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ORIGINAL ARTICLE

Global patterns of interaction specialization in bird-flower networks

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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, plant-animal interactions, ornithophily, specialization, sunbirds.

INTRODUCTION

Specialization is of major importance in ecology and occurs at all levels, from the individual to the community (Devictor *et al.*, 2010). The origin and evolution of specialization are important to understand species interactions (Futuyma & Moreno, 1988), such as plant-animal interactions involved in pollination (Waser *et al.*, 1996; Johnson & Steiner, 2000). Birds include the most abundant and speciose vertebrate pollinators, with flower visitation reported in more than 50 families (Cronk & Ojeda, 2008). Of these families, three are highly specialized for nectarivory: in the New World (NW), hummingbirds (Apodiformes, Trochilidae, 363 species) found throughout the Americas, and in the Old World (OW), sunbirds (Passeriformes, Nectariniidae, 132 species), in Africa, Asia and Oceania/Australia, and honeyeaters (Passeriformes, Meliphagidae, 175 species), in Asia and Oceania/Australia (Stiles, 1981; Fleming & Muchhala, 2008; del Hoyo *et al.*, 2016), with a limited distribution overlap between these two 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). 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 (Pyke, 1980; Stiles, 1981; Collins & Paton, 1989; Fleming, 2005; Cronk & Ojeda, 2008; Fleming & Muchhala, 2008).

Despite the convergent evolution between these families, they vary in the extent of phenotypic specialization towards pollination (*sensu* Ollerton *et al.*, 2007).

Hummingbirds are the most phenotypically specialized for nectarivory, followed by sunbirds, with honeyeaters as the most phenotypically generalized taxa (Stiles, 1981; Fleming & Muchhala, 2008). Bill length in hummingbird communities is more variable than in OW communities (Fleming & Muchhala, 2008), which may likewise facilitate a finer resource partitioning among hummingbird species (Abrahamczyk & Kessler, 2010; Maglianesi *et al.*, 2014). Greater phenotypic specialization of hummingbirds is also manifest by their small size, which is one of their adaptations that allows for hovering flight (Pyke, 1980). Hovering is the prevalent mode of flower foraging among hummingbirds (Collins & Paton, 1989), with perching being predominant in the typically heavier sunbirds and honeyeaters (Pyke, 1980; Fleming & Muchhala, 2008; 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 thought to be the second-most phenotypically specialized 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). Also, flowers visited by sunbirds, as in hummingbird-pollinated species, tend to have tubular or gullet shapes, while honeyeaters tend to visit flowers with less restrictive morphologies (Stiles, 1981; Fleming & Muchhala, 2008). Although phenotypic specialization of nectar-feeding birds and their floral resources clearly decreases from specialized hummingbird to sunbird and then generalized honeyeater communities (Stiles, 1981; Fleming & Muchhala, 2008), it remains unclear whether the interaction specialization of bird-flower communities would 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 types of bird-flower communities, we predicted the following interaction specialization gradient: hummingbird-flower > sunbird-flower > honeyeater-flower. We compiled a dataset of 121 networks, and tested 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, and sampling methods and intensity.

MATERIALS AND METHODS

Bird-flower interaction networks

We gathered published and unpublished data on flower visitation by hummingbirds, sunbirds and honeyeaters sampled at the community-level in a locality (data source and geographical information of each network are available in the Appendix of Supporting Information: Tables S1–S2). 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 absence (0) or 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 included interactions only of the nectar-feeding specialist families: Meliphagidae, Nectariniidae and Trochilidae (Stiles, 1981; Fleming & Muchhala, 2008; del Hoyo *et al.*, 2016). We excluded interactions with known exotic plant species and illegitimate interactions, when the bird did not contact the floral reproductive structures, for example, piercing the corolla to reach the nectar. These interactions were excluded because they are unlikely to involve bird-flower evolutionary relationships. Information about interaction legitimacy was unavailable in four studies that were used in the analyses (Pettet, 1977; Collins & Rebelo, 1987; Brooker *et al.*, 1990; Wester, 2013), in which case we assumed that all interactions were legitimate. We used databases of Flora of the West Indies (botany.si.edu/antilles/WestIndies/query.cfm), Brazilian Flora Checklist (floradobrasil.jbrj.gov.br) and Tropicos (www.tropicos.org) to classify plant species as exotic.

