



Global patterns of interaction specialization in bird–flower networks

Thais B. Zanata^{1,2,3,*}  | Bo Dalsgaard³ | Fernando C. Passos⁴ | Peter A. Cotton⁵ | James J. Roper^{1,6} | Pietro K. Maruyama⁷ | Erich Fischer⁸ | Matthias Schleuning⁹ | Ana M. Martín González^{3,10} | Jeferson Vizentin-Bugoni^{11,12} | Donald C. Franklin¹³ | Stefan Abrahamczyk^{14,15} | Ruben Alárcon¹⁶ | Andréa C. Araujo¹⁷ | Francielle P. Araújo¹⁸ | Severino M. de Azevedo-Junior¹⁹ | Andrea C. Baquero³ | Katrin Böhning-Gaese^{9,20} | Daniel W. Carstensen³ | Henrique Chupil²¹ | Aline G. Coelho²² | Rogério R. Faria²³ | David Hořák²⁴ | Tanja T. Ingversen²⁵ | Štěpán Janeček^{24,26} | Glauco Kohler^{1,27} | Carlos Lara²⁸ | Flor M. G. Las-Casas²⁹ | Ariadna V. Lopes³⁰ | Adriana O. Machado³¹ | Caio G. Machado²² | Isabel C. Machado³⁰ | María A. Maglianesi^{9,32} | Tiago S. Malucelli^{1,2} | Jayasilan Mohd-Azlan^{13,33} | Alan C. Moura²² | Genilda M. Oliveira³⁴ | Paulo E. Oliveira³¹ | Juan Francisco Ornelas³⁵  | Jan Riegert³⁶ | Licléia C. Rodrigues³⁷ | Liliana Rosero-Lasprilla³⁸ | Ana M. Rui³⁹ | Marlies Sazima⁷ | Baptiste Schmid⁴⁰ | Ondřej Sedláček²⁴ | Allan Timmermann⁴¹ | Maximilian G. R. Vollstädt^{9,20} | Zhiheng Wang⁴² | Stella Watts⁴³ | Carsten Rahbek^{3,44} | Isabela G. Varassin²

¹Programa de Pós-Graduação em Ecologia e Conservação, Universidade Federal do Paraná, Curitiba-PR, Brazil

²Laboratório de Ecologia Vegetal, Departamento de Botânica, Universidade Federal do Paraná, Curitiba, Brazil

³Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

⁴Laboratório de Biodiversidade, Conservação e Ecologia de Animais Silvestres, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil

⁵Marine Biology & Ecology Research Centre, University of Plymouth, Plymouth, UK

⁶Graduate Program in Ecosystem Ecology, Universidade Vila Velha, Vila Velha, Brazil

⁷Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, Brazil

⁸Centro de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil

⁹Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt (Main), Germany

¹⁰Pacific Ecoinformatics and Computational Ecology Lab, Berkeley, CA, USA

¹¹Programa de Pós-Graduação em Ecologia, Universidade Estadual de Campinas (Unicamp), Campinas, Brazil

¹²University of Illinois at Urbana-Champaign, Urbana, IL, USA

¹³Research Institute for Environment & Livelihoods, Charles Darwin University, Darwin, NT, Australia

¹⁴Nees Institute for Biodiversity of Plants, University of Bonn, Bonn, Germany

¹⁵Institute of Systematic and Evolutionary Botany, University of Zurich, Zurich, Switzerland

¹⁶Biology Program, California State University Channel Islands, Camarillo, CA, USA

¹⁷Laboratório de Ecologia, Centro de Ciências Biológicas e da Saúde, Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil

¹⁸Universidade Estadual do Rio Grande do Sul, São Francisco de Paula, Brazil

¹⁹Department of Biology, Rural Federal University of Pernambuco, Recife, Brazil



²⁰Institute for Ecology, Evolution and Diversity, Goethe University, Frankfurt am Main, Germany

²¹Programa de Pós-Graduação em Zoologia, Instituto de Pesquisas Cananéia, Cananéia, Brazil

²²Laboratório de Ornitologia, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Feira de Santana, Brazil

²³Campus de Aquidauana, Universidade Federal de Mato Grosso do Sul, Aquidauana, Brazil

²⁴Department of Ecology, Faculty of Science, Charles University in Prague, Praha 2, Czech Republic

²⁵Department of Ecology & Genetics, Institute of Biological Sciences, University of Aarhus, Aarhus, Denmark

²⁶Institute of Botany, Czech Academy of Sciences, Třeboň, Czech Republic

²⁷Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil

²⁸Centro de Investigación en Ciencias Biológicas, Universidad Autónoma de Tlaxcala, Tlaxcala, México

²⁹Laboratory of Ecology, Systematics and Evolution of Birds, Federal University of Pernambuco, Recife, Brazil

³⁰Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Brazil

³¹Instituto de Biologia, Universidade Federal de Uberlândia, Uberlândia, Brazil

³²Vicerrectoría de Investigación, Universidad Estatal a Distancia (UNED), San José, Costa Rica

³³Department of Zoology, Faculty of Resource Science and Technology, Universiti Malaysia Sarawak, Sarawak, Malaysia

³⁴Instituto Federal de Brasília, Brasília, Brazil

³⁵Departamento de Biología Evolutiva, Instituto de Ecología, AC, Xalapa, México

³⁶Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

³⁷Laboratório de Ornitologia, Departamento de Zoologia, ICB, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

³⁸Escuela de Ciencias Biológicas, Grupo de Investigación Biología para la Conservación, Universidad Pedagógica y Tecnológica de Colombia, Tunja, Colombia

³⁹Departamento de Ecologia, Zoologia e Genética, Instituto de Biologia, Universidade Federal de Pelotas, Capão do Leão, Brazil

⁴⁰Swiss Ornithological Institute, Sempach, Switzerland

⁴¹Department of Bioscience, Aarhus University, Aarhus, Denmark

⁴²Department of Ecology and Key Laboratory for Earth Surface Processes of the Ministry of Education, College of Urban and Environmental Sciences, Peking University, Beijing, China

⁴³Landscape and Biodiversity Research Group, Department of Environmental and Geographical Sciences, University of Northampton, Northampton, UK

⁴⁴Department of Life Sciences, Imperial College London, Ascot, UK

Correspondence

Thais B. Zanata, Laboratório de Ecologia Vegetal, Departamento de Botânica, Universidade Federal do Paraná, Centro Politécnico, Curitiba-PR, Brazil.
Email: thaisbzana@gmail.com

Funding information

CAPES Foundation, Grant/Award Number: 8105/2014-6, 8012/2014-08; CNPq, Grant/Award Number: 309453/2013-5, 445405/2014-7; Czech Science Foundation (project no. 14-36098G); British Ornithologists' Union; Wolfson College, University of Oxford; FAPESP, Grant/Award Number: 2015/21457-4; FAPEMIG; FUNDECT; Oticon Fonden Denmark; The Danish Council for Independent Research Natural Sciences; University of Aarhus; CACyPI-Uatx-2016GK; FACEPE; OeAD; FAPESB; CONICIT; MICIT; CCT; UNED; OTS; DAAD; DFG; Hesse's Ministry of Higher Education, Research, and the Arts

Editor: Holger Kreft

Abstract

Aim: Among the world's three major nectar-feeding bird taxa, hummingbirds are the most phenotypically specialized for nectarivory, followed by sunbirds, while the honeyeaters are the least phenotypically specialized taxa. We tested whether this phenotypic specialization gradient is also found in the interaction patterns with their floral resources.

Location: Americas, Africa, Asia and Oceania/Australia.

Methods: We compiled interaction networks between birds and floral resources for 79 hummingbird, nine sunbird and 33 honeyeater communities. Interaction specialization was quantified through connectance (C), complementary specialization (H_2'), binary (Q_B) and weighted modularity (Q), with both observed and null-model corrected values. We compared interaction specialization among the three types of bird–flower communities, both independently and while controlling for potential confounding variables, such as plant species richness, asymmetry, latitude, insularity, topography, sampling methods and intensity.

Results: Hummingbird–flower networks were more specialized than honeyeater–flower networks. Specifically, hummingbird–flower networks had a lower proportion of realized interactions (lower C), decreased niche overlap (greater H_2') and greater modularity (greater Q_B). However, we found no significant differences between hummingbird– and sunbird–flower networks, nor between sunbird– and honeyeater–flower networks.



Main conclusions: As expected, hummingbirds and their floral resources have greater interaction specialization than honeyeaters, possibly because of greater phenotypic specialization and greater floral resource richness in the New World. Interaction specialization in sunbird–flower communities was similar to both hummingbird–flower and honeyeater–flower communities. This may either be due to the relatively small number of sunbird–flower networks available, or because sunbird–flower communities share features of both hummingbird–flower communities (specialized floral shapes) and honeyeater–flower communities (fewer floral resources). These results suggest a link between interaction specialization and both phenotypic specialization and floral resource richness within bird–flower communities at a global scale.

KEYWORDS

honeyeaters, hummingbirds, modularity, niche partitioning, ornithophily, plant–animal interactions, specialization, sunbirds

1 | INTRODUCTION

Specialization is of major importance in ecology and occurs at all levels, from the individual to the community (Devictor et al., 2010). Understanding the origin and evolution of specialization is fundamental to our understanding of species interactions (Futuyma & Moreno, 1988), such as the interactions between plants and animals in pollination (Johnson & Steiner, 2000; Waser et al., 1996). Birds include the most abundant and species rich vertebrate pollinators, with flower visitation reported in more than 50 bird families (Cronk & Ojeda, 2008). Of these families, three are highly specialized for nectarivory: Trochilidae, Nectariniidae and Meliphagidae. Hummingbirds (Apodiformes, Trochilidae, 363 species) occur in the New World (NW) throughout the Americas, while sunbirds (Passeriformes, Nectariniidae, 132 species) and honeyeaters (Passeriformes, Meliphagidae, 175 species) are found in the Old World (OW). Sunbirds occur in Africa, Asia and Oceania/Australia, and honeyeaters are found in Asia and Oceania/Australia (del Hoyo et al., 2016; Fleming & Muchhala, 2008; Stiles, 1981), with a limited distribution overlap between these OW families (Barker et al., 2002). These three families contain most of the specialized nectar-feeding bird species, and are an example of convergent evolution, as they have independently evolved adaptations associated with nectarivory (Prum et al., 2015). Nectar-feeding adaptations include long and/or curved bill, grooved tongue tip, a tongue extensible beyond the bill tip and small body size in relation to non-nectarivorous birds (Stiles, 1981). This pattern of evolution has generated interest in understanding the differences and similarities in the morphology and ecology of these nectar-feeding birds and their floral resources (Collins & Paton, 1989; Cronk & Ojeda, 2008; Fleming, 2005; Fleming & Muchhala, 2008; Pyke, 1980; Stiles, 1981).

Despite the convergent evolution between these families, they vary in their extent of phenotypic specialization for pollination (*sensu* Ollerton et al., 2007). Hummingbirds are the most phenotypically specialized for nectarivory, followed by sunbirds, while

honeyeaters are the least phenotypically specialized taxa (Fleming & Muchhala, 2008; Stiles, 1981). Bill length in hummingbird communities is more variable than in OW communities (Fleming & Muchhala, 2008), which may facilitate a finer resource partitioning among hummingbird species (Abrahamczyk & Kessler, 2010; Maglianesi et al., 2014). Greater phenotypic specialization of hummingbirds is also manifested in their small size, one of their adaptations allowing hovering flight (Pyke, 1980). Hovering is the prevalent mode of flower foraging among hummingbirds (Collins & Paton, 1989), with perching being predominant in the generally heavier sunbirds and honeyeaters (Fleming & Muchhala, 2008; Pyke, 1980; but see Janeček et al., 2011; Wester, 2013). Small size and hovering flight are likely to have favoured the diversification of hummingbird-pollinated plant species, because the evolutionary transition from small and delicate insect-pollinated to hummingbird-pollinated species was probably relatively simple (Castellanos et al., 2003; Thomson & Wilson, 2008). This greater diversification of floral resources may have promoted a greater interaction specialization in NW communities (Dalsgaard et al., 2011).

