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Global patterns of interaction specialization in bird-flower networks

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163 ABSTRACT

164 Aim: Among the world's three major nectar-feeding bird taxa, hummingbirds are the

165 most phenotypically specialized for nectarivory, followed by sunbirds, while the

166 honeyeaters are the least phenotypically specialized taxa. We tested whether this

167 phenotypic specialization gradient is also found in the interaction patterns with their

168 floral resources.

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

170   Methods: We compiled interaction networks between birds and floral resources for 79

171   hummingbird, nine sunbird and 33 honeyeater communities. Interaction specialization

172   was quantified through connectance (C), complementary specialization (H_2'), binary

173   (Q_B) and weighted modularity (Q), with both observed and null-model corrected

174   values. We compared interaction specialization among the three types of bird–flower

175   communities, both independently and while controlling for potential confounding

176   variables, such as plant species richness, asymmetry, latitude, insularity, topography,

177   sampling methods and intensity.

178   Results: Hummingbird-flower networks were more specialized than honeyeater-

179   flower networks. Specifically, hummingbird-flower networks had a lower proportion

180   of realized interactions (lower C), decreased niche overlap (greater H_2') and greater

181   modularity (greater Q_B). However, we found no significant differences between

182   hummingbird– and sunbird–flower networks, nor between sunbird– and honeyeater–

183   flower networks.

184   Main conclusions: As expected, hummingbirds and their floral resources have greater

185   interaction specialization than honeyeaters, possibly because of greater phenotypic

186   specialization and greater floral resource richness in the New World. Interaction

187   specialization in sunbird–flower communities was similar to both hummingbird–

188   flower and honeyeater–flower communities. This may either be due to the relatively

189   small number of sunbird–flower networks available, or because sunbird–flower

190   communities share features of both hummingbird–flower communities (specialized

191   floral shapes) and honeyeater–flower communities (fewer floral resources). These

192   results suggest a link between interaction specialization and both phenotypic

193   specialization and floral resource richness within bird–flower communities at a global

194   scale.

195   Keywords: Honeyeaters, hummingbirds, modularity, niche partitioning, plant-animal

196   interactions, ornithophily, specialization, sunbirds.

197   INTRODUCTION

198   Specialization is of major importance in ecology and occurs at all levels, from the

199   individual to the community (Devictor *et al.*, 2010). The origin and evolution of

200   specialization are important to understand species interactions (Futuyma & Moreno,

201   1988), such as plant-animal interactions involved in pollination (Waser *et al.*, 1996;

202   Johnson & Steiner, 2000). Birds include the most abundant and speciose vertebrate

203   pollinators, with flower visitation reported in more than 50 families (Cronk & Ojeda,

204   2008). Of these families, three are highly specialized for nectarivory: in the New

205   World (NW), hummingbirds (Apodiformes, Trochilidae, 363 species) found

206   throughout the Americas, and in the Old World (OW), sunbirds (Passeriformes,

207   Nectariniidae, 132 species), in Africa, Asia and Oceania/Australia, and honeyeaters

208   (Passeriformes, Meliphagidae, 175 species), in Asia and Oceania/Australia (Stiles,

209   1981; Fleming & Muchhala, 2008; del Hoyo *et al.*, 2016), with a limited distribution

210   overlap between these two OW families (Barker *et al.*, 2002). These three families

211   contain most of the specialized nectar-feeding bird species, and are an example of

212   convergent evolution, as they have independently evolved adaptations associated with

213   nectarivory (Prum *et al.*, 2015). This pattern of evolution has generated interest in

214   understanding the differences and similarities in the morphology and ecology of these

215   nectar-feeding birds and their floral resources (Pyke, 1980; Stiles, 1981; Collins &

216   Paton, 1989; Fleming, 2005; Cronk & Ojeda, 2008; Fleming & Muchhala, 2008).

217   Despite the convergent evolution between these families, they vary in the

218   extent of phenotypic specialization towards pollination (*sensu* Ollerton *et al.*, 2007).

219   Hummingbirds are the most phenotypically specialized for nectarivory, followed by

220   sunbirds, with honeyeaters as the most phenotypically generalized taxa (Stiles, 1981;

221   Fleming & Muchhala, 2008). Bill length in hummingbird communities is more

222   variable than in OW communities (Fleming & Muchhala, 2008), which may likewise

223   facilitate a finer resource partitioning among hummingbird species (Abrahamczyk &

224   Kessler, 2010; Maglianesi *et al.*, 2014). Greater phenotypic specialization of

225   hummingbirds is also manifest by their small size, which is one of their adaptations

226   that allows for hovering flight (Pyke, 1980). Hovering is the prevalent mode of flower

227   foraging among hummingbirds (Collins & Paton, 1989), with perching being

228   predominant in the typically heavier sunbirds and honeyeaters (Pyke, 1980; Fleming

229   & Muchhala, 2008; but see Janeček *et al.*, 2011; Wester, 2013). Small size and

230   hovering flight are likely to have favoured the diversification of hummingbird-

231   pollinated plant species, because the evolutionary transition from small and delicate

232   insect-pollinated to hummingbird-pollinated species was probably relatively simple

233   (Castellanos *et al.*, 2003; Thomson & Wilson, 2008). This greater diversification of

234   floral resources may have promoted a greater interaction specialization in NW

235   communities (Dalsgaard *et al.*, 2011).