We compiled a total of 121 bird-flower interaction networks, of which 79 described hummingbird-, 9 sunbird- and 33 honeyeater-flower interactions. Interaction frequency was available for 67 (85%) hummingbirds (HU), 5 (55%) sunbirds (SU) and 23 (70%) honeyeaters (HO) networks. Bird species richness ranged from 2 to 24 in the HU, 2 to 13 in the SU and 2 to 12 in the HO networks, while plant species richness ranged from 2 to 65 in the HU, 2 to 26 in the SU and 2 to 39 in the HO networks (for detailed values of each network, see Table S2).

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 (Jordano, 1987; Blüthgen, 2010). 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 (Olesen *et al.*, 2007; Dormann & Strauss, 2014; Maruyama *et al.*, 2014). 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* package (Dormann *et al.*, 2008) in R (R Core Team, 2017). Although metric values were correlated (Pearson's $r > 0.8$, $p < 0.05$ 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).

Null-model corrections of network metrics

Network metrics are often influenced by species richness and sampling effort. Thus, null models were proposed to control for these effects (Schleuning *et al.*, 2014; Martín González *et al.*, 2015; Dalsgaard *et al.*, 2017) The idea behind the use of null models is 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 used Patefield's algorithm (Patefield, 1981) to generate randomized networks, an algorithm 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 algorithm requires interaction frequency to generate randomized networks, and so we only use null-model corrections on weighted networks. Thus, sample size was larger for observed connectance and binary modularity than null-model corrected connectance and binary modularity (see above; Table S2). 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 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 how the observed network values depart from the null expectation, we calculated the null-model corrected values, by subtracting the observed metric value from the mean value across all randomized networks (Δ-transformation; Schleuning *et al.*, 2014; Martín González *et al.*, 2015; Dalsgaard *et al.*, 2017).

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 types of communities. First, for data with equal variances, we compared them using one-way ANOVA with Tukey's multiple comparison test, and for data with unequal variances we used Kruskal-Wallis test with Dunn's multiple comparison test. Analysis and graphs were plotted in GraphPad Prism 6.0 (GraphPad Software, La Jolla, California, USA; Morgan, 1998). Second, we compared interaction specialization between the three types of bird-flower communities while controlling for potentially confounding variables (see below), using linear multiple regression models and corrected Akaike Information Criterion (AICc). We used the threshold of $\Delta AICc \leq 2$ to identify minimum adequate models (MAM; Burnham & Anderson, 2002).

In the linear models, the three types of bird-flower communities were 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 more generalized 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; 7) the method used to record species interactions, included because it may influence network structure (Ramírez-Burbano *et al.*, 2017), where focal observations were classified as “0” and sampling pollen loads on visiting birds as “1”; 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 (Schleuning *et al.*, 2012; Dalsgaard *et al.*, 2017). As interaction frequency is required to quantify sampling intensity, we were only able to estimate this variable on the weighted networks (Table S2).

Model selection was performed using the *dredge* function in *MuMIn* 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). We used an importance threshold value of ≥ 0.80 to identify relevant predictor variables (Sebastián-González *et al.*, 2015). When the bird-flower community variable was selected in the MAM, we used partial regressions to detect the total and individual variation explained by this variable. The differences between the three types of bird-flower communities were tested by Tukey contrasts for general linear hypothesis, using the *glht* function in *multcomp* 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 *car* package (Fox & Weisberg, 2011). We checked for positive spatial autocorrelation in the residuals of the MAM with the lowest ΔAICc computing Moran's *I* in 14-equally spaced distance classes and applying a permutation test with 10,000 iterations, using the *correlog* function in *pgirmess* package (Giraudoux, 2016). Initial analyses found that interaction specialization was associated with the method of recording interactions (Tables 1–2). Therefore, we checked the consistency of our results by repeating all analyses using networks sampled only through focal observations (Tables S3–S4). Analyses were conducted using R (R Core Team, 2017).