Sunbirds and the plants they visit are considered the second-most phenotypically specialized bird–flower community. Sunbirds have bills, tongues and digestive tracts that are better adapted to nectar-feeding than those of honeyeaters, the least specialized group (Stiles, 1981). In addition, as in hummingbird-pollinated species, flowers visited by sunbirds tend to have tubular or gullet shapes, while honeyeaters tend to visit flowers with less restrictive morphologies (Fleming & Muchhala, 2008; Stiles, 1981). Although phenotypic specialization of nectar-feeding birds and their floral resources clearly decrease from specialized hummingbird to sunbird and then less specialized honeyeater communities (Fleming & Muchhala, 2008; Stiles, 1981), it remains unclear whether the interaction specialization of bird–flower communities reflect the same phenotypic specialization gradient.

Species interaction patterns, such as bird–flower interactions, can be investigated by a network approach. This approach can reveal



emergent properties at the community-level that are not apparent in pairwise interactions (Bascompte & Jordano, 2007). Some of the main network metrics that quantify interaction specialization at the community-level are connectance, complementary specialization and modularity (Blüthgen, 2010). Community-level specialization quantified by these metrics is associated with the concept of ecological specialization (*sensu* Ollerton et al., 2007) and the realized Eltonian niche (Devictor et al., 2010), where interactions are treated as one dimension of the ecological niche and the degree of interaction specialization represents niche partitioning among species (Blüthgen, 2010).

Because of the observed phenotypic specialization in the three main bird–flower communities, we predicted the following interaction specialization gradient: hummingbird–flower > sunbird–flower > honeyeater–flower. To test this, we compiled a dataset of 121 networks, and examined the differences of bird–flower interaction specialization between these three bird families, both independently and while controlling for potential confounding variables such as plant species richness, asymmetry, latitude, insularity, topography, sampling methods and intensity.

2 | MATERIALS AND METHODS

2.1 | Bird–flower interaction networks

We gathered published and unpublished data on flower visitation by hummingbirds, sunbirds and honeyeaters sampled at the community-level (a list of data source of each network is available in the Appendix 1). For each study, interaction lists between bird and plant species were transformed into adjacency matrices, with birds as columns and plants as rows. In these matrices, flower visits by birds were represented in binary networks by their absence (0) or occurrence (1), or in weighted networks by their interaction frequency (Bascompte & Jordano, 2007). Interaction frequency represents the number of observations of birds either visiting or carrying pollen from a given plant species. We only included interactions for the nectar-feeding specialist families: Trochilidae, Nectariniidae and Meliphagidae (del Hoyo et al., 2016; Fleming & Muchhala, 2008; Stiles, 1981). In addition, we excluded illegitimate interactions, when the bird did not contact the floral reproductive structures, for example, piercing the corolla to reach the nectar. We also excluded interactions with known exotic plant species, because they are unlikely to involve bird–flower evolutionary relationships. Information about interaction legitimacy was unavailable in four of the studies used in the analyses (Brooker et al., 1990; Collins & Rebelo, 1987; Pettet, 1977; Wester, 2013). In these cases, we assumed that all interactions were legitimate. We classified plant species as exotic using the databases of Flora of the West Indies (botany.si.edu/antilles/WestIndies/query.cfm), the Brazilian Flora Checklist (floradobrasil.jbrj.gov.br) and Tropicos (www.tropicos.org).

We compiled a total of 121 bird–flower interaction networks, of which 79 described hummingbird–flower, nine sunbird–flower and 33 honeyeater–flower interactions. Interaction frequency was

available for 67 (85%) hummingbird networks, five (55%) sunbird networks and 23 (70%) honeyeater networks. Bird species richness within networks ranged from two to 24 in the hummingbird, two to 13 in the sunbird and two to 12 in the honeyeater communities, while plant species richness ranged from two to 65 in the hummingbird, two to 26 in the sunbird and two to 39 in the honeyeater communities (detailed values of each network are available in the Appendix S1: Table S1).

2.2 | Measuring specialization of interaction networks

To quantify interaction specialization, we used two binary metrics, connectance (C) and binary modularity (Q_B), and two weighted metrics, complementary specialization (H_2') and weighted modularity (Q). These metrics range from 0 to 1, where the most generalized network has a value of 0 and the most specialized network has a value of 1 (H_2' , Q_B , Q), with the inverse for connectance (C).

Connectance is defined as the proportion of observed pairwise interactions relative to the total number of possible interactions in the community, where the total number of possible interactions is calculated as the richness of visited plant species multiplied by the richness of nectar-feeding birds (Blüthgen, 2010; Jordano, 1987). Complementary specialization is derived from two-dimensional Shannon entropy, and quantifies the niche partitioning among species considering partner availability, defined by the marginal totals in the interaction matrix, and so measures the exclusiveness of interactions (Blüthgen et al., 2006; Martín González et al., 2015). Finally, modularity is a network pattern that emerges when some species interact strongly with each other, but less so with the remaining species, thereby creating strongly connected sub-groups within a less connected network (Dormann & Strauss, 2014; Maruyama et al., 2014; Olesen et al., 2007). Binary modularity was measured using the Barber metric (Barber, 2007), with simulated annealing as the search algorithm in the MODULAR software (Marquitti et al., 2014). Weighted modularity was calculated with the standard specifications of the QuanBiMo algorithm and using the greatest modularity value after five independent runs (Dormann & Strauss, 2014; Schleuning et al., 2014). Connectance, complementary specialization and weighted modularity were calculated with the “bipartite” 2.08 package (Dormann et al., 2008) in R 3.2.5 (R Core Team, 2016). Although metric values were correlated (Pearson's $r > 0.80$, $p < 0.05$ for spatial and non-spatial correlation), we analysed all metrics separately because they can describe complementary patterns of interaction specialization (Martín González et al., 2015).

2.3 | Null-model corrections of network metrics

Network metrics are often influenced by species richness and sampling effort. Thus, we constructed null models to control for these effects (Dalsgaard et al., 2017; Martín González et al., 2015; Schleuning et al., 2014). The use of null models allows us to calculate deviations between observed values and null-model expectations,



assuming random species interactions, while controlling network properties that may be related to species richness and sampling effort (Dalsgaard et al., 2017). We generated randomized networks using Patefield's algorithm (Patefield, 1981), an approach commonly used in geographical analyses of interaction networks (Dalsgaard et al., 2017). This algorithm constrains network size (representing species richness) and the interaction matrix marginal totals (the sum of interaction frequencies of each bird and plant species, which may be a consequence of species abundance or sampling effort; Dormann et al., 2009). Patefield's algorithm requires interaction frequency to generate randomized networks, and so we could only use null-model corrections on weighted networks. Thus, sample size was larger for observed connectance and binary modularity than for null-model corrected connectance and binary modularity (see above; Table S1). For each of the observed networks, we generated 1,000 randomized networks to estimate connectance and complementary specialization and 100 to estimate binary and weighted modularity. We used fewer randomizations for modularity metrics because their calculation requires excessively time-consuming algorithms (Olesen et al., 2007; Schleuning et al., 2014; Sebastián-González et al., 2015). For each of the randomized networks, we calculated the network metrics following the same procedure as adopted for the observed networks (see above). To quantify the departure of the observed network values from the null expectation, we calculated null-model corrected values by subtracting the observed metric value from the mean value across all randomized networks (Δ -transformation; Dalsgaard et al., 2017; Martín González et al., 2015; Schleuning et al., 2014).

2.4 | Comparing hummingbird, sunbird and honeyeater interaction specialization

We compared observed and null-model corrected metrics of hummingbird-, sunbird- and honeyeater-flower networks, testing for differences of interaction specialization between the three community types. First, for data with equal variances, we compared them using one-way ANOVA with Tukey's multiple comparison test, for data with unequal variances we used the Kruskal–Wallis test with Dunn's multiple comparison test. Analysis and graphs were plotted in GRAPHPAD PRISM 6.0 (Morgan, 1998). Second, we compared the interaction specialization between the three types of bird–flower community while controlling for potentially confounding variables (see below), using linear multiple regression models and corrected Akaike information criterion (AIC_c). We used the threshold of $\Delta AIC_c \leq 2$ to identify minimum adequate models (MAM; Burnham & Anderson, 2002).

In the linear models, bird–flower community was assigned as a categorical variable with three levels (hummingbirds, sunbirds and honeyeaters). Nine potentially confounding variables were also included in the models: (1) plant species richness (\log_{10} transformed), included because species-rich communities are expected to have greater specialization (Dalsgaard et al., 2011; Martín González et al., 2015; but see Vázquez & Stevens, 2004; Schleuning et al., 2012); (2) asymmetry (\log_{10} transformed), described as the ratio between bird and plant species richness and included because connectance

decreases when asymmetry increases (Blüthgen et al., 2006); (3) absolute latitude, because several studies have found greater network specialization towards the tropics (Olesen & Jordano, 2002; Dalsgaard et al., 2011; but see Vázquez & Stevens, 2004; Schleuning et al., 2012); (4) insularity, where mainland communities were classified as “0” and island communities as “1” and included in the models because insular communities are expected to be less specialized than mainland communities (Martín González et al., 2015; Traveset et al., 2015); (5) topography (square root transformed), defined as the elevational range of the sampled localities calculated in 1×1 km grid cells within a concentric distance of 10 km from each sampled locality; (6) duration of each study (\log_{10} transformed), based on the number of sampling months, included because sampling effort can affect interaction specialization (Dalsgaard et al., 2017); (7) the method used to record species interactions, where focal observations were classified as “0” and sampling pollen loads on visiting birds as “1”, included because it may influence network structure (Ramírez-Burbano et al., 2017); (8) sampling coverage, where “1” represents studies that sampled the supposed entire communities of bird and plant species, and “0” represents studies that sampled only a subset of the community (for example, studies focusing on ornithophilous plant species or a given plant family); and (9) sampling intensity (\log_{10} transformed), calculated as the ratio between the square root of the total number of interactions and the square root of the product of the number of bird and plant species in the network (Dalsgaard et al., 2017; Schleuning et al., 2012). As interaction frequency is required to quantify sampling intensity, we were only able to estimate this variable for the weighted networks (Table S1).

Model selection was performed using the *dredge* function in the “MuMIn” 1.15.6 package (Barton, 2016). We reported the standardized coefficients for an averaged model (AVM) and the importance (Σw_i) of each predictor variable measured across all models (Burnham & Anderson, 2002). To identify relevant predictor variables, we used an importance threshold value of ≥ 0.80 (Sebastián-González et al., 2015). The importance (Σw_i) of each predictor variable is measured by the sum of the Akaike weights in the subset of models that include the given predictor variable. Akaike weights (w_i) describe the weight of evidence of a given model to be the best model among the set of possible models. In this sense, the larger the values of Σw_i for a given predictor variable, the greater is its importance in relation to other predictor variables (Burnham & Anderson, 2002). When the bird–flower community variable was selected in the MAM, we used partial regressions to detect the total and unique variation explained by this variable. The differences between the bird–flower community types were tested using Tukey contrasts for general linear hypotheses, using the *glht* function in the “multcomp” 1.4-6 package (Hothorn et al., 2008). We considered multicollinearity to be absent when the variance inflation factor (VIF) or the generalized variance inflation factor (GVIF) was ≤ 10 (Hair et al., 2009); both indices were measured using the *vif* function in the “car” 2.1-4 package (Fox & Weisberg, 2011). We checked for positive spatial autocorrelation in the residuals of the MAM with the lowest ΔAIC_c by computing Moran's *I* in 14-equally spaced distance classes and applying a

permutation test with 10,000 iterations, using the *correlog* function in the “pgirmess” 1.6.7 package (Giraudeau, 2016). Initial analyses found that interaction specialization was associated with the method of recording interactions (Tables 1 and 2). Therefore, we checked the consistency of our results by repeating all analyses using networks sampled only through focal observations (Appendix S2, Tables S2–S3). Analyses were conducted using R.

