Global patterns of interaction specialization in bird–flower networks


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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 (H2'), binary (Q0) 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 H2') and greater modularity (greater Q0). 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 (DeVitore 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 (Abrahacmycz & 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 Janecek 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 (Qb), and two weighted metrics, complementary specialization (H2) 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 (H2, Qb, 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; Martin 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 (AICc). We used the threshold of ΔAICc ≤ 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 (log10 transformed), included because species-rich communities are expected to have greater specialization (Dalsgaard et al., 2011; Martin González et al., 2015; but see Vázquez & Stevens, 2004; Schleuning et al., 2012); (2) asymmetry (loB10 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 (Martin González et al., 2015; Traveset et al., 2015); (5) topography (square root transformed), defined as the elevation 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 (log10 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 (log10 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 (Δwi) 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 (Δwi) 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 (wi) 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 Δwi, 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 ΔAICc by computing Moran’s I in 14-equally spaced distance classes and applying a
permutation test with 10,000 iterations, using the corregol function in the "pgirmess" 1.6.7 package (Giraudoux, 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 x 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).

### 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–flower networks.

#### Table 1

<table>
<thead>
<tr>
<th>Predictor variables</th>
<th>Connectance (C)</th>
<th>Complementary specialization (H2')</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OBS (121)</td>
<td>MAM (94)</td>
</tr>
<tr>
<td></td>
<td>wi AVM MAM</td>
<td>wi AVM MAM</td>
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<tr>
<td>Bird-flower community</td>
<td>1.00</td>
<td>1.00</td>
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<tr>
<td></td>
<td>–0.11 0.11 (A)</td>
<td>–0.11 0.12 (A)</td>
</tr>
<tr>
<td>Hummingbirds</td>
<td>0.02 0.03 (B)</td>
<td>0.09 0.09 (B)</td>
</tr>
<tr>
<td>Sunbirds</td>
<td>1.01 1.00 (B)</td>
<td>0.16 0.17 (B)</td>
</tr>
<tr>
<td>Honeyeaters</td>
<td>1.00 –0.55</td>
<td>–0.54 0.02</td>
</tr>
<tr>
<td>Asymmetry</td>
<td>1.00 –0.33</td>
<td>–0.32 0.19</td>
</tr>
<tr>
<td>Insularity</td>
<td>0.63 0.07</td>
<td>0.07 0.24</td>
</tr>
<tr>
<td>Topography</td>
<td>0.23 0.01</td>
<td>–0.29 –0.01</td>
</tr>
<tr>
<td>Latitude</td>
<td>0.36 0.01</td>
<td>–0.37 0.01</td>
</tr>
<tr>
<td>Sampling method</td>
<td>0.94 0.14</td>
<td>0.15 0.98</td>
</tr>
<tr>
<td>Duration</td>
<td>0.25 –0.01</td>
<td>–0.30 –0.02</td>
</tr>
<tr>
<td>Sampling coverage</td>
<td>0.23 –0.01</td>
<td>–0.21 –0.01</td>
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<tr>
<td>Sampling intensity</td>
<td>1.00 –0.17</td>
<td>–0.17 0.57</td>
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<td>AICc</td>
<td>–146.96</td>
<td>–168.06</td>
</tr>
<tr>
<td>R2 adjusted</td>
<td>0.69</td>
<td>0.50</td>
</tr>
<tr>
<td>R2 total Bird-flower community</td>
<td>0.32</td>
<td>0.29</td>
</tr>
<tr>
<td>R2 only Bird-flower community</td>
<td>0.04</td>
<td>0.16</td>
</tr>
<tr>
<td>Moran’s I</td>
<td>≤0.04NS</td>
<td>≤0.13NS</td>
</tr>
</tbody>
</table>

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; R2 adjusted, variation explained by the minimum adequate model with the lowest ΔAICc; R2 only Bird-flower community, adjusted unique variation explained by the difference between the bird-flower community types; 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; R2 adjusted, variation explained by the minimum adequate model with the lowest ΔAICc; R2 only Bird-flower community, adjusted unique variation explained by the difference between bird-flower community types; Wi, importance of each predictor variable measured across all models; NS p > 0.05; number of models with ΔAICc ≤ 2: a – three; b – four; c – eleven; d – six. For all models with ΔAICc ≤ 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.
flower networks, and neither between sunbird–flower and honeysuckle–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 honeysuckle–flower networks, and greater complementary specialization and null-model corrected binary modularity than honeysuckle–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 honeysuckle–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 honeysuckle communities (Kruskal–Wallis test: $K = 28.32, p < 0.001$; Dunn's multiple comparison tests: hummingbirds > sunbirds = honeysuckers).

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 observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity. Sampling method also influenced specialization, with greater specialization observed and null-model corrected weighted modularity.
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 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 (H2₀) 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.
modularity, when compared to honeyletter-flower networks. However, interaction specialization of sunbird-flower networks was similar to both hummingbird-flower and honeyletter-flower networks.

The greater overall specialization between hummingbirds and their floral resources indicates that their interactions are more species-restricted than the interactions of honeyleters 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 honeyleters, 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; Vizentin-Bugoni et al., 2014). Indeed, in most hummingbird-flower communities, there is a subset of flowers with long, curved

FIGURE 2 Specialization of bird-flower interaction networks in hummingbird, sunbird and honeyletter 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 honeyleters 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 (Abrahmczyk & 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

**FIGURE 3** Specialization of bird-flower interaction networks in hummingbird, sunbird and honeyeater communities, measured by observed binary ($Q_{\text{B-OBS}}$) and weighted modularity ($Q_{\text{OBS}}$). 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]
hummimgbirds (Feinsinger & Colwell, 1978), resulting in greater niche partitioning in NW than in OW networks. Conversely, the lower specialization of honeeyesr 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 honeeyesrs 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 honeeye-flower communities may result in lower interaction specialization, when compared to hummingbird-flower networks. Honeyeyesrs 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 hummimgbirds also forage for insects as a source of protein (Stiles, 1995). These diverse feeding habits of honeeyesrs 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 $\beta$-diversity of interactions (Trejelsgaard 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 $\beta$-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 honeeey-flower networks, respectively. Second, sunbird-flower communities share ecological traits with both hummingbird-flower and honeeye-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 trapping between resources (Padyšákova & Janecék, 2016). In contrast, we have demonstrated that in comparison to hummingbird communities, honeeye 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; Martin González et al., 2015; Sebastián-González et al., 2015, but see Schleunig 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, favoring generalized over specialized bird species (Dalsgaard et al., 2009).

In conclusion, we confirmed that interactions are more specialized in hummingbird-flower than in honeeye-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 honeeyer-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.

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AUTHOR CONTRIBUTIONS

TBZ, BD and IGV conceived the ideas; BD, PAC, JKR, 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, IC, 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, JKR, PKM, EF, MSc, AMMG, JVB, DCF and IGV led the writing.

REFERENCES


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

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HONEYEATERS (Meliphagidae)


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