To determine how our sample of networks spanned the global nectar-feeding bird species richness gradient in each bird family, we compared the cumulative frequency distribution of bird species richness in grid cells across the global distribution and the richness in the grid cells containing the sampled networks. Comparisons were done using a two-sample Kolmogorov-Smirnov test in GraphPad Prism 6.0 (Morgan, 1998). The global richness dataset was based on presence-absence data for Trochilidae, Nectariniidae and Meliphagidae at the spatial resolution of 1 × 1 latitudinal-longitudinal degree grid following Rahbek & Graves (2001). This global richness dataset was also used to build the richness maps in ArcMap 9.2 (ESRI, 2009; Figs. 2–3).

RESULTS

Hummingbird-flower networks had lower connectance than sunbird- and honeyeater-flower networks. Furthermore, hummingbird-flower networks had greater complementary specialization and modularity than honeyeater-flower networks. However, no differences were found between the complementary specialization and modularity of hummingbird- and sunbird-flower networks, and neither between sunbird- and honeyeater-flower networks. Likewise, using null-model corrected values, a similar pattern of interaction specialization was observed (Fig. 1). Additionally, when potentially confounding variables were included in the linear models, hummingbird-flower networks still had lower connectance than sunbird- and honeyeater-flower networks and greater complementary specialization and null-model corrected binary modularity than honeyeater-flower networks. Moreover, no differences were found between complementary specialization and binary modularity of hummingbird- and sunbird-flower networks, and neither between sunbird- and honeyeater-flower networks. Only weighted modularity did not differ between the networks of these bird-flower communities when including potentially confounding variables (Tables 1–2). Hummingbird communities visited more plant species than sunbird and 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 1–2). Notably, specialization increased with plant species richness for both observed and null-model corrected metrics (Fig. S1). Moreover, communities with greater bird than plant species richness exhibited greater specialization, with lower observed connectance, but not in null-model corrected connectance, where the pattern was reversed. On islands, networks were less specialized, with lower observed and null-model corrected weighted modularity. Sampling also influenced specialization, with greater specialization detected in networks sampled by focal observations (Tables 1–2). 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, with the same pattern described above for interaction specialization between the bird-flower communities (Tables S3–S4). Intensity of sampling affected interaction specialization, with decreased null-model corrected connectance and weighted modularity when sampling intensity was high (Tables 1–2).

Hummingbird-flower networks were geographically widely distributed, but with some parts of North America and the Amazon region being poorly sampled. Also, when the cumulative frequency distribution of nectar-feeding bird species richness was compared between the global and the sampled localities, we found that species-poor communities were disproportionately less sampled than species-rich hummingbird communities (Fig. S2). In the Old World, in contrast, network distributions were more restricted and some species-rich regions, especially in Central Africa, India, Southeast Asia and Southeast Australia, had few or no studies of bird-flower interactions at the community-level (Figs. 2–3). Nonetheless, the included networks encompassed well the global bird species richness gradient in sunbird and honeyeater communities (Fig. S2).

DISCUSSION

We found that New World (NW) hummingbird-flower interaction networks are more specialized than Old World (OW) honeyeater-flower networks, as predicted. Notably, hummingbird-flower networks have fewer realized interactions, lower niche overlap and greater binary modularity, as compared to honeyeater-flower networks. Interaction specialization of sunbird-flower networks, however, was similar to both hummingbird- and honeyeater-flower networks, contrarily to the prediction that they would have intermediate values (see below).