To determine how our sample of networks spanned the global species richness gradient in the three nectar-feeding bird family of interest (Trochilidae, Nectariniidae and Meliphagidae), we compared the cumulative frequency distribution of their species richness in grid cells across the globe with the richness in the grid cells containing the sampled networks. Comparisons were done using a two-sample Kolmogorov–Smirnov test in GRAPHPAD PRISM. The global richness dataset was based on presence–absence data for Trochilidae, Nectariniidae and Meliphagidae, obtained from a global distributional

database (Rahbek et al., 2012). Species ranges were recorded at a spatial resolution of 1×1 latitudinal–longitudinal degree and represent a conservative estimate of the extent of occurrence (Rahbek & Graves, 2000, 2001). This global distributional database was also used to build the richness maps in QGIS 2.18 (QGIS Development Team, 2017; Figures 2 and 3).

3 | RESULTS

Hummingbird–flower networks had lower connectance than sunbird–flower and honeyeater–flower networks. Furthermore, hummingbird–flower networks had greater complementary specialization and modularity than honeyeater–flower networks. However, we found no significant differences between the complementary specialization and modularity of hummingbird–flower and sunbird–

TABLE 1 Multiple linear regression models predicting observed (OBS) and null-model corrected (Δ) connectance (C) and complementary specialization (H_2') of bird-flower interaction networks. Connectance is the realized proportion of possible interactions in a community while complementary specialization measures niche overlap among species. Predictor variables are described in the Material and Methods. Numbers in bold are predictor variables whose importance (Σw_i) is ≥ 0.80 . A dash indicates that the predictor variable was absent from the MAM. Numbers in parenthesis are the sample size used in each analysis. Letters next to the standardized coefficients represent the group that each bird-flower community belongs to, based on Tukey contrasts for general linear hypotheses.

	Connectance (C)						Complementary specialization (H_2')					
	C_{OBS} (121)			ΔC (94)			$H_2'_{OBS}$ (94)			$\Delta H_2'$ (94)		
	Σw_i	AVM	MAM ^a	Σw_i	AVM	MAM ^b	Σw_i	AVM	MAM ^c	Σw_i	AVM	MAM ^d
Predictor variables												
Bird-flower community	1.00			1.00			0.96			0.98		
Hummingbirds		−0.11	−0.11 (A)		−0.11	−0.12 (A)		0.16	0.13 (A)		0.17	0.17 (A)
Sunbirds		0.02	0.03 (B)		0.09	0.09 (B)		0.05	0.01 (AB)		0.08	0.10 (AB)
Honeyeaters		1.01	1.00 (B)		0.16	0.17 (B)		0.11	0.11 (B)		−0.04	−0.04 (B)
Plant species richness	1.00	−0.55	−0.54	1.00	−0.23	−0.24	0.92	0.18	0.17	1.00	0.22	0.22
Asymmetry	1.00	−0.33	−0.32	1.00	0.19	0.19	0.28	−0.03	–	0.31	−0.07	–
Insularity	0.63	0.07	0.07	0.24	0.02	–	0.45	−0.08	–	0.33	−0.05	–
Topography	0.23	0.01	–	0.29	−0.01	–	0.43	0.03	0.03	0.38	0.03	–
Latitude	0.36	0.01	–	0.37	0.01	–	0.42	−0.02	−0.03	0.27	−0.01	–
Sampling method	0.94	0.14	0.15	0.98	0.19	0.20	0.97	−0.36	−0.33	0.99	−0.38	−0.39
Duration	0.25	−0.01	–	0.30	−0.02	–	0.26	0.02	–	0.29	0.02	–
Sampling coverage	0.23	−0.01	–	0.21	−0.01	–	0.25	0.03	–	0.23	0.02	–
Sampling intensity				1.00	−0.17	−0.17	0.57	−0.12	–	0.25	0.03	–
AIC _c			−146.96			−168.06			−58.51			−64.07
R^2 adjusted			0.69			0.50			0.34			0.38
R^2 total Bird-flower community			0.32			0.29			0.21			0.25
R^2 only Bird-flower community			0.04			0.16			0.04			0.08
Moran's I			$\leq 0.04^{NS}$			$\leq 0.13^{NS}$			$\leq 0.06^{NS}$			$\leq 0.08^{NS}$

AIC_c, corrected Akaike's information criterion; AVM, standardized coefficients of the averaged model measured across all models; MAM, standardized coefficients of the minimum adequate model with the lowest ΔAIC_c ; R^2 adjusted, variation explained by the minimum adequate model with the lowest ΔAIC_c ; R^2 only Bird-flower community, adjusted unique variation explained by the difference between the bird-flower community types; R^2 total Bird-flower community, adjusted total variation explained by the difference between bird-flower community types; Σw_i , importance of each predictor variable measured across all models; ^{NS} $p > 0.05$; number of models with $\Delta AIC_c \leq 2$: a – three; b – four; c – eleven; d – six. For all models with $\Delta AIC_c \leq 2$, the predictor variable that represents the difference between the bird-flower community types was selected. Multicollinearity between predictor variables is absent, as generalized variance inflation factor (GVIF) ≤ 1.72 .



TABLE 2 Multiple linear regression models predicting observed (OBS) and null-model corrected (Δ) binary (Q_B) and weighted modularity (Q) of bird-flower interaction networks. Modularity is a network metric that detects preferentially interacting subsets of species within the community. Predictor variables are described in the Material and Methods. Numbers in bold are predictor variables whose importance (Σw_i) is ≥ 0.80 . A dash indicates that the predictor variable was absent from the MAM. Numbers in parenthesis are the sample size used in each analysis. Letters next to the standardized coefficients represent the group that each bird-flower community belongs, based on Tukey contrasts for general linear hypotheses.

Predictor variables	Binary modularity (Q_B)						Weighted modularity (Q)					
	Q_{B-OBS} (121)			ΔQ_B (94)			Q_{OBS} (94)			ΔQ (94)		
	Σw_i	AVM	MAM ^a	Σw_i	AVM	MAM ^b	Σw_i	AVM	MAM ^c	Σw_i	AVM	MAM ^d
Bird-flower community	0.99			1.00			0.28			0.27		
Hummingbirds		0.07	0.07 (A)		0.08	0.08 (A)		0.06	–		0.05	–
Sunbirds		–0.01	–0.01 (AB)		0.01	0.01 (AB)		0.06	–		0.05	–
Honeyeaters		0.12	0.09 (B)		–0.06	–0.02 (B)		0.12	–		–0.07	–
Plant species richness	1.00	0.14	0.17	1.00	0.12	0.08	1.00	0.21	0.21	1.00	0.26	0.23
Asymmetry	0.57	0.08	0.09	0.64	–0.06	–	0.24	–0.03	–	0.60	–0.09	–
Insularity	0.43	–0.04	–	0.71	–0.04	–0.05	0.99	–0.11	–0.11	0.82	–0.08	–0.09
Topography	0.33	0.01	–	0.63	0.01	0.02	0.74	0.03	0.03	0.68	0.02	0.03
Latitude	0.52	–0.01	–	0.60	–0.01	–0.01	0.23	–0.01	–	0.22	–0.01	–
Sampling method	0.63	–0.08	–0.08	1.00	–0.15	–0.14	0.91	–0.21	–0.20	0.95	–0.21	–0.20
Duration	0.25	–0.01	–	0.22	–0.01	–	0.23	–0.01	–	0.27	0.01	–
Sampling coverage	0.24	0.01	–	0.27	0.02	–	0.22	0.01	–	0.22	0.01	–
Sampling intensity				0.39	0.03	–	1.00	–0.15	–0.15	0.25	0.02	–
AIC _c			–211.75			–241.09			–138.50			–154.64
R^2 adjusted			0.35			0.55			0.52			0.49
R^2 total Bird-flower community			0.23			0.34			–			–
R^2 only Bird-flower community			0.06			0.09			–			–
Moran's I			$\leq 0.06^{NS}$			$\leq 0.17^{NS}$			$\leq 0.07^{NS}$			$\leq 0.06^{NS}$

AIC_c, corrected Akaike's information criterion; AVM, standardized coefficients of the averaged model measured across all models; MAM, standardized coefficients of the minimum adequate model with the lowest ΔAIC_c ; R^2 adjusted, variation explained by the minimum adequate model with the lowest ΔAIC_c ; R^2 only Bird-flower community, adjusted unique variation explained by the difference between the s-flower community types; R^2 total Bird-flower community, adjusted total variation explained by the difference between the bird-flower community types; Σw_i , importance of each predictor variable measured across all models; ^{NS} $p > 0.05$; number of models with $\Delta AIC_c \leq 2$: a – eleven; b – nine; c – one; d – five. Only for binary modularity, all models with $\Delta AIC_c \leq 2$ the predictor variable that represents the difference between the bird-flower community types was selected. Multicollinearity between predictor variables is absent in binary modularity models, as generalized variance inflation factor (GVIF) ≤ 1.60 and in weighted modularity models, as variance inflation factor (VIF) ≤ 2.30 .

flower networks, and neither between sunbird–flower and honeyeater–flower networks. Furthermore, we found a very similar pattern of interaction specialization when using null-model corrected values (Figure 1). When potentially confounding variables were included in the linear models, hummingbird–flower networks still showed lower connectance than sunbird–flower and honeyeater–flower networks, and greater complementary specialization and null-model corrected binary modularity than honeyeater–flower networks. Moreover, we found no differences between complementary specialization and binary modularity of hummingbird–flower and sunbird–flower networks, nor between sunbird–flower and honeyeater–flower networks. Weighted modularity of networks was the only variable that did not differ between these bird–flower communities when including potentially confounding variables (Tables 1 and 2). Finally, hummingbird–flower communities contained more plant species than those involving sunbird or honeyeater communities (Kruskal–Wallis

test: $K = 28.32$, $p < 0.001$; Dunn's multiple comparison tests: hummingbirds > sunbirds = honeyeaters).

Several of the confounding variables were associated with estimates of interaction specialization (Tables 1 and 2). Notably, specialization increased with plant species richness for both observed and null-model corrected metrics (Appendix S3: Figure S1). Moreover, communities with a greater richness of birds than plant species exhibited greater specialization, with lower observed connectance; this pattern was reversed when looking at null-model corrected connectance. On islands, networks were less specialized, with lower observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization shown in networks sampled by focal observations (Tables 1 and 2). Nonetheless, restricting the analysis to networks sampled through focal observations, the most important predictor variables ($\Sigma w_i \geq 0.80$) were the same as in the complete dataset, and showed

