dajoz, I., Meriguet, J., & Loreau, M. (2005). Functional diversity of plant–
646 pollinator interaction webs enhances the persistence of plant communities. *PLoS*
647 *Biology*, 4, e1.

648 Fründ, J., Dormann, C. F., Holzschuh, A., & Tschardtke, T. (2013). Bee diversity effects on
649 pollination depend on functional complementarity and niche shifts. *Ecology*, 94,
650 2042–2054.

651 Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., ... Bommarco, R.
652 (2015). Functional identity and diversity of animals predict ecosystem functioning
653 better than species-based indices. *Proceedings of the Royal Society Biological*
654 *Sciences*, 282, 20142620.

655 Graham, C. H., Parra, J. L., Tinoco, B. A., Stiles, F. G., & McGuire, J. (2012). Untangling the
656 influence of ecological and evolutionary factors on trait variation across hummingbird
657 assemblages. *Ecology*, 93, S99–S111.

658 Grass, I., Berens, D. G., & Farwig, N. (2014). Natural habitat loss and exotic plants reduce the
659 functional diversity of flower visitors in a heterogeneous subtropical landscape.
660 *Functional Ecology*, 28, 1117–1126.

661 Gravel, D., Albouy, C., & Thuiller, W. (2016). The meaning of functional trait composition of
662 food webs for ecosystem functioning. *Philosophical Transactions of the Royal Society*
663 *Biological Sciences*, 371, 20150268.

664 Guimarães Jr, P. R., Jordano, P., & Thompson, J. N. (2011). Evolution and coevolution in
665 mutualistic networks. *Ecology Letters*, 14, 877–885.

666 Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high
 667 resolution interpolated climate surfaces for global land areas. *International Journal of*
 668 *Climatology*, 25, 1965–1978.

669 Inouye, D.W. (1978). Resource partitioning in bumblebees: experimental studies of foraging
 670 behavior. *Ecology*, 59, 672–678.

671 Jordano, P., Bascompte, J., & Olesen, J. M. (2006). The ecological consequences of complex
 672 topology and nested structure in pollination webs. In N. M. Waser & J. Ollerton
 673 (Eds.), *Plant-pollinator interactions: From specialization to generalization* (pp. 173–
 674 199). Chicago, IL: University of Chicago Press.

675 Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, M. H., & Stang,
 676 M. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and
 677 as structuring mechanism of ecological networks. *Functional Ecology*, 27, 329–341.

678 Junker, R. R., Blüthgen, N., & Keller, A. (2015). Functional and phylogenetic diversity of
 679 plant communities differently affect the structure of flower-visitor interactions and
 680 reveal convergences in floral traits. *Evolutionary Ecology*, 29, 437–450.

681 K-1 Model Developers. (2004). K-1 Coupled GCM (MIROC) description. *K-1 Technical*
 682 *Report*, No.1.

683 Kissling, W. D., & Schleuning, M. (2015). Multispecies interactions across trophic levels at
 684 macroscales: retrospective and future directions. *Ecography*, 38, 346–357.

685 Kissling, W. D., & Carl, G. (2008). Spatial autocorrelation and the selection of simultaneous
 686 autoregressive models. *Global Ecology and Biogeography*, 17, 59–71.

687 Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity.
688 *Proceedings of the National Academy of Sciences USA*, *104*, 5925–5930.

689 Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional
690 diversity from multiple traits. *Ecology*, *91*, 299–305.

691 Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009).
692 The velocity of climate change. *Nature*, *462*, 1052–1055.

693 López-Segoviano, G., Bribiesca, R., & Arizmendi, M. C. (2018). The role of size and
694 dominance in the feeding behavior of coexisting hummingbirds. *Ibis*, *160*, 283–292.

695 MacArthur, R. H., & Levins, R. (1967). Limiting similarity convergence and divergence of
696 coexisting species. *The American Naturalist*, *101*, 377–385.

697 Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014).
698 Morphological traits determine specialization and resource use in plant-hummingbird
699 networks in the Neotropics. *Ecology*, *95*, 3325–3334.

700 Maglianesi, M. A., Böhning-Gaese, K., & Schleuning, M. (2015). Different foraging
701 preferences of hummingbirds on artificial and natural flowers reveal mechanisms
702 structuring plant–pollinator interactions. *Journal of Animal Ecology*, *84*, 655–664.