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 (Fleming, 2005; Abrahamczyk & Kessler, 2015; 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; Vizentin-Bugoni *et al.*, 2014). Indeed, in most hummingbird-flower communities, there is a subset of flowers with long, curved corollas visited by one or few long and curve-billed birds (Feinsinger & Colwell, 1978; Maglianesi *et al.*, 2014). Thus, increased range of bill and corolla lengths in hummingbird-flower networks may contribute to reduced niche overlap and increased community-level specialization (Cotton, 1998b; Abrahamczyk & Kessler, 2010; Maruyama *et al.*, 2014; Maglianesi *et al.*, 2015). 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 understory of NW in comparison to OW forests (LaFrankie *et al.*, 2006). This greater diversity may create new interaction opportunities for hummingbirds, resulting in greater niche partitioning in the NW than in the 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), particularly 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 lerp more frequently than hummingbirds do (Pyke, 1980; Higgins *et al.*, 2016). Although hummingbirds also forage for insects as a source of protein (Stiles, 1995). These diversified feeding habits of honeyeaters may decrease competition for nectar resources, producing the more generalized interactions with flowers demonstrated here (though see Dalsgaard *et al.*, 2017 for an opposed example on frugivorous birds networks). The greatest overall specialization in hummingbird networks implies in narrower niche overlaps of interactions. If combined to species turnover across continental scales, this greater specialization may imply in a larger spatial variability of interactions, resulting in a larger spatial β-diversity of interactions (Trojelsgaard *et al.*, 2015) for hummingbird networks. Additionally, temporal variation of resources spanning across the entire year in NW communities (Bawa *et al.*, 2003) 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 two reasons: First, relatively few sunbird-flower networks were available, resulting in wider confidence intervals (Fig. 1). Perhaps more networks would 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 are ecologically similar to both hummingbird- and honeyeater-flower communities, and indeed have intermediate interaction specialization levels (Fig. 1). For instance, although sunbirds are considered less phenotypically specialized for nectar-feeding than hummingbirds (Stiles, 1981), the flowers they visit may 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 species, as tubular and gullet corolla shapes may be inaccessible to some species of the nectar-feeding bird community (Pettet, 1977; Temeles *et al.*, 2002). This morphological mismatch in both communities may produce the similar interaction specialization of sunbird- and hummingbird-flower networks that we detected in this study. Additionally, some sunbirds may have specialized feeding behaviours, similar to hummingbirds, of hovering and traplining while visiting flowers (Padyšáková & Janeček, 2016). However, this is not consistent with the observation that interaction specialization was also similar between sunbird- and honeyeater-flower communities. The specialization similarity of honeyeater and sunbird communities may be related to their lower floral resource richness in comparison to hummingbird communities, as demonstrated in this study. This lower resource diversity may increase niche overlap, producing the more generalized feeding-niches found in OW networks. However, we suggest that it is likely that a larger sample size of sunbird-flower networks would have resolved these possibilities in favour of our first explanation because the sunbird interaction specialization tends to be intermediate between those of hummingbirds and honeyeaters (Fig. 1).

The correlation between plant species richness and interaction specialization may be 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 be a consequence of their species-poor communities (MacArthur & Wilson, 1963; Dalsgaard *et al.*, 2009; Abrahamczyk *et al.*, 2015), but may also be due to the tendency of generalist species having greater establishment success on islands than specialist species (Olesen *et al.*, 2002; Maldonado *et al.*, 2013; Traveset *et al.*, 2015). Moreover, at least for hummingbirds, generalized interactions on islands may have been influenced by their rather recent colonization (McGuire *et al.*, 2014; Abrahamczyk *et al.*, 2015) and a greater level of strong and periodic disturbances in islands in comparison to mainland communities, which may favour generalized over specialized bird species (Dalsgaard *et al.*, 2009).

In conclusion, we confirmed that interactions are more specialized in hummingbird- than in honeyeater-flower networks, but we were unable to show that sunbird-flower networks differ from those of hummingbirds and honeyeaters. 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 (Stiles, 1981; Fleming & Muchhala, 2008). These results suggest that there is a potential link between phenotypic specialization and floral resource richness with interaction specialization among nectarivorous bird-flower communities across global scales.

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SUPPORTING INFORMATION

Supporting information can be found in the online version of this article:

Appendix S1 – Data source (Table S1), geographical and sampling details of each study used to build the interaction networks of bird-flower communities (Table S2).

Appendix S2 – Multiple linear regression models of bird-flower interaction networks sampled through focal observation (Table S3–S4).

Appendix S3 – Linear regressions between network metrics and the plant species richness (Fig. S1) and two-sample Kolmogorov-Smirnov test comparing the global and sampled cumulative species richness frequency of the three bird families (Fig. S2).

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 proposed by Fleming & Muchhala (2008). Authors 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. All authors read and approved the final version of the manuscript.

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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 (C) is the realized proportion of possible interactions in a community while complementary specialization (H_2’) 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 $\geq$ 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.