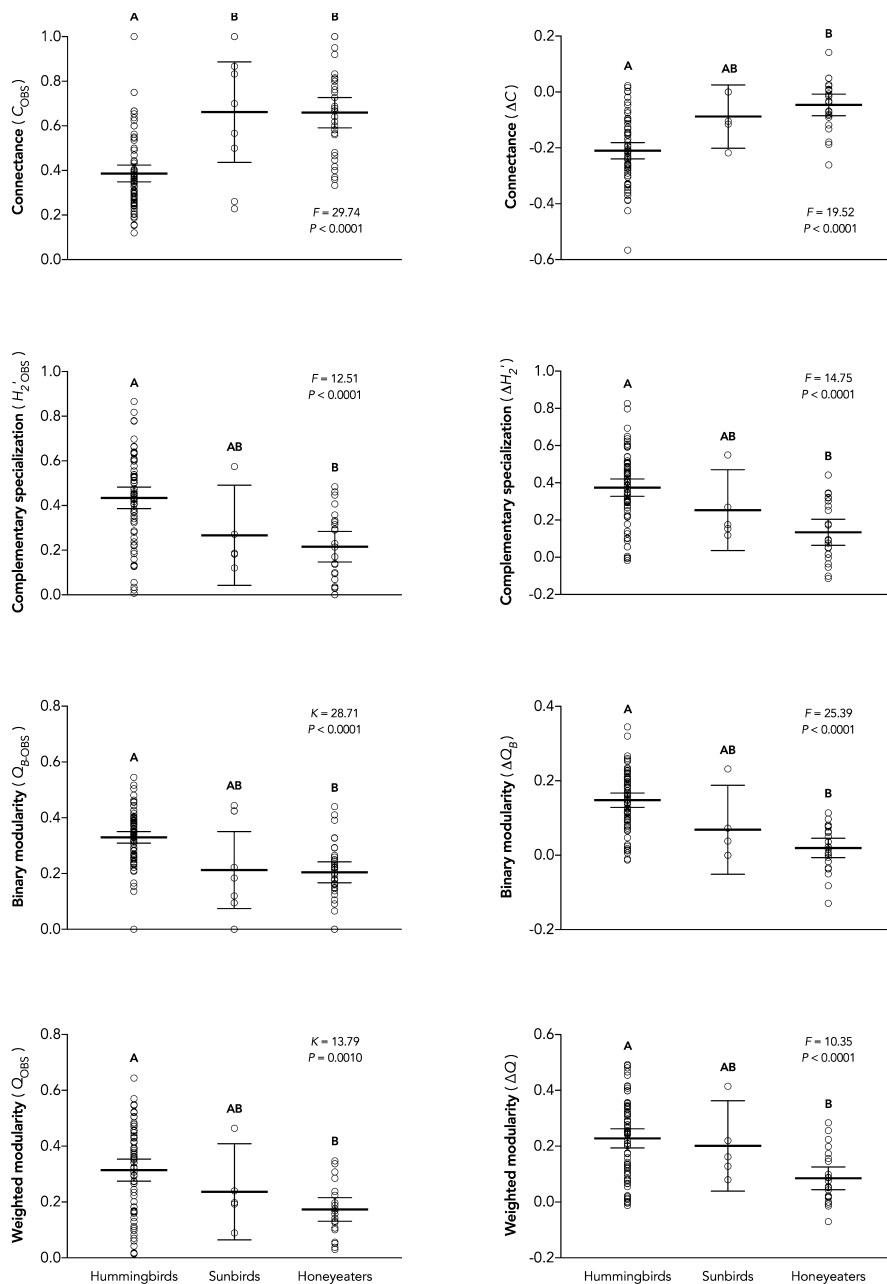


FIGURE 1 Comparison of the observed (OBS, first column) and null-model corrected (Δ , second column) metrics of bird-flower interaction networks of the three types of bird communities (hummingbirds, sunbirds and honeyeaters). Connectance (C) is the realized proportion of possible interactions in a community, complementary specialization (H_2') measures niche overlap among species and modularity (Q_B and Q) detects preferentially interacting subsets of species within the community. Observed connectance and binary modularity have a sample size of 121 networks, while the other metrics have a sample size of 94 networks. Dots represent each network and lines indicate mean and confidence interval at 95% confidence level. Letters represent the group that each bird-flower community belongs, based on Tukey's or Dunn's multiple comparison tests.

the same pattern described above for interaction specialization between different bird-flower communities (Tables S2 and S3). Intensity of sampling affected interaction specialization, with decreased null-model corrected connectance and weighted modularity when sampling intensity was high (Tables 1 and 2).

Hummingbird-flower networks were geographically widely spread, although some parts of North America and the Amazon region were poorly sampled (Figures 2 and 3). In addition, by comparing the cumulative frequency distribution of the global species richness of hummingbirds with their species richness in the sampled localities, we found that species-poor communities were disproportionately less sampled than species-rich communities (Appendix S3: Figure S2). Throughout the Old World, in contrast, the distribution of available networks was more restricted and

some species-rich regions, especially Central Africa, India, Southeast Asia and Southeast Australia, had few or no community-level studies of bird-flower interactions (Figures 2 and 3). Nonetheless, the species richness of the sunbird and honeyeater networks included in our study encompassed much of the global species richness gradient (Figure S2).

4 | DISCUSSION

As predicted, we found that New World (NW) hummingbird-flower interaction networks are more specialized than Old World (OW) honeyeater-flower networks. Hummingbird-flower networks have fewer realized interactions, lower niche overlap and greater binary

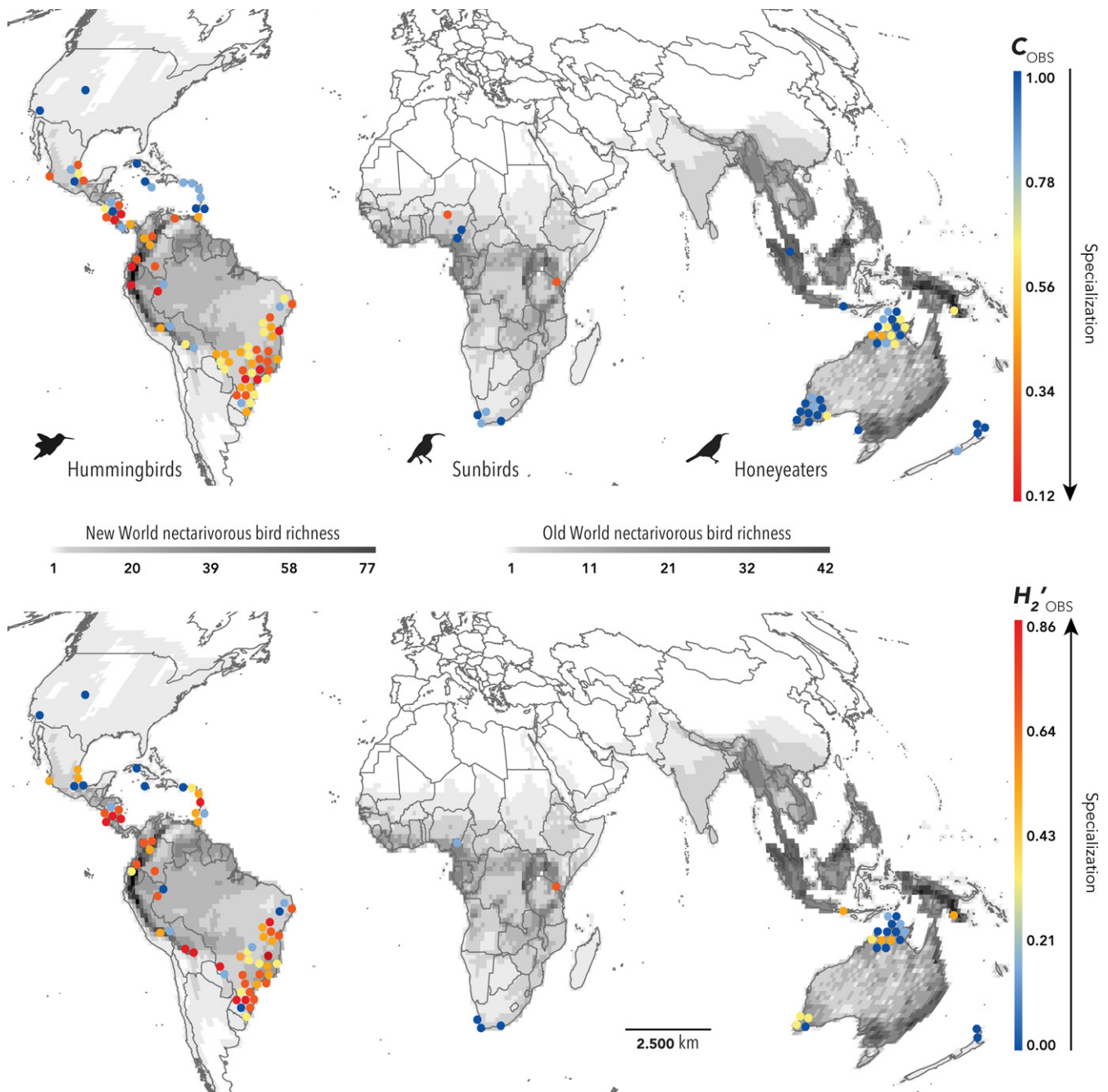


FIGURE 2 Specialization of bird-flower interaction networks in hummingbird, sunbird and honeyeater communities, measured by observed connectance (C_{OBS}), which describes the realized proportion of possible interactions in a community, and observed complementary specialization (H'_2_{OBS}), which calculates the niche overlap among species. Observed connectance has a sample size of 121 networks, while complementary specialization has a sample size of 94 networks. The species richness of hummingbirds, sunbirds and honeyeaters are represented in grey shades, intensifying with an increase in species richness. Points were moved slightly to improve visualization. Maps were built using Mollweide's equal-area projection. [Colour figure can be viewed at wileyonlinelibrary.com]

modularity, when compared to honeyeater-flower networks. However, interaction specialization of sunbird-flower networks was similar to both hummingbird-flower and honeyeater-flower networks.

The greater overall specialization between hummingbirds and their floral resources indicates that their interactions are more species-restricted than the interactions of honeyeaters with their flowers (Blüthgen, 2010). This greater interaction partitioning in hummingbird networks may be a consequence of the greater

variation in bill length among hummingbirds than honeyeaters, as well as the greater richness of bird-pollinated plant species in the NW (Abrahamczyk & Kessler, 2015; Fleming, 2005; Higgins et al., 2016). Hummingbird bill morphology in combination with corolla morphology may play a key role in constraining interactions via morphological mismatching (Cotton, 1998a; Temeles et al., 2002; Vizzintin-Bugoni et al., 2014). Indeed, in most hummingbird-flower communities, there is a subset of flowers with long, curved