703 Maglianesi M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2015). Functional
704 structure and specialization in three tropical plant-hummingbird interaction networks
705 across an elevational gradient in Costa Rica. *Ecography*, *38*, 1119–1128.

706 Martín González, A. M., Dalsgaard, B., Nogués-Bravo, D., Graham, C. H., Schleuning, M.,
707 Maruyama, P. K., ... Martinez, N. D. (2015). The macroecology of phylogenetically

708 structured hummingbird-plant networks. *Global Ecology and Biogeography*, 24,
709 1212–1224.

710 Maruyama, P. K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I., & Sazima, M. (2015).
711 Nectar robbery by a hermit hummingbird: association to floral phenotype and its
712 influence on flowers and network structure. *Oecologia*, 178, 783–793.

713 Maruyama, P. K., Vizentin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B.
714 (2014). Morphological and spatio-temporal mismatches shape a Neotropical savanna
715 plant-hummingbird network. *Biotropica*, 46, 740–747.

716 McGill, B., Enquist, B. J., Weiher, E., & Westoby, M. (2006) Rebuilding community ecology
717 from functional traits. *Trends in Ecology and Evolution*, 21, 178–185.

718 Mouillot, D., Graham, N. A., Villéger, S., Mason, N. W. & Bellwood, D. R. (2013). A
719 functional approach reveals community responses to disturbances. *Trends in Ecology*
720 *and Evolution*, 28, 167–177.

721 Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M., ...
722 Bennett, P. M. (2009). Global biogeography and ecology of body size in birds.
723 *Ecology Letters*, 12, 249–259.

724 Ordonez, A., & Svenning, J.C. (2017). Consistent role of Quaternary climate change in
725 shaping current plant functional diversity patterns across European plant orders.
726 *Scientific Reports*, 7, 42988.

727 Otto-Bliesner, B. L., Brady, E. C., Clauzet, G., Tomas, R., Levis, S., & Kothavala, Z. (2006).
728 Last glacial maximum and Holocene climate in CCSM3. *Journal of Climate*, 19,
729 2526–2544.

730 R Core Team (2016). *R: A language and environment for statistical computing*. R Foundation
731 for Statistical Computing, Vienna, Austria.

732 Rader, R., Bartomeus, I., Tylianakis, J. M., & Laliberté, E. (2014). The winners and losers of
733 land use intensification: pollinator community disassembly is non-random and alters
734 functional diversity. *Diversity and Distributions*, 20, 908–917.

735 Rosseel, Y. (2012). lavaan: An R Package for structural Equation Modeling. *Journal of*
736 *Statistical Software*, 48, 1–36.

737 Schleuning, M., Fründ, J., & Garcia, D. (2015). Predicting ecosystem functions from
738 biodiversity and mutualistic networks: an extension of trait-based concepts to plant–
739 animal interactions. *Ecography*, 38, 380–392.

740 Schleuning, M., Fründ, J., Klein, A. M., Abrahamczyk, S., Alarcón, R., Albecht, M., ...
741 Blüthgen, N. (2012). Specialization of mutualistic interaction networks decreases
742 towards tropical latitudes. *Current Biology*, 22, 1925–408.

743 Schleuning, M., Ingmann, L., Strauss, R., Fritz, S. A., Dalsgaard, B., Dehling, D. M., ...
744 Dormann, C. (2014). Ecological, historical and evolutionary determinants of
745 modularity in weighted seed-dispersal networks. *Ecology Letters*, 17, 454–463.

746 Shipley, B. (2002). *Cause and correlation in biology: a user's guide to path analysis,*
747 *structural equations and causal inference*. Cambridge University Press, UK.

748 Souza, C. S., Maruyama, P. K., Aoki, C., Sigrist, M. R., Raizer, J., Gross, C., & Araujo, A. C.
749 (2018). Temporal variation in plant-pollinator networks from seasonal tropical
750 environments: higher specialization when resources are scarce. *Journal of Ecology*, in
751 press.

752 Snow, B. K., & Snow, D. W. (1972). Feeding niches of hummingbirds in a Trinidad valley.
753 *Journal of Animal Ecology*, 41, 471–485.

754 Sonne, J., Martín González, A. M., Maruyama, P. K., Sandel, B., Vizentin-Bugoni, J.,
755 Schleuning, M., ... Dalsgaard, B. (2016). High proportion of smaller-ranged
756 hummingbird species coincides with ecological specialization across the Americas.
757 *Proceedings of the Royal Society Biological Sciences*, 283, 20152512.