		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	–
	AICc			-146.96			-168.06			-58.51			-64.07
	R^2 adjusted			0.69			0.50			0.34			0.38
	$R^2_{\text{total Bird-flower community}}$			0.32			0.29			0.21			0.25
	$R^2_{\text{only Bird-flower community}}$			0.04			0.16			0.04			0.08
	Moran´s *I*			$\leq 0.04^{NS}$			$\leq 0.13^{NS}$			$\leq 0.06^{NS}$			$\leq 0.08^{NS}$

AICc – 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 ΔAICc; R^2 adjusted – variation explained by the minimum adequate model with the lowest ΔAICc; $R^2_{\text{only Bird-flower community}}$ – adjusted unique variation explained by the difference between the three types of bird-flower communities; $R^2_{\text{total Bird-flower community}}$ – adjusted total variation explained by the difference between the three types of bird-flower communities ; Σw_i – importance of each predictor variable measured across all models; $^{NS}p > 0.05$; number of models with $\Delta AICc \leq 2$: a - three; b - four; c - eleven; d - six. For all models with $\Delta AICc \leq 2$, the predictor variable that represents the difference between the three types of bird-flower communities was selected. Letters next to the standardized coefficients represent the group that each bird-flower community belongs, based on Tukey contrasts for general linear hypotheses. 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 $\geq$ 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.

		Binary modularity (Q_B)						Weighted modularity (Q)					
		$Q_{B\text{-}OBS}$ (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]
Predictor variables	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	–
	AICc			-211.75			-241.09			-138.50			-154.64
	R^2 adjusted			0.35			0.55			0.52			0.49
	$R^2_{\text{total Bird-flower community}}$			0.23			0.34			–			–
	$R^2_{\text{only Bird-flower community}}$			0.06			0.09			–			–
	Moran´s *I*			$\underline{<}0.06^{NS}$			$\underline{<}0.17^{NS}$			$\underline{<}0.07^{NS}$			$\underline{<}0.06^{NS}$

AICc – Akaike’s Information Criterion corrected; AVM – standardized coefficients of the averaged model measured across all models; MAM – standardized coefficients of the minimum adequate model with the lowest ΔAICc; R^2 adjusted – variation explained by the minimum adequate model with the lowest ΔAICc; $R^2_{\text{only Bird-flower community}}$ – adjusted unique variation explained by the difference between the three types of bird-flower communities; $R^2_{\text{total Bird-flower community}}$ – adjusted total variation explained by the difference between the three types of bird-flower communities; Σw_i - importance of each predictor variable measured across all models; $^{NS}p > 0.05$; number of models with $\Delta AICc \leq 2$: a - eleven; b - nine; c - one; d - five. Only for binary modularity, all models with $\Delta AICc \leq 2$ the predictor variable that represents the difference between the three types of bird-flower communities was selected. Letters next to the standardized coefficients represent the group that each bird-flower community belongs, based on Tukey contrasts for general linear hypotheses. Multicollinearity between predictor variables is absent in binary modularity models, as generalized variance inflation factor (GVIF) $\leq$ 1.60 and in weighted modularity models, as variance inflation factor (VIF) $\leq$ 2.30.