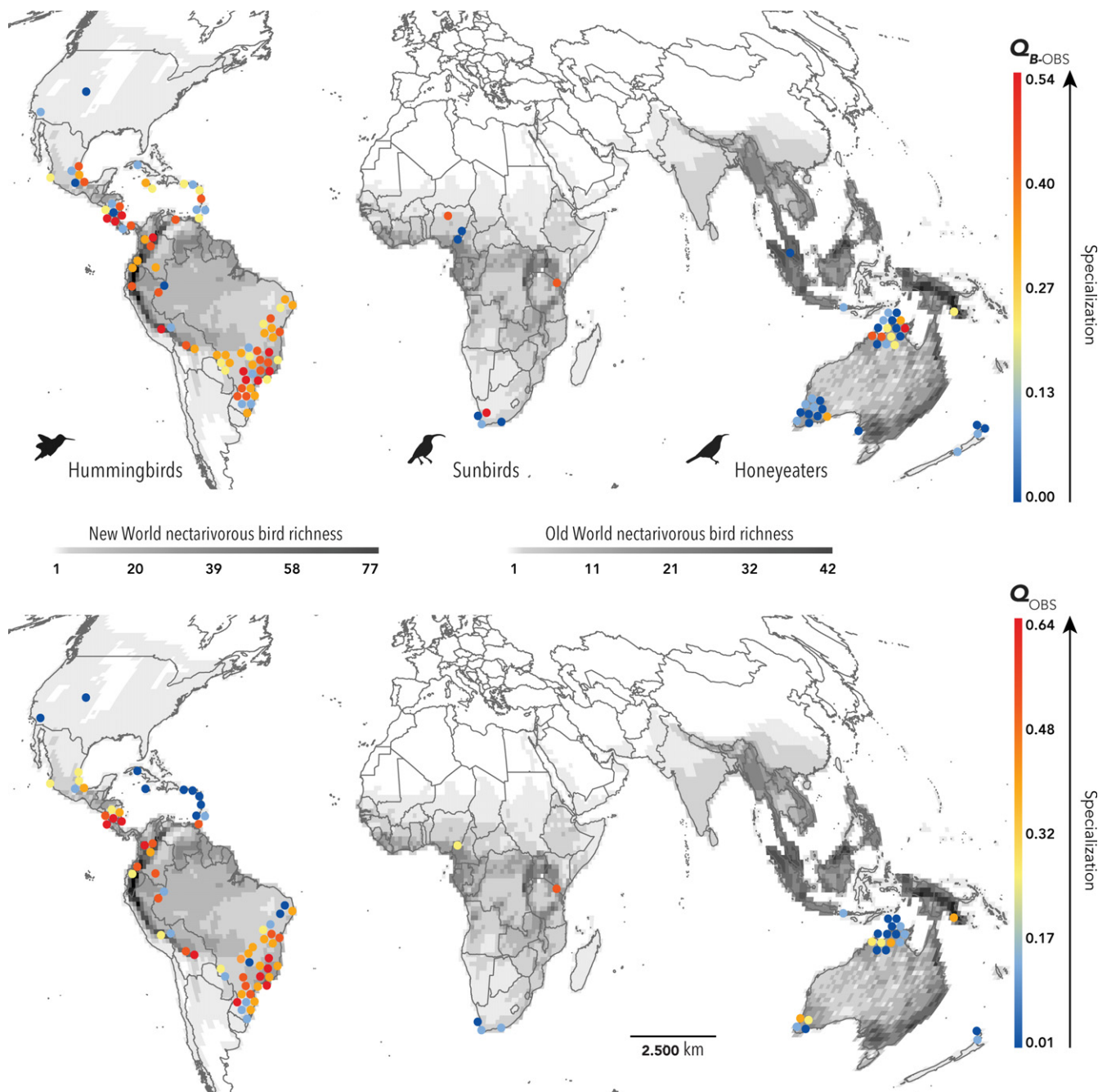


FIGURE 3 Specialization of bird-flower interaction networks in hummingbird, sunbird and honeyeater communities, measured by observed binary (Q_{B-OBS}) and weighted modularity (Q_{OBS}). Modularity is a network metric that detects preferentially interacting subsets of species within the community. Observed binary modularity has a sample size of 121 networks, while weighted modularity has a sample size of 94 networks. The species richness of hummingbirds, sunbirds and honeyeaters are represented in grey shades, intensifying with an increase in species richness. Points were moved slightly to improve visualization. Maps were built using Mollweide's equal-area projection. [Colour figure can be viewed at wileyonlinelibrary.com]

corollas visited by only one or a few long- and curve-billed birds (Feinsinger & Colwell, 1978; Maglianesi et al., 2014). Thus, the increased range of bill and corolla lengths in hummingbird-flower networks may contribute to reduced niche overlap and increased community-level specialization (Abrahamczyk & Kessler, 2010; Cotton, 1998b; Maglianesi et al., 2015; Maruyama et al., 2014). A greater specialization in hummingbird-flower networks could also

be due to a greater spatio-temporal floral resource predictability (Fleming & Muchhala, 2008). NW annual flowering cycles tend to be more predictable (Bawa et al., 2003) than, for instance, the supra-annual mass flowering in South Asian forests (Sakai, 2002). Additionally, flowers are more diverse and abundant in the understorey of NW forests in comparison to OW forests (LaFrankie et al., 2006). This greater diversity may create more interaction opportunities for



hummingbirds (Feinsinger & Colwell, 1978), resulting in greater niche partitioning in NW than in OW networks. Conversely, the lower specialization of honeyeater communities compared to hummingbird communities, is likely to be due to the much less variable bill length and corolla shapes in those communities (Ford & Paton, 1977). This is particularly the case in northern Australia, where most of the flowers visited by honeyeaters have an open or cup-shaped corolla that is morphologically accessible to several bird species (Ford et al., 1979; Franklin & Noske, 2000). Hence, more uniform bill lengths and more generalized corolla shapes among honeyeater–flower communities may result in lower interaction specialization, when compared to hummingbird–flower networks. Honeyeaters also tend to have broader dietary preferences in general, feeding on other resources, such as fruits, insects and honeydew more frequently than hummingbirds do (Higgins et al., 2016; Pyke, 1980), although hummingbirds also forage for insects as a source of protein (Stiles, 1995). These diverse feeding habits of honeyeaters may decrease competition for nectar resources, resulting in the more generalized interactions with flowers demonstrated here (although see Dalsgaard et al., 2017 for contradictory example in frugivorous bird–plant networks). Hummingbird networks had the highest overall specialization, implying in reduced niche overlaps. If combined with species turnover across continental scales, this greater specialization in hummingbird networks may imply a larger spatial variability of interactions, resulting in a greater spatial β -diversity of interactions (Trøjelsgaard et al., 2015). Additionally, temporal variation of resources spanning the entire year in NW communities (Bawa et al., 2003; Cotton, 2007) may also cause a temporal variation in interactions, resulting in a larger temporal β -diversity of interactions.

The similarity between sunbird–flower networks and the other two bird–flower communities is likely to be due to two reasons: first, relatively few sunbird–flower networks were available, resulting in wider confidence intervals (Figure 1). More networks may have reduced that variability and made it possible to detect differences between sunbird–flower networks and hummingbird– and honeyeater–flower networks, respectively. Second, sunbird–flower communities share ecological traits with both hummingbird–flower and honeyeater–flower communities. For instance, although sunbirds are considered less phenotypically specialized for nectar-feeding than hummingbirds (Stiles, 1981), the flowers they visit often have rather restrictive morphologies, with tubular and gullet shapes, similar to those of hummingbird-pollinated flowers (Fleming & Muchhala, 2008). This greater morphological restriction of flowers may decrease niche overlap among sunbird species, as these corolla shapes may be inaccessible to some species within the community (Pettet, 1977; Temeles et al., 2002). This morphological mismatch between bird–flower species may produce similar levels of interaction specialization in both sunbird–flower and hummingbird–flower networks, as we detected in this study. Additionally, some sunbirds have specialized feeding behaviours similar to hummingbirds, hovering while visiting flowers and traplining between resources (Padyšáková & Janeček, 2016). In contrast, we have demonstrated that in comparison to hummingbird communities, honeyeater and sunbird communities have lower floral resource

richness, which may explain the similarity in their level of interaction specialization. This lower resource diversity may increase niche overlap, producing the more generalized feeding niches found in OW networks.

The correlation between plant species richness and interaction specialization is likely to arise because niche availability is greater in species-rich than species-poor communities, thereby promoting greater niche partitioning among species (Dalsgaard et al., 2011; Martín González et al., 2015; Sebastián-González et al., 2015; but see Schleuning et al., 2012). The greater generalization of interactions of insular compared to mainland networks may therefore be a consequence of their species-poor communities (Abrahamczyk et al., 2015; Dalsgaard et al., 2009; MacArthur & Wilson, 1963), but may also be due to the tendency of generalist species to have greater establishment success on islands than specialist species (Maldonado et al., 2013; Olesen et al., 2002; Traveset et al., 2015). Moreover, at least for hummingbirds, generalized interactions on islands may have been influenced by their rather recent colonization (Abrahamczyk et al., 2015; McGuire et al., 2014) and a greater level of strong and periodic disturbances in islands in comparison to mainland communities, favouring generalized over specialized bird species (Dalsgaard et al., 2009).

In conclusion, we confirmed that interactions are more specialized in hummingbird–flower than in honeyeater–flower networks, and that sunbird–flower networks have similar interaction specialization with the other two bird–flower communities. The increased interaction specialization in the hummingbird–flower networks may be a consequence of their greater floral resource richness and phenotypic specialization, in contrast to honeyeater–flower communities (Fleming & Muchhala, 2008; Stiles, 1981). These results suggest that there is a link between phenotypic specialization, floral resource richness and interaction specialization among nectarivorous bird–flower communities across global scales.

ACKNOWLEDGEMENTS

We thank Marco A. R. Mello for his comments on a previous version of the manuscript; Louis A. Hansen and Bjørn Hermansen for their help in building the bird species richness map; and André C. Guaraldo for his help with the analysis. CAPES Foundation supported TBZ (PDSE scholarship proc. 8105/2014-6), JVB (PDSE scholarship proc. 8012/2014-08), AGC, RRF, AVL and LCR; CNPq supported FCP, EF, ACA, AVL, CGM, ICM, LCR, MSa and IGV (grant number 2013-5 and 445405/2014-7); Czech Science Foundation supported DH, SJ and OS (project n. 14-36098G); PAC was supported by the British Ornithologists' Union and Wolfson College, University of Oxford; PKM by FAPESP (proc. 2015/21457-4); ACA and RRF by FUNDECT; ACB by Oticon Fonden Denmark; DWC and TTJ by The Danish Council for Independent Research Natural Sciences; TTJ by F-HF, KHF, TFNS, University of Aarhus; CL by the CACyPI-Uatx-2016GK; AVL by FACEPE and OeAD; CGM by FAPESB; MAM by the CONICIT, MICIT, CCT and UNED from Costa Rica, OTS, DAAD, and the research-funding program "LOEWE" of Hesse's Ministry of Higher



Education, Research, and the Arts (Germany). JMA thanks Michael J. Lawes, RIEL, DCC, NTDP&I, RAAF, P&WCNT, and NTP&W; LRL by Unicamp and Ministerio del Medio Ambiente de Colombia; PEO by FAPEMIG; ZW by National Natural Science Foundation of China; AGC thanks Reserva Ecológica Michelin; GK thanks Valentim Casett, owner of the Prima Luna Reserve; MSc, KBG, BS, MGRV thank the German Research Foundation (DFG) for funding; TBZ, BD, AMMG and CR thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate (grant number DNRF96).

AUTHOR CONTRIBUTIONS

TBZ, BD and IGV conceived the ideas; BD, PAC, JJR, PKM, EF, MSc, AMMG, JVB, DCF, SA, RA, ACA, FPA, SMAJ, ACB, KBG, DWC, HC, AGC, RRF, DH, TTI, SJ, GK, CL, FMGLC, AVL, AOM, CMG, ICM, MAM, TSM, JMA, ACM, GMO, PEO, JFO, JR, LCR, LRL, AMR, MSA, BS, OS, AT, MGRV, ZW, SW, CR and IGV collected the data and helped with discussion; TBZ analysed the data; and TBZ, BD, FCP, PAC, JJR, PKM, EF, MSc, AMMG, JVB, DCF and IGV led the writing.