236   Sunbirds and the plants they visit are thought to be the second-most

237   phenotypically specialized community. Sunbirds have bills, tongues and digestive

238   tracts that are better adapted to nectar-feeding than those of honeyeaters, the least

239   specialized group (Stiles, 1981). Also, flowers visited by sunbirds, as in

240   hummingbird-pollinated species, tend to have tubular or gullet shapes, while

241   honeyeaters tend to visit flowers with less restrictive morphologies (Stiles, 1981;

242   Fleming & Muchhala, 2008). Although phenotypic specialization of nectar-feeding

243   birds and their floral resources clearly decreases from specialized hummingbird to

244   sunbird and then generalized honeyeater communities (Stiles, 1981; Fleming &

245   Muchhala, 2008), it remains unclear whether the interaction specialization of bird-

246   flower communities would reflect the same phenotypic specialization gradient.

247   Species interaction patterns, such as bird-flower interactions, can be

248   investigated by a network approach. This approach can reveal emergent properties at

249   the community-level that are not apparent in pairwise interactions (Bascompte &

250   Jordano, 2007). Some of the main network metrics that quantify interaction

251   specialization at the community-level are connectance, complementary specialization

252   and modularity (Blüthgen, 2010). Community-level specialization quantified by these

253   metrics is associated with the concept of ecological specialization (*sensu* Ollerton *et*

254   *al.*, 2007) and the realized Eltonian niche (Devictor *et al.*, 2010), where interactions

255   are treated as one dimension of the ecological niche and the degree of interaction

256   specialization represents niche partitioning among species (Blüthgen, 2010).

257   Because of the observed phenotypic specialization in the three types of bird-

258   flower communities, we predicted the following interaction specialization gradient:

259   hummingbird-flower > sunbird-flower > honeyeater-flower. We compiled a dataset of

260   121 networks, and tested the differences of bird-flower interaction specialization

261   between these three bird families, both independently and while controlling for

262   potential confounding variables such as plant species richness, asymmetry, latitude,

263   insularity, topography, and sampling methods and intensity.

264   MATERIALS AND METHODS

265   Bird-flower interaction networks

266   We gathered published and unpublished data on flower visitation by hummingbirds,

267   sunbirds and honeyeaters sampled at the community-level in a locality (data source

268   and geographical information of each network are available in the Appendix of

269   Supporting Information: Tables S1–S2). For each study interaction lists between bird

270   and plant species were transformed into adjacency matrices, with birds as columns

271   and plants as rows. In these matrices, flower visits by birds were represented in binary

272   networks by their absence (0) or occurrence (1), or in weighted networks by their

273   absence (0) or their interaction frequency (Bascompte & Jordano, 2007). Interaction

274   frequency represents the number of observations of birds either visiting or carrying

275   pollen from a given plant species. We included interactions only of the nectar-feeding

276   specialist families: Meliphagidae, Nectariniidae and Trochilidae (Stiles, 1981;

277   Fleming & Muchhala, 2008; del Hoyo *et al.*, 2016). We excluded interactions with

278   known exotic plant species and illegitimate interactions, when the bird did not contact

279   the floral reproductive structures, for example, piercing the corolla to reach the nectar.

280   These interactions were excluded because they are unlikely to involve bird-flower

281   evolutionary relationships. Information about interaction legitimacy was unavailable

282   in four studies that were used in the analyses (Pettet, 1977; Collins & Rebelo, 1987;

283   Brooker *et al.*, 1990; Wester, 2013), in which case we assumed that all interactions

284   were legitimate. We used databases of Flora of the West Indies

285   (botany.si.edu/antilles/WestIndies/query.cfm), Brazilian Flora Checklist

286   (floradobrasil.jbrj.gov.br) and Tropicos (www.tropicos.org) to classify plant species

287   as exotic.

288   We compiled a total of 121 bird-flower interaction networks, of which 79

289   described hummingbird-, 9 sunbird- and 33 honeyeater-flower interactions.

290   Interaction frequency was available for 67 (85%) hummingbirds (HU), 5 (55%)

291   sunbirds (SU) and 23 (70%) honeyeaters (HO) networks. Bird species richness ranged

292   from 2 to 24 in the HU, 2 to 13 in the SU and 2 to 12 in the HO networks, while plant

293   species richness ranged from 2 to 65 in the HU, 2 to 26 in the SU and 2 to 39 in the

294   HO networks (for detailed values of each network, see Table S2).

295   Measuring specialization of interaction networks

296   To quantify interaction specialization, we used two binary metrics, connectance (C)

297   and binary modularity (Q_B), and two weighted metrics, complementary specialization

298   (H_2') and weighted modularity (Q). These metrics range from 0 to 1, where the most

299   generalized network has a value of 0 and the most specialized network has a value of

300   1 (H_2', Q_B, Q), with the inverse for connectance (C).