758 Stiles, F.G. (1981). Geographical aspects of bird-flower coevolution, with particular reference
759 to Central America. *Annals of the Missouri Botanical Garden*, 68, 323–351.

760 Swenson, N. G., Enquist, B. J., Pither, J., Kerkhoff, A. J., Boyle, B., Weiser, M. D., ...
761 Nolting, K. M. (2012). The biogeography and filtering of woody plant functional
762 diversity in North and South America. *Global Ecology and Biogeography*, 21, 798–
763 808.

764 Tinoco, B. A., Graham, C. H., Aguilar, J. M., & Schleuning, M. (2017). Effects of
765 hummingbird morphology on specialization in pollination networks vary with
766 resource availability. *Oikos*, 126, 52–60.

767 Traveset, A., Olesen, J. M., Nogales, M., Vargas, P., Jaramillo, P., Antolín, E., ... Heleno, R.
768 (2015). Bird–flower visitation networks in the Galápagos unveil a widespread
769 interaction release. *Nature Communications*, 6, 6376.

770 Traveset, A., Tur, C., Trøjelsgaard, K., Heleno, R., Castro-Urgal, R., & Olesen, J. M. (2015).
771 Global patterns of mainland and insular pollination networks. *Global Ecology and*
772 *Biogeography*, 25, 880–890.

773 Trøjelsgaard, K., & Olesen, J. M. (2013). Macroecology of pollination networks. *Global*
774 *Ecology and Biogeography*, 22, 149–162.

775 Trøjelsgaard, K., & Olesen, J. M. (2016). Ecological networks in motion: micro-and
776 macroscopic variability across scales. *Functional Ecology*, 30, 1926–1935.

777 Tylianakis, J. M. & Morris, R. J. (2017). Ecological networks across environmental gradients.
778 *Annual Review of Ecology, Evolution, and Systematics*, 48, 25–48.

779 Vamosi, J. C., Knight, T. M., Steets, J. A., Mazer, S. J., Burd, M., & Ashman, T. L. (2006).
780 Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of*
781 *Sciences USA*, 103, 956–961.

782 Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional
783 diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89,
784 2290–2301.

785 Vizentin-Bugoni, J., Maruyama, P. K., & Sazima, M. (2014). Processes entangling
786 interactions in communities: forbidden links are more important than abundance in a
787 hummingbird–plant network. *Proceedings of the Royal Society Biological Sciences*,
788 281, 20132397.

789 Vizentin-Bugoni, J., Maruyama, P. K., Debastiani, V. J., Duarte, L. S., Dalsgaard, B., &
790 Sazima, M. (2016). Influences of sampling effort on detected patterns and structuring
791 processes of a Neotropical plant-hummingbird network. *Journal of Animal Ecology*,
792 85, 262–272.

793 Weinstein, B. G., & Graham, C. H. (2017). On comparing traits and abundance for predicting
794 species interactions with imperfect detection. *Food Webs*, 11, 17–25.

Wilson, P., Castellanos, M. C., Hogue, J. N., Thomson, J. D., & Armbruster, W. S. (2004). A multivariate search for pollination syndromes among penstemons. *Oikos*, 104, 345–361.

Zanata, T. B., Dalsgaard, B., Passos, F. C., Cotton, P. A., Roper, J. J., Maruyama, P. K., ..., Varassin, I. G. (2017). Global patterns of interaction specialization in bird–flower networks. *Journal of Biogeography*, 44, 1891–1910.