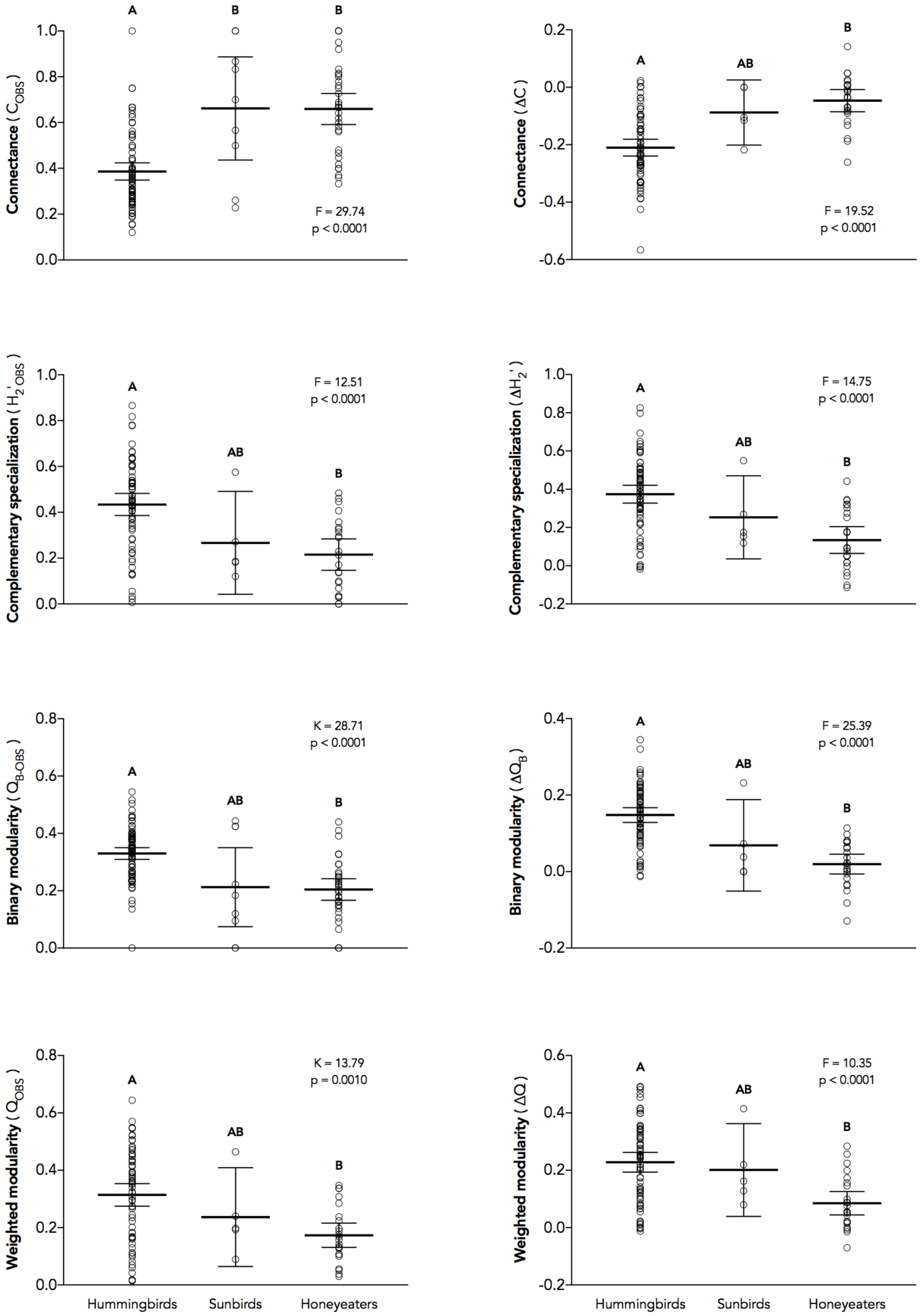
Figure legends

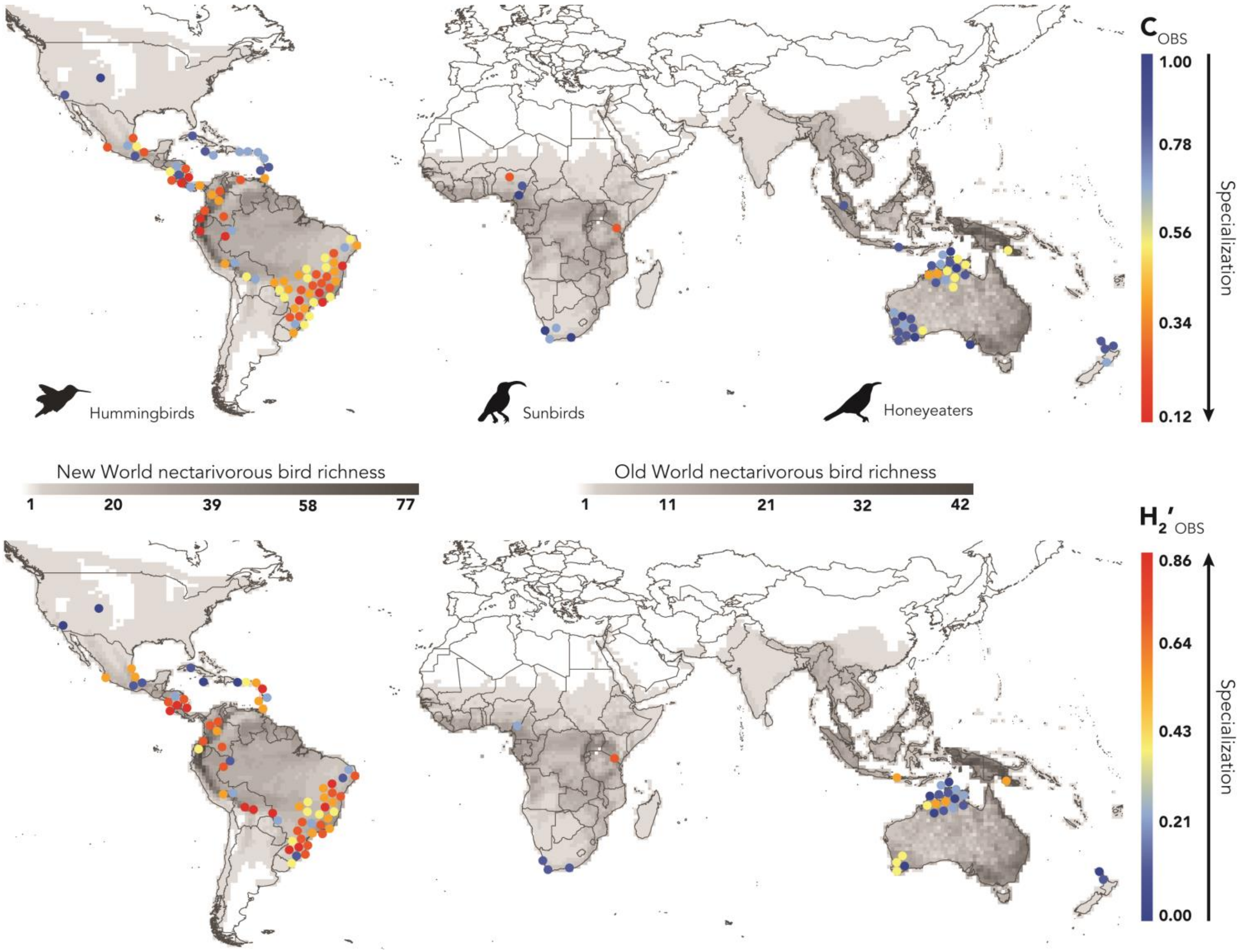
Fig. 1 – Comparison of the observed (OBS, first column) and null-model corrected (Δ, second column) metrics of bird-flower interaction networks of the three types of bird communities (hummingbirds, sunbirds and honeyeaters). Connectance (C) is the realized proportion of possible interactions in a community, 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.