REFERENCES

- Abrahamczyk, S., & Kessler, M. (2010). Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology*, 151, 615–625.
- Abrahamczyk, S., & Kessler, M. (2015). Morphological and behavioural adaptations to feed on nectar: how feeding ecology determines the diversity and composition of hummingbird assemblages. *Journal of Ornithology*, 156, 333–347.
- Abrahamczyk, S., Souto-Vilarós, D., McGuire, J. A., & Renner, S. S. (2015). Diversity and clade ages of West Indian hummingbirds and the largest plant clades dependent on them: a 5–9 Myr young mutualistic system. *Biological Journal of the Linnean Society*, 114, 848–859.
- Barber, M. J. (2007). Modularity and community detection in bipartite networks. *Physical Review E*, 76, 1–11.
- Barker, F. K., Barrowclough, G. F., & Groth, J. G. (2002). A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society B: Biological Sciences*, 269, 295–308.
- Barton, K. (2016). *MuMIn: multi-model inference - R package*. R Foundation for Statistical Computing.
- Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution and Systematics*, 38, 567–593.
- Bawa, K. S., Kang, H., & Grayum, M. H. (2003). Relationships among the time, frequency, and duration of flowering in tropical rain forest trees. *American Journal of Botany*, 90, 877–887.
- Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. *Basic and Applied Ecology*, 11, 185–195.
- Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, 6, 1–12.
- Brooker, M., Braithwaite, R., & Estbergs, J. (1990). Foraging ecology of some insectivorous and nectarivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. *Emu*, 90, 215–230.
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.
- Castellanos, M. C., Wilson, P., & Thomson, J. D. (2003). Pollen transfer by hummingbirds and bumblebees, and the divergence of pollination modes in *Penstemon*. *Evolution*, 57, 2742–2752.
- Collins, B. G., & Paton, D. C. (1989). Consequences of differences in body mass, wing length and leg morphology for nectar-feeding birds. *Australian Journal of Ecology*, 14, 269–289.
- Collins, B. G., & Rebelo, T. (1987). Pollination biology of the Proteaceae in Australia and southern Africa. *Austral Ecology*, 12, 387–421.
- Cotton, P. A. (1998a). Coevolution in an Amazonian hummingbird-plant community. *Ibis*, 140, 639–646.
- Cotton, P. A. (1998b). The hummingbird community of a lowland Amazonian rainforest. *Ibis*, 140, 512–521.
- Cotton, P. A. (2007). Seasonal resource tracking by Amazonian hummingbirds. *Ibis*, 149, 135–142.
- Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany*, 59, 715–727.
- Dalsgaard, B., Magård, E., Fjeldsø, J., Martín González, A. M., Rahbek, C., Olesen, J. M., ... Svenning, J. C. (2011). Specialization in plant-hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. *PLoS ONE*, 6, e25891.
- Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. *Oecologia*, 159, 757–766.
- Dalsgaard, B., Schleuning, M., Maruyama, P. K., Dehling, D. M., Sonne, J., Vizentin-Bugoni, J., ... Rahbek, C. (2017). Opposed latitudinal patterns of network-derived and dietary specialization in avian plant-frugivore interaction systems. *Ecography*, <https://doi.org/10.1111/ecog.02604>
- del Hoyo, J., Elliot, A., Sargatal, J., Christie, D. A., & Juana, E. (2016). *Handbook of the birds of the world alive*. Barcelona: Lynx Edicions.
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., ... Mouquet, N. (2010). Defining and measuring ecological specialization. *Journal of Applied Ecology*, 47, 15–25.
- Dormann, C. F., Frund, J., Bluthgen, N., & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, 2, 7–24.
- Dormann, C. F., Gruber, B., & Fründ, J. (2008). Introducing the bipartite package: analysing ecological networks. *R News*, 8, 8–11.
- Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, 5, 90–98.
- Feinsinger, P., & Colwell, R. K. (1978). Community organization among Neotropical nectar-feeding birds. *American Zoologist*, 18, 779–795.
- Fleming, T. H. (2005). The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos*, 111, 556–562.
- Fleming, T. H., & Muchhala, N. (2008). Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *Journal of Biogeography*, 35, 764–780.
- Ford, H. A., & Paton, D. C. (1977). The comparative ecology of ten species of honeyeaters in South Australia. *Australian Journal of Ecology*, 2, 399–407.
- Ford, H. A., Paton, D. C., & Forde, N. (1979). Birds as pollinators of Australian plants. *New Zealand Journal of Botany*, 17, 509–519.
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*. Thousand Oaks, CA: SAGE.
- Franklin, D. C., & Noske, R. A. (2000). Nectar sources used by birds in monsoonal north-western Australia: a regional survey. *Australian Journal of Botany*, 48, 461–474.
- Futuyama, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, 19, 207–233.



- Giraudoux, P. (2016). *Pgirmess: data analysis in Ecology - R package*. R Foundation for Statistical Computing.
- Hair, J. F., Black, W. C., & Babin, B. J. (2009). *Multivariate data analysis: A global perspective*. Upper Saddle River, NJ: Prentice Hall.
- Higgins, P., Christidis, L., Ford, H., & Bonan, A. (2016). Honeyeaters (Meliphagidae). In J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie & E. Juana (Eds.), *Handbook of the birds of the world alive* (retrieved from <http://www.hbw.com/>). Barcelona: Lynx Edicions.
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal*, 50, 346–363.
- Janeček, Š., Patáčová, E., Bartoš, M., Padyšáková, E., Spitzer, L., & Tropek, R. (2011). Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? *Oikos*, 120, 178–183.
- Johnson, S. D., & Steiner, K. E. (2000). Generalization versus specialization in plant pollination systems. *Trends in Ecology and Evolution*, 15, 140–143.
- Jordano, P. (1987). Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. *The American Naturalist*, 129, 657–677.
- LaFrankie, J. V., Ashton, P. S., Chuyong, G. B., Co, L., Condit, R., Davies, S. J., ... Villa, G. (2006). Contrasting structure and composition of the understory in species-rich tropical rain forests. *Ecology*, 87, 2298–2305.
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- Maglianesi, M. A., Bluthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, 95, 3325–3334.
- Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2015). Functional structure and specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. *Ecography*, 38, 1119–1128.
- Maldonado, M. B., Lomáscolo, S. B., & Vázquez, D. P. (2013). The importance of pollinator generalization and abundance for the reproductive success of a generalist plant. *PLoS ONE*, 8, e75482.
- Marquitti, F. M. D., Guimarães, P. R., Pires, M. M., & Bittencourt, L. F. (2014). MODULAR: software for the autonomous computation of modularity in large network sets. *Ecography*, 37, 221–224.
- Martín González, A. M., Dalsgaard, B., Nogués-Bravo, D., Graham, C. H., Schleuning, M., Maruyama, P. K., ... Martinez, N. D. (2015). The macroecology of phylogenetically structured hummingbird-plant networks. *Global Ecology and Biogeography*, 24, 1212–1224.
- Maruyama, P. K., Vizentin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B. (2014). Morphological and spatio-temporal mismatches shape a Neotropical savanna plant-hummingbird network. *Biotropica*, 46, 740–747.
- McGuire, J. A., Witt, C. C., Remsen, J. V., Corl, A., Rabosky, D. L., Altshuler, D. L., & Dudley, R. (2014). Molecular phylogenetics and the diversification of hummingbirds. *Current Biology*, 24, 910–916.
- Morgan, W. T. (1998). A review of eight statistics software package for general use. *The American Statistician*, 52, 70–82.
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 19891–19896.
- Olesen, J. M., Eskildsen, L. I., & Venkatasamy, S. (2002). Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Diversity and Distributions*, 8, 181–192.
- Olesen, J. M., & Jordano, P. (2002). Geographic patterns in plant-pollinator mutualistic networks. *Ecology*, 83, 2416–2424.
- Ollerton, J., Killick, A., Lamborn, E., Watts, S., & Whiston, M. (2007). Multiple meanings and modes: on the many ways to be a generalist flower. *Taxon*, 56, 717–728.
- Padyšáková, E., & Janeček, Š. (2016). Sunbird hovering behavior is determined by both the forager and resource plant. *Biotropica*, 48, 687–693.
- Patefield, W. M. (1981). Algorithm AS 159: an efficient method of generating random $R \times C$ tables with given row and column totals. *Journal of the Royal Statistical Society Series C (Applied Statistics)*, 30, 91–97.
- Pettet, A. (1977). Seasonal changes in nectar-feeding by birds at Zaria, Nigeria. *Ibis*, 119, 291–308.
- Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Moriarty Lemmon, E., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573.
- Pyke, G. H. (1980). The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Australian Journal of Ecology*, 5, 343–369.
- QGIS Development Team (2017). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from <http://www.qgis.org/>
- R Core Team (2016). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rahbek, C., & Graves, G. R. (2000). Detection of macro-ecological patterns in South American hummingbirds is affected by spatial scale. *Proceedings of the Royal Society B: Biological Sciences*, 267, 2259–2265.
- Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 4534–4539.
- Rahbek, C., Hansen, L. A., & Fjeldså, J. (2012). Data from “One degree resolution database of the global distribution of birds.” The Natural History Museum of Denmark, University of Copenhagen, Denmark. <http://macroecology.ku.dk/resources/>
- Ramírez-Burbano, M. B., Stiles, G., González, C., Amorim, F., Dalsgaard, B., & Maruyama, P. K. (2017). The role of the endemic and critically endangered Colorful Puffleg *Eriocnemis mirabilis* in plant-hummingbird networks of the Colombian Andes. *Biotropica*, <https://doi.org/10.1111/btp.12442>.
- Sakai, S. (2002). General flowering in lowland mixed dipterocarp forests of south-east Asia. *Biological Journal of the Linnean Society*, 75, 233–247.
- Schleuning, M., Fründ, J., Klein, A. M., Abrahamczyk, S., Alarcón, R., Albrecht, M., ... Blüthgen, N. (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, 22, 1925–1931.
- Schleuning, M., Ingmann, L., Strauß, R., Fritz, S. A., Dalsgaard, B., Dehling, D. M., ... Dormann, C. F. (2014). Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecology Letters*, 17, 454–463.
- Sebastián-González, E., Dalsgaard, B., Sandel, B., & Guimarães, P. R. Jr (2015). Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters. *Global Ecology and Biogeography*, 24, 293–303.
- Stiles, F. G. (1981). Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Annals of the Missouri Botanical Garden*, 68, 323–351.
- Stiles, F. G. (1995). Behavioral, ecological and morphological correlates of foraging for arthropods by the hummingbirds of a tropical wet forest. *The Condor*, 97, 853–878.
- Temeles, E. J., Linhart, Y. B., Masonjones, M., & Masonjones, H. D. (2002). The role of flower width in hummingbird bill length-flower length relationships. *Biotropica*, 34, 68–80.



- Thomson, J. D., & Wilson, P. (2008). Explaining evolutionary shifts between bee and hummingbird pollination: convergence, divergence, and directionality. *International Journal of Plant Sciences*, 169, 23–38.
- Traveset, A., Olesen, J. M., Nogales, M., Vargas, P., Jaramillo, P., Antolín, E., ... Heleno, R. (2015). Bird–flower visitation networks in the Galápagos unveil a widespread interaction release. *Nature Communications*, 6, 6376.
- Trøjelsgaard, K., Jordano, P., Carstensen, D. W., & Olesen, J. M. (2015). Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142925.
- Vázquez, D. P., & Stevens, R. D. (2004). The latitudinal gradient in niche breadth: Concepts and evidence. *The American Naturalist*, 164, 1–19.
- Vizentin-Bugoni, J., Maruyama, P. K., & Sazima, M. (2014). Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132397.
- Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in pollination systems, and why it matters. *Ecology*, 77, 1043–1060.
- Wester, P. (2013). Sunbirds hover at flowers of *Salvia* and *Lycium*. *Ostrich: Journal of African Ornithology*, 84, 27–32.

BIOSKETCH

Thais B. Zanata is an ecologist interested in mutualistic interactions, specifically in the effects of morphology, evolution and climate on interaction patterns across broad geographical scales. This working group, a collaboration among researchers that study bird–flower interactions in different continents, was established to test the ideas of Fleming and Muchhala (2008).

SUPPORTING INFORMATION

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

How to cite this article: Zanata TB, Dalsgaard B, Passos FC, et al. Global patterns of interaction specialization in bird–flower networks. *J Biogeogr.* 2017;44:1891–1910. <https://doi.org/10.1111/jbi.13045>