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

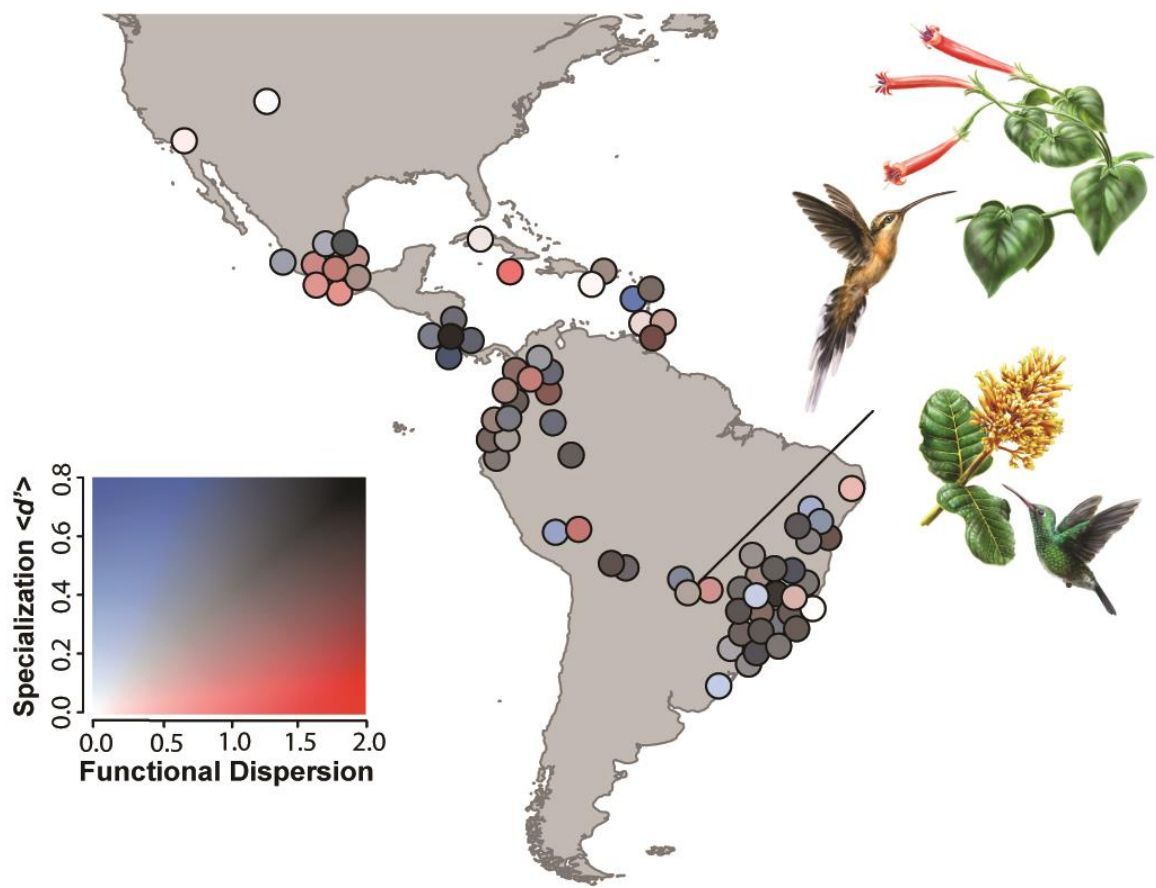
Pietro K. Maruyama is an ecologist, with a broad interest ranging from natural history to macroecology of plant–animal mutualistic interactions. This study is part of the HumLab research team (www.humlab.weebly.com), an ongoing research collaboration on plant–hummingbird networks across the Americas involving numerous researchers from a wide range of institutions and countries.

814 **TABLE 1** Model selection and averaging results of the multi-predictor linear models explaining the variation of hummingbird specialization
815 $\langle d' \rangle$ and network modularity ΔQ , corrected by the Patefield null model. We used two functional diversity measures, functional dispersion
816 (FDis) and minimum spanning tree (MST) reflecting different aspects of trait diversity in hummingbird communities. Important predictors in
817 explaining network indices variation ($\Sigma w_i > 0.8$) are highlighted in bold. We also show the AICc: corrected Akaike's information criterion;
818 AVM: standardized coefficients of the averaged model across all models; MAM: standardized coefficients of the minimum adequate model with
819 the lowest AICc value; R^2 adj: variation explained by the minimum adequate model with the lowest AICc. Acronyms of the predictors - FDis:
820 functional dispersion; MST: minimum spanning tree; Plants: plant richness; MAP: mean annual precipitation; TS: temperature seasonality; PS:
821 precipitation seasonality; AnomT: temperature anomaly; AnomP: precipitation anomaly; Topography: topographical variation; SI: sampling
822 intensity. See Methods for details.