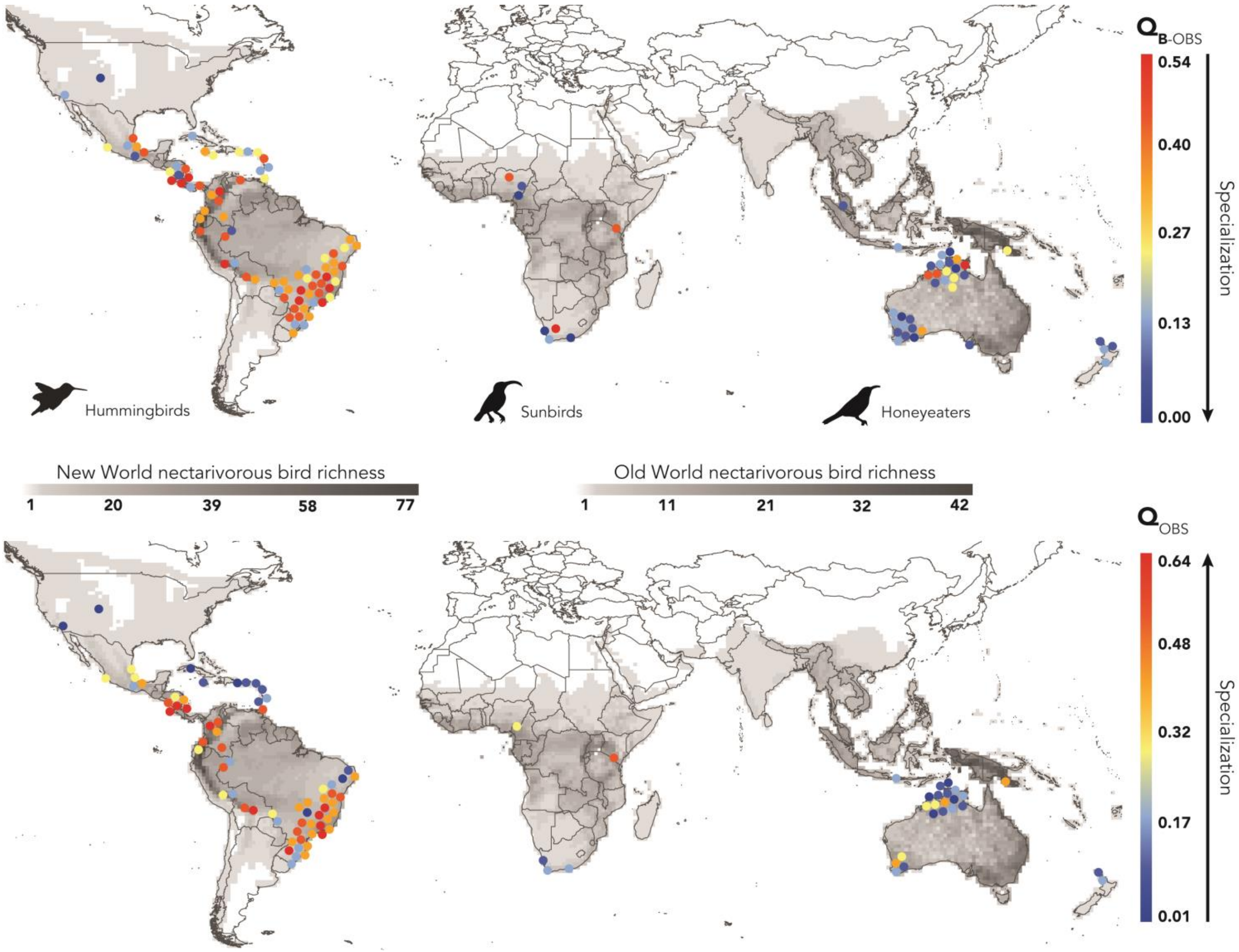
Fig. 2 – Specialization of bird-flower interaction networks in hummingbird, sunbird and honeyeater communities, measured by observed connectance (C_{OBS}), which describes the realized proportion of possible interactions in a community, and observed complementary specialization ($H_2'_{OBS}$), which 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.

Fig. 3 – Specialization of bird-flower interaction networks in in hummingbird, sunbird and honeyeater communities, measured by observed binary ($Q_{B\text{-}OBS}$) 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.


Connectance (C_{OBS})
A
B
B
F = 29.74
p < 0.0001
1.0
0.8
0.6
0.4
0.2
0.0
Connectance (ΔC)
A
AB
B
F = 19.52
p < 0.0001
0.2
0.0
-0.2
-0.4
-0.6
Complementary specialization ($H_2'_{OBS}$)
A
AB
B
F = 12.51
p < 0.0001
1.0
0.8
0.6
0.4
0.2
0.0
Complementary specialization ($\Delta H_2'$)
A
AB
B
F = 14.75
p < 0.0001
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Binary modularity ($Q_{B\text{-}OBS}$)
A
AB
B
K = 28.71
p < 0.0001
0.8
0.6
0.4
0.2
0.0
Binary modularity (ΔQ_B)
A
AB
B
F = 25.39
p < 0.0001
0.4
0.2
0.0
-0.2
Weighted modularity (Q_{OBS})
A
AB
B
K = 13.79
p = 0.0010
0.8
0.6
0.4
0.2
0.0
Weighted modularity (ΔQ)
A
AB
B
F = 10.35
p < 0.0001
0.6
0.4
0.2
0.0
-0.2
Hummingbirds
Sunbirds
Honeyeaters
Hummingbirds
Sunbirds
Honeyeaters


C_{OBS}
1.00
0.78
0.56
0.34
0.12
Specialization
Hummingbirds
Sunbirds
Honeyeaters
New World nectarivorous bird richness
1
20
39
58
77
Old World nectarivorous bird richness
1
11
21
32
42
$H_2'_{OBS}$
0.86
0.64
0.43
0.21
0.00
Specialization


$Q_{B\text{-OBS}}$
0.54
0.40
0.27
0.13
0.00
Specialization
Hummingbirds
Sunbirds
Honeyeaters
New World nectarivorous bird richness
1
20
39
58
77
Old World nectarivorous bird richness
1
11
21
32
42
Q_{OBS}
0.64
0.48
0.32
0.17
0.01
Specialization