APPENDIX 1 DATA SOURCE OF EACH STUDY USED TO BUILD THE INTERACTION NETWORKS OF BIRD-FLOWER COMMUNITIES

ID	Data source
HUMMINGBIRDS (Trochilidae)	
1	Ollerton, J., Alarcón, R., Waser, N. M., Price, M. V., Watts, S., Cranmer, L., Hingston, A., Peter, C. I., & Rotenberry, J. (2009). A global test of the pollination syndrome hypothesis. <i>Annals of Botany</i> , 103, 1471–1480.
2	Alarcón, R., Waser, N. M., & Ollerton, J. (2008). Year-to-year variation in the topology of a plant-pollinator interaction network. <i>Oikos</i> , 117, 1796–1807.
3	Baquero, A. C. (2014). <i>Evolutionary and ecological insight into hummingbird-plant communities in the Caribbean</i> . M.Sc. Thesis, University of Copenhagen, Denmark.
4	Arizmendi, M. C., & Ornelas, J. F. (1990). Hummingbirds and their floral resources in a tropical dry forest in Mexico. <i>Biotropica</i> , 22, 172–180.
5	Juan Francisco Ornelas, <i>unpublished data</i> .
6	Carlos Lara, <i>unpublished data</i> .
7	Carlos Lara, <i>unpublished data</i> .
8	Lara, C. (2006). Temporal dynamics of flower use by hummingbirds in a highland temperate forest in Mexico. <i>Ecoscience</i> , 13, 23–29.
9	Toledo, V. M. (1975). La estacionalidad de las flores utilizadas por los colibríes de una selva tropical húmeda en México. <i>Biotropica</i> , 7, 63–70.
10	Ingversen, T. (2006). <i>Plant-pollinator interactions on Jamaica and Dominica - the centrality, asymmetry, and modularity of networks</i> . M.Sc. Thesis, University of Aarhus, Denmark.
11	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
12	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
13	Percival, M. (1974). Floral ecology of coastal scrub in southeast Jamaica. <i>Biotropica</i> , 6, 104–129.
14	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
15	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
16	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
17	Dalsgaard, B., Martín González, A. M., Olesen, J. M., Ollerton, J., Timmermann, A., Andersen, L. H., & Tossas, A. G. (2009). Plant-hummingbird interactions in the West Indies: floral specialisation gradients associated with environment and hummingbird size. <i>Oecologia</i> , 159, 757–766.
18	Snow, B. K., & Snow, D. W. (1972). Feeding niches of hummingbirds in a Trinidad valley. <i>Journal of Animal Ecology</i> , 41, 471–485.
19	Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the Neotropics. <i>Ecology</i> , 95, 3325–3334.
20	Stiles, F. G. (1975). Ecology, flowering phenology and hummingbird pollination of some Costa Rican <i>Heliconia</i> species. <i>Ecology</i> , 56, 285–301.
21	Seres, A., & Ramirez, N. (1995). Biología floral y polinización de algunas monocotiledóneas de un bosque nublado venezolano. <i>Annals of the Missouri Botanical Garden</i> , 82, 61–81.
22	Wolf, L. L. (1970). The impact of seasonal flowering on the biology of some tropical hummingbirds. <i>The Condor</i> , 72, 1–14.
23	Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the Neotropics. <i>Ecology</i> , 95, 3325–3334.
24	Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the Neotropics. <i>Ecology</i> , 95, 3325–3334.
25	Stiles, F. G. (1985). Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. <i>Ornithological Monographs</i> , 36, 757–787.
26	Feinsinger, P. (1978). Ecological interactions between plants and hummingbirds in a successional tropical community. <i>Ecological Monographs</i> , 48, 269–287.
27	Wolf, L. L., Stiles, F. G., & Hainsworth, F. R. (1976). Ecological organization of a tropical, highland hummingbird community. <i>The Journal of Animal Ecology</i> , 45, 349–379.
28	Wolf, L. L., Stiles, F. G., & Hainsworth, F. R. (1976). Ecological organization of a tropical, highland hummingbird community. <i>The Journal of Animal Ecology</i> , 45, 349–379.

(Continues)



APPENDIX 1 (Continued)

ID	Data source
29	Snow, D. W., & Snow, B. (1980). Relationships between hummingbirds and flowers in the Andes of Colombia. <i>Bulletin of the British Museum Natural History (Zoology)</i> , 38, 105–139.
30	Snow, D. W., & Snow, B. (1980). Relationships between hummingbirds and flowers in the Andes of Colombia. <i>Bulletin of the British Museum Natural History (Zoology)</i> , 38, 105–139.
31	Snow, D. W., & Snow, B. (1980). Relationships between hummingbirds and flowers in the Andes of Colombia. <i>Bulletin of the British Museum Natural History (Zoology)</i> , 38, 105–139.
32	Gutierrez Zamora, E. A., & Rojas Nossa, S. V. (2001). <i>Dinámica anual de la interacción colibrí-flor en ecosistemas alto andinos del volcán Galeras, sur de Colombia</i> . B.Sc. Thesis, Universidad Nacional de Colombia, Colombia.
33	Rosero-Lasprilla, L. (2003). <i>Interações planta/beija-flor em três comunidades vegetais da parte sul do Parque Nacional Natural Chiribiquete, Amazonas (Colômbia)</i> . PhD. Thesis, Universidade Estadual de Campinas, Brasil. Rosero Lasprilla L. & Sazima M. (2004). Interacciones planta-colibrí en tres comunidades vegetales de la parte suroriental del Parque Nacional Natural Chiribiquete, Colombia. <i>Ornitología Neotropical</i> , 15, 183–190.
34	Walther, B. A., & Brieschke, H. (2001). Hummingbird-flower relationships in a mid-elevation rainforest near Mindo, north-western Ecuador. <i>International Journal of Ornithology</i> , 4, 115–135.
35	Cotton, P. A. (1998). The hummingbird community of a lowland Amazonian rainforest. <i>Ibis</i> , 140, 512–521.
36	Amaya-Márquez, M., Stiles, G., & Rangel-Ch, O. (2001). Interacción planta-colibrí en Amacayacu (Amazonas, Colombia): una perspectiva palinológica. <i>Caldasia</i> , 23, 301–322.
37	Dziedzich, C., Stevens, A.-D., & Gottsberger, G. (2003). The hummingbird plant community of a tropical montane rain forest in southern Ecuador. <i>Plant Biology</i> , 5, 331–337.
38	Las-Casas, F. M. G., Azevedo Júnior, S. M., & Dias Filho, M. M. (2012). The community of hummingbirds (Aves: Trochilidae) and the assemblage of flowers in a Caatinga vegetation. <i>Brazilian Journal of Biology</i> , 72, 51–58.
39	Lopes, A. V. F. (2002). <i>Polinização por beija-flores em remanescente da Mata Atlântica pernambucana, nordeste do Brasil</i> . Ph.D. Thesis, Universidade Estadual de Campinas, Brasil.
40	Leal, F. C., Lopes, A. V., & Machado, I. C. (2006). Polinização por beija-flores em uma área de caatinga no Município de Floresta, Pernambuco, Nordeste do Brasil. <i>Revista Brasileira de Botânica</i> , 29, 379–389.
41	Moura, A. C. (2012). <i>Beija-flores (Aves: Trochilidae) e as plantas em que forrageiam em uma comunidade de Caatinga de altitude da Chapada Diamantina, Bahia</i> . M.Sc. Thesis, Universidade Estadual de Feira de Santana, Brasil.
42	Watts, S. (2008). <i>Plant-flower visitor interactions in the Sacred Valley of Peru</i> . Ph.D. Thesis, University of Northampton, United Kingdom.
43	Machado, C. G., Coelho, A. G., Santana, C. S., & Rodrigues, M. (2007). Beija-flores e seus recursos florais em uma área de campo rupestre da Chapada Diamantina, Bahia. <i>Revista Brasileira de Ornitologia</i> , 15, 267–279.
44	Santana, C. S., & Machado, C. G. (2010). Fenologia de floração e polinização de espécies ornitófilas de bromeliáceas em uma área de campo rupestre da Chapada Diamantina, BA, Brasil. <i>Revista Brasileira de Botânica</i> , 33, 469–477.
45	Machado, C. G. (2009). Beija-flores (Aves: Trochilidae) e seus recursos florais em uma área de caatinga da Chapada Diamantina, Bahia, Brasil. <i>Zoologia</i> , 26, 255–265.
46	Machado, C. G. (2014). The hummingbird community and the plants which they visit at a savannah in the Chapada Diamantina, Bahia, Brazil. <i>Bioscience Journal</i> , 30, 1578–1587.
47	Watts, S., Dormann, C. F., Martín González, A. M., & Ollerton, J. (2006). The influence of floral traits on specialization and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes. <i>Annals of Botany</i> , 118, 415–429.
48	Coelho, A.G. (2013). <i>A comunidade de plantas utilizada por beija-flores no sub-bosque de um fragmento de Mata Atlântica da Bahia, Brasil</i> . Ph.D. Thesis, Universidade Estadual de Feira de Santana, Brasil.
49	Abrahamczyk, S., & Kessler, M. (2010). Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. <i>Journal of Ornithology</i> , 151, 615–625.
50	Abrahamczyk, S., & Kessler, M. (2010). Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. <i>Journal of Ornithology</i> , 151, 615–625.
51	Machado, A. O. (2012). <i>Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região</i> . Ph.D. Thesis, Universidade Federal de Uberlândia, Brasil.
52	Machado, A. O. (2012). <i>Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região</i> . Ph.D. Thesis, Universidade Federal de Uberlândia, Brasil. Araújo, F. P., Sazima, M., & Oliveira, P. E. (2013). The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. <i>Plant Systematics and Evolution</i> , 299, 1119–1133. Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B., & Oliveira, P. E. (2013). Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. <i>Naturwissenschaften</i> , 100, 1061–1068.

(Continues)



APPENDIX 1 (Continued)

ID	Data source
53	Machado, A. O. (2012). <i>Diversidade de recursos florais para beija-flores nos cerrados do Triângulo mineiro e região</i> . Ph.D. Thesis, Universidade Federal de Uberlândia, Brasil. Araújo, F. P., Sazima, M., & Oliveira, P. E. (2013). The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. <i>Plant Systematics and Evolution</i> , 299, 1119–1133. Maruyama, P. K., Oliveira, G. M., Ferreira, C., Dalsgaard, B., & Oliveira, P. E. (2013). Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. <i>Naturwissenschaften</i> , 100, 1061–1068.
54	Rodrigues, L. C., & Rodrigues, M. (2014). Flowers visited by hummingbirds in the open habitats of the south-eastern Brazilian mountain tops: species composition and seasonality. <i>Brazilian Journal of Biology</i> , 74, 659–676.
55	Araujo, A. C., & Sazima, M. (2003). The assemblage of flowers visited by hummingbirds in the “capões” of southern Pantanal, Mato Grosso do Sul, Brazil. <i>Flora</i> , 198, 427–435.
56	Vasconcelos, M. F., & Lombardi, J. A. (1999). Padrão sazonal na ocorrência de seis espécies de beija-flores (Apodiformes: Trochilidae) em uma localidade de campo rupestre na Serra do Curral, Minas Gerais. <i>Ararajuba</i> , 7, 71–79.
57	Varassin, I. G., & Sazima, M. (2012). Spatial heterogeneity and the distribution of bromeliad pollinators in the Atlantic Forest. <i>Acta Oecologica</i> , 43, 104–112.
58	Rodrigues, L. C., & Araujo, A. C. (2011). The hummingbird community and their floral resources in an urban forest remnant in Brazil. <i>Brazilian Journal of Biology</i> , 71, 611–622.
59	Faria, R. R. (2007). <i>Fenologia de floração e polinização de espécies ornitófilas na Serra da Bodoquena, Mato Grosso Do Sul, Brasil</i> . M.Sc. Thesis. Universidade Federal do Mato Grosso do Sul, Brasil. Faria, R. R., & Araujo, A. C. (2010). Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso Do Sul, Brazil. <i>Anais da Academia Brasileira de Ciências</i> , 82, 843–855. Faria, R. R., & Araujo, A. C. (2010). Pollination ecology of <i>Ruellia angustiflora</i> (Ness) Lindau ex Rambo (Acanthaceae) in the Serra da Bodoquena, Mato Grosso do Sul, Brazil. <i>Flora</i> , 205, 106–111. Camargo, E., Rodrigues, L. C., & Araujo, A. C. (2011). Pollination biology and reproduction of <i>Seemannia sylvatica</i> (Kunth) Hanstein (Gesneriaceae) in the Serra da Bodoquena National Park, Mato Grosso do Sul. <i>Biota Neotropica</i> , 11, 125–130.
60	Faria, R. R. (2007). <i>Fenologia de floração e polinização de espécies ornitófilas na Serra da Bodoquena, Mato Grosso Do Sul, Brasil</i> . M.Sc. Thesis. Universidade Federal do Mato Grosso do Sul, Brasil. Faria, R. R., & Araujo, A. C. (2010). Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso Do Sul, Brazil. <i>Anais da Academia Brasileira de Ciências</i> , 82, 843–855. Faria, R. R., & Araujo, A. C. (2010). Pollination ecology of <i>Ruellia angustiflora</i> (Ness) Lindau ex Rambo (Acanthaceae) in the Serra da Bodoquena, Mato Grosso do Sul, Brazil. <i>Flora</i> , 205, 106–111. Camargo, E., Rodrigues, L. C., & Araujo, A. C. (2011). Pollination biology and reproduction of <i>Seemannia sylvatica</i> (Kunth) Hanstein (Gesneriaceae) in the Serra da Bodoquena National Park, Mato Grosso do Sul. <i>Biota Neotropica</i> , 11, 125–130.
61	Faria, R. R. (2007). <i>Fenologia de floração e polinização de espécies ornitófilas na Serra da Bodoquena, Mato Grosso Do Sul, Brasil</i> . M.Sc. Thesis. Universidade Federal do Mato Grosso do Sul, Brasil. Faria, R. R., & Araujo, A. C. (2010). Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso Do Sul, Brazil. <i>Anais da Academia Brasileira de Ciências</i> , 82, 843–855. Faria, R. R., & Araujo, A. C. (2010). Pollination ecology of <i>Ruellia angustiflora</i> (Ness) Lindau ex Rambo (Acanthaceae) in the Serra da Bodoquena, Mato Grosso do Sul, Brazil. <i>Flora</i> , 205, 106–111. Camargo, E., Rodrigues, L. C., & Araujo, A. C. (2011). Pollination biology and reproduction of <i>Seemannia sylvatica</i> (Kunth) Hanstein (Gesneriaceae) in the Serra da Bodoquena National Park, Mato Grosso do Sul. <i>Biota Neotropica</i> , 11, 125–130.
62	Abreu, C. R. M., & Vieira, M. F. (2004). Os beija-flores e seus recursos florais em um fragmento florestal de Viçosa, sudeste brasileiro. <i>Lundiana</i> , 5, 129–134.
63	Machado, C. G., & Semir, J. (2006). Fenologia da floração e biologia floral de bromeliáceas ornitófilas de uma área da Mata Atlântica do Sudeste brasileiro. <i>Revista Brasileira de Botânica</i> , 29, 163–174.
64	Canela, M. B. F. (2006). <i>Interações entre plantas e beija-flores numa comunidade de floresta atlântica montana em Itatiaia, RJ</i> . Ph.D. Thesis, Universidade Estadual de Campinas, Brasil.
65	Sazima, I., Buzato, S., & Sazima, M. (1996). An assemblage of hummingbird-pollinated flowers in a montane forest in south-eastern Brazil. <i>Botanica Acta</i> , 109, 149–160.
66	Vizentin-Bugoni, J., Maruyama, P. K., & Sazima, M. (2014). Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird-plant network. <i>Proceedings of the Royal Society B: Biological Sciences</i> , 281, 20132397.
67	Maruyama, P. K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I., & Sazima, M. (2015). Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. <i>Oecologia</i> , 178, 783–793.
68	Maruyama, P. K., Vizentin-Bugoni, J., Dalsgaard, B., Sazima, I., & Sazima, M. (2015). Nectar robbery by a hermit hummingbird: association to floral phenotype and its influence on flowers and network structure. <i>Oecologia</i> , 178, 783–793.