823

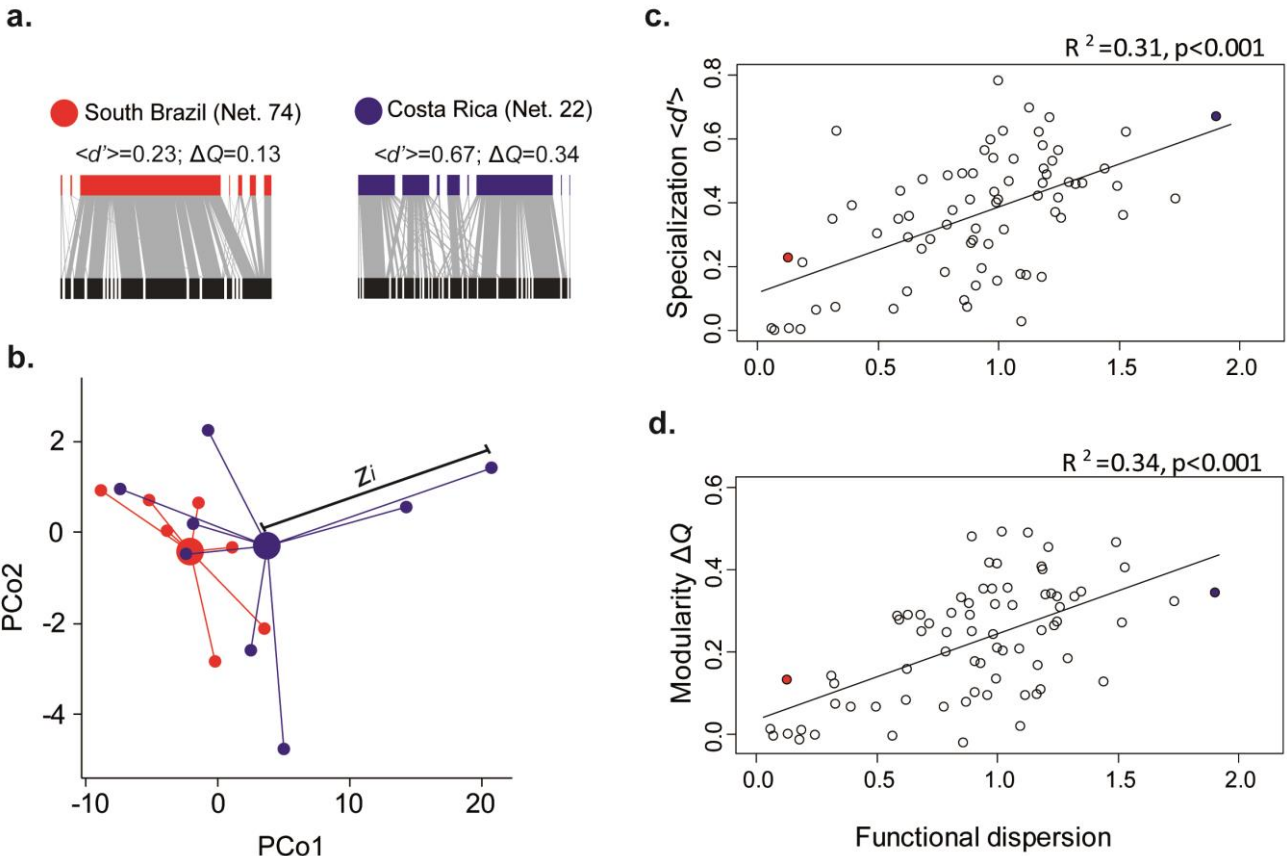
	Complementary specialization $\langle d' \rangle$						Modularity ΔQ					
	FDis			MST			FDis			MST		
	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM	Σw_i	AVM	MAM
FD index	0.97	0.33	0.31	0.28	0.02	-	1.00	0.43	0.43	0.55	0.12	-
Plants	0.75	0.16	0.19	0.89	0.23	0.26	0.98	0.28	0.28	0.98	0.34	0.35
MAP	0.92	0.30	0.33	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

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

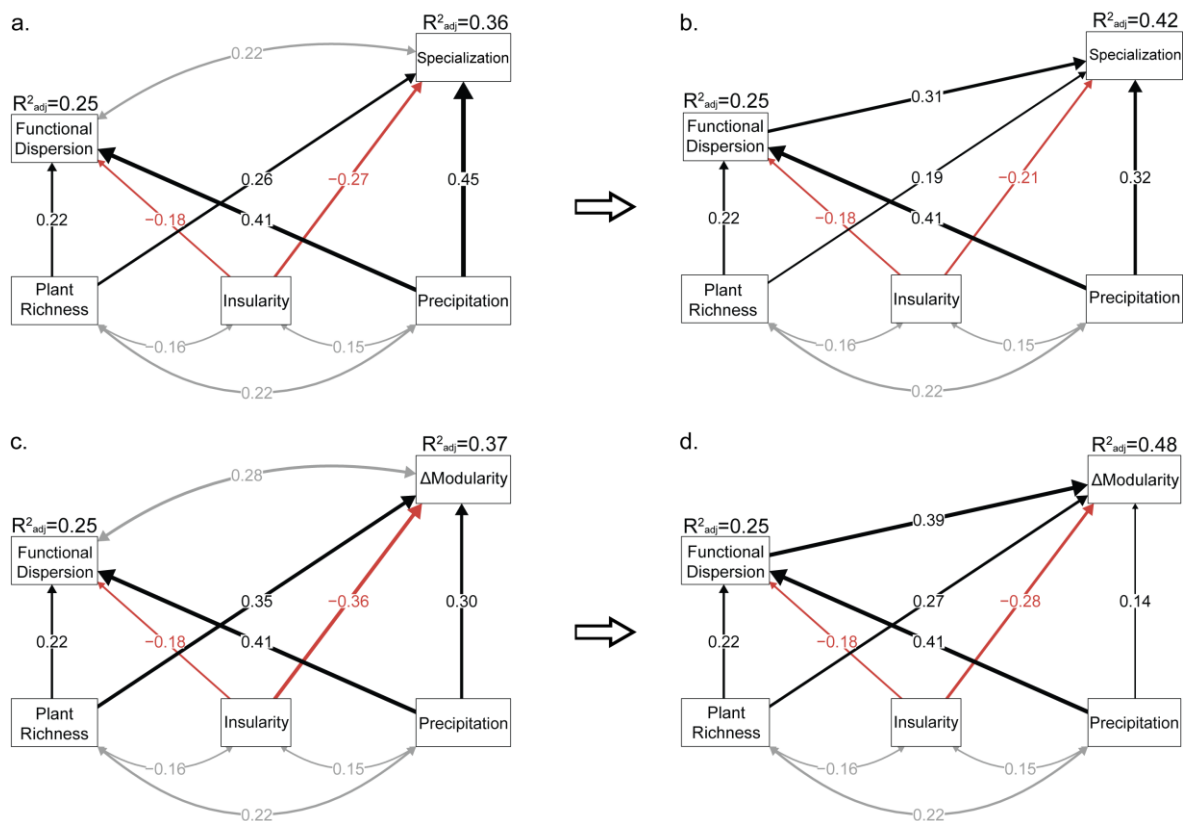


833

834 **FIGURE 2** The relationship between hummingbird functional dispersion (FDis) and network
 835 structure. (a) An example illustrating two networks with similar number of hummingbird
 836 species (Net 74 = 7, Net 22 = 8), but with contrasting FDis. Networks on top depict the
 837 interaction networks with hummingbird species indicated by red and blue boxes at the top and
 838 plant species indicated by black boxes at the bottom (with the interactions indicated by grey
 839 lines). (b) FDis is measured as the mean of the distance (Z_i) of a species (small circles) to its
 840 community centroid (large circles) in multivariate trait space generated by a Principal
 841 Coordinate Analysis. Notice that the community from Costa Rica (blue/right) includes several
 842 species located distantly from the community centroid, in contrast to the community from
 843 Southern Brazil (red/left). Linear regressions showing the relationship between hummingbird
 844 (c) specialization $\langle d' \rangle$ and (d) modularity ΔQ with FDis. Note that the two networks from (a)
 845 are indicated with their respective colors.



847 **FIGURE 3** Structural equation models (SEMs) showing the direct and indirect associations
 848 among environmental and richness predictors, functional dispersion (FDis) with
 849 complementary specialization ($\langle d' \rangle$; 3a, b) and modularity (ΔQ ; 3c, d). Models in (a) and (c)
 850 assume a covariation between FDis and networks structure, while (b) and (d) consider a
 851 directional relationship between FDis and network structure. In both cases, the value of R^2 is
 852 substantially higher in the models that include the direct link between FDis and network
 853 metrics. Black arrows indicate positive relationships while red arrows indicate negative
 854 relationships, with the thickness of each arrow reflecting their standardized path coefficients.
 855 Double-headed grey arrows indicate covariance links.