(Continues)



APPENDIX 1 (Continued)

ID	Data source
69	Araujo, A. C. (1996). <i>Beija-flores e seus recursos florais numa área de planície costeira do litoral norte de São Paulo, Brasil</i> . M.Sc. Thesis, Universidade Estadual de Campinas, Brasil.
70	Snow, D. W., & Snow, B. K. (1986). Feeding ecology of hummingbirds in the Serra do Mar, south-eastern Brazil. <i>El Hornero</i> , 12, 286–296.
71	Erich Fischer, <i>unpublished data</i> .
72	Piacentini, V. D. Q., & Varassin, I. G. (2007). Interaction network and the relationships between bromeliads and hummingbirds in an area of secondary Atlantic rain forest in southern Brazil. <i>Journal of Tropical Ecology</i> , 23, 663–671.
73	Malucelli, T. S. (2014). <i>Fatores envolvidos na estruturação das redes de polinização beija-flor-planta em um gradiente sucessional</i> . M.Sc. Thesis, Universidade Federal do Paraná, Brasil.
74	Kaehler, M., Varassin, I. G., & Goldenberg, R. (2005). Polinização em uma comunidade de bromélias em Floresta Atlântica Alto-montana no Estado do Paraná, Brasil. <i>Revista Brasileira de Botânica</i> , 28, 219–228.
75	Chupil, H. (2012). <i>Uso de grãos de pólen na identificação de plantas e para examinar a partição de nicho alimentar entre beija-flores no sul do Brasil</i> . M.Sc. Thesis, Universidade Federal do Paraná, Brasil. Chupil, H., & Roper, J. J. (2014). Assembleia de beija-flores (Família Trochilidae) em uma região de ecótono no município de Piraquara, Paraná. <i>Atualidades Ornitológicas</i> , 177, 7–9.
76	Kohler, G. (2011). <i>Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no sul do Brasil</i> . M.Sc. Thesis, Universidade Federal do Paraná, Brasil.
77	Kohler, G. (2011). <i>Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no sul do Brasil</i> . M.Sc. Thesis, Universidade Federal do Paraná, Brasil.
78	Kohler, G. (2011). <i>Redes de interação planta-beija-flor em um gradiente altitudinal de Floresta Atlântica no sul do Brasil</i> . M.Sc. Thesis, Universidade Federal do Paraná, Brasil.
79	Jeferson Vizentin-Bugoni & Ana M. Rui, <i>unpublished data</i> .

SUNBIRDS (Nectariniidae)

1	Pettet, A. (1977). Seasonal changes in nectar-feeding by birds at Zaria, Nigeria. <i>Ibis</i> , 119, 291–308.
2	Weston, K. A., Chapman, H. M., Kelly, D., & Moltchanova, E. V. (2012). Dependence on sunbird pollination for fruit set in three West African montane mistletoe species. <i>Journal of Tropical Ecology</i> , 28, 205–213.
3	Janeček, Š., Riegert, J., Sedláček, O., Bartoš, M., Hořák, D., Reif, J., Padyšáková, E., Fainová, D., Antczak, M., Pešata, M., Mikeš, V., Patáčová, E., Altman, J., Kantorová, J., Hrázský, Z., Brom, J., & Doležal, J. (2012). Food selection by avian floral visitors: an important aspect of plant-flower visitor interactions in West Africa. <i>Biological Journal of the Linnean Society</i> , 107, 355–367.
4	Maximilian, G. R. Vollstädt, Katrin Böhning-Gaese & Matthias Schleuning, <i>unpublished data</i> .
5	Schmid, B., Nottebrock, H., Esler, K. J., Pagel, J., Pauw, A., Böhning-Gaese, K., Schurr, F. M., & Schleuning, M. (2015). Responses of nectar-feeding birds to floral resources at multiple spatial scales. <i>Ecography</i> , 38, 1–11.
6	Noske, R. A. (1995). The ecology of mangrove forest birds in Peninsular Malaysia. <i>Ibis</i> , 137, 250–263.
7	Wester, P. (2013). Sunbirds hover at flowers of <i>Salvia</i> and <i>Lycium</i> . <i>Ostrich: Journal of African Ornithology</i> , 84, 27–32.
8	Botes C., Johnson S.D., & Cowling R.M. (2008). Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. <i>Oikos</i> , 117, 875–882.
9	Collins G.C. & Rebelo T. (1987). Pollination biology of the Proteaceae in Australia and southern Africa. <i>Australian Journal of Ecology</i> , 12, 387–421.

HONEYEATERS (Meliphagidae)

1	Brown, E. D., & Hopkins, M. J. G. (1995). A test of pollinator specificity and morphological convergence between nectarivorous birds and rainforest tree flowers in New Guinea. <i>Oecologia</i> , 103, 89–100.
2	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
3	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.

(Continues)



APPENDIX 1 (Continued)

ID	Data source
4	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
5	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
6	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
7	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
8	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
9	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
10	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
11	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
12	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
13	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
14	Mohd-Azlan, J. (2010). <i>Community ecology of mangrove birds</i> . Ph.D. Thesis, Charles Darwin University, Darwin, Australia. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2015). The role of habitat heterogeneity in structuring mangrove bird assemblages. <i>Diversity</i> , 7, 118–136. Mohd-Azlan, J., Noske, R. A., & Lawes, M. J. (2014). Resource partitioning by mangrove bird communities in North Australia. <i>Biotropica</i> , 46, 331–340.
15	Noske, R. A. (1996). Abundance, zonation and foraging ecology of birds in mangroves of Darwin Harbour, Northern Territory. <i>Wildlife Research</i> , 23, 443–474.

(Continues)



APPENDIX 1 (Continued)

ID	Data source
16	Franklin, D. C. (1997). The foraging behaviour of avian nectarivores in a monsoonal Australian woodland over a six-month period. <i>Corella</i> , 21, 48–54.
17	Brooker, M., Braithwaite, R., & Estbergs, J. (1990). Foraging ecology of some insectivorous and nectarivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. <i>Emu</i> , 90, 215–230.
18	Hopper, S. D. (1981). Honeyeaters and their winter food plants on Granite Rocks in the central wheat belt of Western Australia. <i>Australian Wildlife Research</i> , 8, 187–197.
19	Hopper, S. D. (1981). Honeyeaters and their winter food plants on Granite Rocks in the central wheat belt of Western Australia. <i>Australian Wildlife Research</i> , 8, 187–197.
20	Collins, B., & Briffa, P. (1982). Seasonal variation of abundance and foraging of three species of Australian honeyeaters. <i>Wildlife Research</i> , 9, 557–569.
21	Hopper, S. D. (1981). Honeyeaters and their winter food plants on Granite Rocks in the central wheat belt of Western Australia. <i>Australian Wildlife Research</i> , 8, 187–197.
22	Whelan, R. J., & Burbidge, A. H. (1980). Flowering phenology, seed set and bird pollination of five Western Australian <i>Banksia</i> species. <i>Australian Journal of Ecology</i> , 5, 1–7.
23	Collins, B. G. (1985). Energetics of foraging and resource selection by honeyeaters in forest and woodland habitats of Western Australia. <i>New Zealand Journal of Zoology</i> , 12, 577–587.
24	Hopper, S. D. (1981). Honeyeaters and their winter food plants on Granite Rocks in the central wheat belt of Western Australia. <i>Australian Wildlife Research</i> , 8, 187–197.
25	Comer, S. J., & Wooller, R. D. (2002). A comparison of the passerine avifauna of a rehabilitated mine site and a nearby reserve in southwestern Australia. <i>Emu</i> , 102, 305–311.
26	Recher, H. F., & Davis Jr., W. E. (2011). Observations on the foraging ecology of honeyeaters (Meliphagidae) at <i>Dryandra</i> woodland, Western Australia. <i>Western Australian Journal of Ornithology</i> , 3, 19–29.
27	Collins, B. G., Grey, J., & McNee, S. (1990). Foraging and nectar use in nectarivorous bird communities. In: M.L. Morrison, C.J. Ralph, J. Verner, and J.R. Jehl Jr. (Eds.), <i>Avian foraging: theory, methodology and applications</i> (pp. 110–122). Kansas: Cooper Ornithological Society.
28	Hopper, S. D. (1980). Bird and mammal pollen vectors in <i>Banksia</i> communities at Cheyne beach, Western Australia. <i>Australian Journal of Botany</i> , 28, 61–75.
29	Ford, H. A., & Paton, D. C. (1982). Partitioning of nectar sources in an Australian honeyeater community. <i>Australian Journal of Ecology</i> , 7, 149–159.
30	Merton, D. V. (1966). Foods and feeding behaviour of some forest birds on Hen island in May. <i>Notornis</i> , 13, 179–184.
31	Gravatt, D. J. (1970). Honeyeater movements and the flowering cycle of vegetation on Little Barrier island. <i>Notornis</i> , 17, 96–101.
32	Anderson, S. H. (2003). The relative importance of birds and insects as pollinators of the New Zealand flora. <i>New Zealand Journal of Ecology</i> , 27, 83–94.
33	Castro, I., & Robertson, A. W. (1997). Honeyeaters and the New Zealand forest flora: the utilization and profitability of small flowers. <i>New Zealand Journal of Ecology</i> , 21, 169–179.