858 **APPENDIX 1: Data sources and supporting references**

- 859 Abrahamczyk, S., & Kessler, M. (2010). Hummingbird diversity, food niche characters, and
860 assemblage composition along a latitudinal precipitation gradient in the Bolivian
861 lowlands. *Journal of Ornithology*, 151, 615–625.
- 862 Abreu, C. R. M., & Vieira, M. F. (2004). Os beija-flores e seus recursos florais em um
863 fragmento florestal de Viçosa, sudeste brasileiro. *Lundiana*, 5, 129–134.
- 864 Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a
865 plant-pollinator interaction network. *Oikos*, 117, 1796–1807.
- 866 Araujo, A. C., & Sazima, M. (2003). The assemblage of flowers visited by hummingbirds in
867 the “capões” of Southern Pantanal, Mato Grosso do Sul, Brazil. *Flora*, 198, 427–435.
- 868 Araújo, F. P., Barbosa, A. A. A., & Oliveira, P. E. (2011). Floral resources and hummingbirds
869 on an island of flooded forest in Central Brazil. *Flora*, 206, 827–835.
- 870 Araújo, F. P., Sazima, M., & Oliveira, P. E. (2013). The assembly of plants used as nectar
871 sources by hummingbirds in a Cerrado area of Central Brazil. *Plant Systematics and*
872 *Evolution*, 299, 1119–1133.
- 873 Arizmendi, M. C., & Ornelas, J. F. (1990). Hummingbirds and their floral resources in a
874 tropical dry forest in Mexico. *Biotropica*, 22, 172–180.
- 875 Barbosa-Filho, W. G., & Araujo, A. C. (2013). Flowers visited by hummingbirds in an urban
876 Cerrado fragment, Mato Grosso do Sul, Brazil. *Biota Neotropica*, 13, 21–27.
- 877 Berns, C. M., & Adams, D. C. (2010). Bill shape and sexual shape dimorphism between two
878 species of temperate hummingbirds: Black-Chinned hummingbird (*Archilochus*
879 *alexandri*) and Ruby-Throated hummingbird (*A. colubris*). *The Auk*, 127, 626–635.

- 880 Cotton, P. A. (2007). Seasonal resource tracking by Amazonian hummingbirds. *Ibis*, 149, 135–
881 142.
- 882 Cotton, P. A. (1998). The hummingbird community of a lowland Amazonian rainforest. *Ibis*,
883 140, 512–521.
- 884 Dunning Jr., J. B. (2007). *CRC Handbook of Avian Body Masses*, 2nd edition. Purdue
885 University, West Lafayette, Indiana, USA.
- 886 Fonseca, L. C., Vizentin-Bugoni, J., Rech, A. R. & Alves, M. A. S. (2015). Plant-hummingbird
887 interactions and temporal nectar availability in arestinga from Brazil. *Anais da*
888 *Academia Brasileira de Ciências*, 87, 2163–2175.
- 889 Grantsau, R. (1988). *Os beija-flores do Brasil*. Expressão e Cultura.
- 890 Lara, C. (2006). Temporal dynamics of flower use by hummingbirds in a highland temperate
891 forest in México. *Ecoscience*, 13, 23–29.
- 892 Las Casas, F. M. G., Azevedo Júnior, S. M., & Dias Filho, M. M. (2012). The community of
893 hummingbirds (Aves: Trochilidae) and the assemblage of flowers in a Caatinga
894 vegetation. *Brazilian Journal of Biology*, 72, 51–58.
- 895 Machado, A. O., & Oliveira, P. E. (2015). β -Diversity of hummingbird plants in cerrado areas
896 of Central Brazil. *Rodriguésia*, 66, 1–19.
- 897 Machado, C. G. (2009). Hummingbirds (Aves: Trochilidae) and their floral resources in an area
898 of caatinga vegetation in the Chapada Diamantina, Bahia State, Northeast Brazil.
899 *Zoologia*, 26, 55–65.

900 Machado, C. G. (2014). The hummingbird community and the plants which they visit at a
 901 savannah in the Chapada Diamantina, Bahia, Brazil. *Bioscience Journal*, 30, 1578–
 902 1587.

903 Machado, C. G., Coelho, A. G., Santana, C. S. & Rodrigues, M. (2007). Hummingbirds and
 904 their flowers in the ‘campos rupestres’ of Chapada Diamantina, Bahia, northeastern
 905 Brazil. *Revista Brasileira de Ornitologia*, 15, 215–227.

906 Martínez-García, V., & Ortiz-Pulido, R. (2014). Redes mutualistas colibrí-planta: comparación
 907 en dos escalas espaciales, *Ornitologia Neotropical*, 25, 273–289.

908 Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B. & Oliveira, P. E. (2013).
 909 Pollination syndromes ignored: importance of non-ornithophilous flowers to
 910 Neotropical savanna hummingbirds. *Naturwissenschaften*, 100, 1061–1068.

911 Patefield, W. M. (1981). An efficient method of generating random RxC tables with given row
 912 and column totals. *Applied Statistics*, 30, 91–97.

913 Plein, M., Längsfeld, L., Neuschulz, E. L., Schultheiß, C., Ingmann, L., Töpfer, T., ...
 914 Schleuning, M. (2013). Constant properties of plant-frugivore networks despite
 915 fluctuations in fruit and bird communities in space and time. *Ecology*, 94, 1296–1306.

916 Ramírez-Burbano, M. B., Stiles, F. G., González, C., Amorim, F. W., Dalsgaard, B.,
 917 Maruyama, P. K. (2017). The role of the endemic and critically endangered Colorful
 918 Puffleg *Eriocnemis mirabilis* in plant-hummingbird networks of Colombian Andes.
 919 *Biotropica*, 49, 555–564.

920 Rodrigues, L. C., & Araujo, A. C. (2011). The hummingbird community and their floral
 921 resources in an urban forest remnant in Brazil. *Brazilian Journal of Biology*, 71, 611–
 922 622.

923 Rodrigues, L. C., & Rodrigues, M. (2014). Flowers visited by hummingbirds in the open
 924 habitats of the southeastern Brazilian moutaintops: species composition and seasonality.
 925 *Brazilian Journal of Biology*, 74, 659–676.

926 Rosero-Lasprilla, L., & Sazima, M. (2004). Interacciones planta-colibrí en tres comunidades
 927 vegetales de la parte suroriental del Parque Nacional Natural Chiribiquete, Colombia.
 928 *Ornitologia Neotropical*, 15, 183–190.

929 Sazima, I., Buzato, S., & Sazima, M. (1996). An assemblage of hummingbird-pollinated
 930 flowers in a montane forest in southeastern Brazil. *Botanica Acta*, 109, 149–160.

931 Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of
 932 image analysis. *Nature Methods*, 9, 671–675.

933 Snow D. W., & Snow, B. K. (1986). Feeding ecology of hummingbirds in the Serra do Mar,
 934 southeastern Brazil. *Hornero*, 12, 286–296.

935 Snow, D. W., & Snow, B. K. (1980). Relationships between hummingbirds and flowers in the
 936 Andes of Colombia. *Bulletin of the British Museum of Natural History (Zoology)*, 38,
 937 105–139.

938 Vasconcelos, M. F., & Lombardi, J. A. (1999). Padrão sazonal na ocorrência de deis espécie de
 939 beija-flores (Apodiformes: Trochilidae) em uma localidade de campo rupestre na Serra
 940 do Curral, Minas Gerais. *Ararajuba*, 7, 71–79.

- 941 Walther, B. A., & Brieschke, H. (2001). Hummingbird-flower relationships in a mid-elevation
942 rainforest near Mindo, northwestern Ecuador. *International Journal of Ornithology*, 4,
943 115–135.
- 944 Wolf, L. L., Stiles, F. G., & Hainsworth, F. R. (1976). Ecological organization of a tropical,
945 highland hummingbird community. *Journal of Animal Ecology*, 45, 349–379.

946 **Additional Supporting Information:**

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

948 Appendix S2. List of hummingbirds occurring in the studied networks

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

950 [Appendix S4: List of plant species occurring in the subset of 28 networks with data on plant](#)
951 [traits and abundances. The same nomenclature as in Appendix 3 is used.](#)

952 [Appendix S5: Details and sources of the subset plant-hummingbird networks.](#)

953 Appendix [S6](#). Additional details on Methods

954 Appendix [S7](#). Hummingbird abundance correlations

955 Appendix [S8](#). A plot showing the relationship between the values of FDis calculated using two
956 measures of hummingbird abundance

957 Appendix [S9](#). Model selection results for null model corrected specialization and un-corrected
958 modularity

959 Appendix [S10](#). Model selection results using Velocity, instead of Anomalies as measure of
960 historical climate

961 Appendix [S11](#). Model selection results using unweighted Functional Dispersion index

962 Appendix [S12](#). Model selection results using hummingbird richness

963