301   Connectance is defined as the proportion of observed pairwise interactions

302   relative to the total number of possible interactions in the community, where the total

303   number of possible interactions is calculated as the richness of visited plant species

304   multiplied by the richness of nectar-feeding birds (Jordano, 1987; Blüthgen, 2010).

305   Complementary specialization is derived from two-dimensional Shannon entropy, and

306   quantifies the niche partitioning among species considering partner availability,

307   defined by the marginal totals in the interaction matrix, and so measures the

308   exclusiveness of interactions (Blüthgen *et al.*, 2006; Martín González *et al.*, 2015).

309   Finally, modularity is a network pattern that emerges when some species interact

310   strongly with each other but less so with the remaining species, thereby creating

311   strongly-connected sub-groups within a less connected network (Olesen *et al.*, 2007;

312   Dormann & Strauss, 2014; Maruyama *et al.*, 2014). Binary modularity was measured

313   using the Barber metric (Barber, 2007), with simulated annealing as the search

314   algorithm in the MODULAR software (Marquitti *et al.*, 2014). Weighted modularity

315   was calculated with the standard specifications of the QuanBiMo algorithm and using

316   the greatest modularity value after five independent runs (Dormann & Strauss, 2014;

317   Schleuning *et al.*, 2014). Connectance, complementary specialization and weighted

318   modularity were calculated with the *bipartite* package (Dormann *et al.*, 2008) in R (R

319   Core Team, 2017). Although metric values were correlated (Pearson's r > 0.8, p <

320   0.05 for spatial and non-spatial correlation), we analysed all metrics separately

321   because they can describe complementary patterns of interaction specialization

322   (Martín González *et al.*, 2015).

323   Null-model corrections of network metrics

324   Network metrics are often influenced by species richness and sampling effort. Thus,

325   null models were proposed to control for these effects (Schleuning *et al.*, 2014;

326   Martín González *et al.*, 2015; Dalsgaard *et al.*, 2017) The idea behind the use of null

327   models is to calculate deviations between observed values and null-model

328   expectations, assuming random species interactions, while controlling network

329   properties that may be related to species richness and sampling effort (Dalsgaard *et*

330   *al.*, 2017). We used Patefield's algorithm (Patefield, 1981) to generate randomized

331   networks, an algorithm commonly used in geographical analyses of interaction

332   networks (Dalsgaard *et al.*, 2017). This algorithm constrains network size

333   (representing species richness) and the interaction matrix marginal totals (the sum of

334   interaction frequencies of each bird and plant species, which may be a consequence of

335   species abundance or sampling effort; Dormann *et al.*, 2009). Patefield algorithm

336   requires interaction frequency to generate randomized networks, and so we only use

337   null-model corrections on weighted networks. Thus, sample size was larger for

338   observed connectance and binary modularity than null-model corrected connectance

339   and binary modularity (see above; Table S2). For each of the observed networks, we

340   generated 1,000 randomized networks to estimate connectance and complementary

341   specialization and 100 to estimate binary and weighted modularity. We used fewer

342   randomizations for modularity metrics because their calculation requires time-

343   consuming algorithms (Olesen *et al.*, 2007; Schleuning *et al.*, 2014; Sebastián-

344   González *et al.*, 2015). For each of the randomized networks, we calculated the

345   network metrics following the same procedure as adopted for the observed networks

346   (see above). To quantify how the observed network values depart from the null

347   expectation, we calculated the null-model corrected values, by subtracting the

348   observed metric value from the mean value across all randomized networks (Δ-

349   transformation; Schleuning *et al.*, 2014; Martín González *et al.*, 2015; Dalsgaard *et*

350   *al.*, 2017).

351   Comparing hummingbird, sunbird and honeyeater interaction specialization

352   We compared observed and null-model corrected metrics of hummingbird-, sunbird-

353   and honeyeater-flower networks, testing for differences of interaction specialization

354   between the three types of communities. First, for data with equal variances, we

355   compared them using one-way ANOVA with Tukey's multiple comparison test, and

356   for data with unequal variances we used Kruskal-Wallis test with Dunn's multiple

357   comparison test. Analysis and graphs were plotted in GraphPad Prism 6.0 (GraphPad

358   Software, La Jolla, California, USA; Morgan, 1998). Second, we compared

359   interaction specialization between the three types of bird-flower communities while

360   controlling for potentially confounding variables (see below), using linear multiple

361   regression models and corrected Akaike Information Criterion (AICc). We used the

362   threshold of $\Delta AICc \leq 2$ to identify minimum adequate models (MAM; Burnham &

363   Anderson, 2002).

364   In the linear models, the three types of bird-flower communities were assigned

365   as a categorical variable with three levels (hummingbirds, sunbirds and honeyeaters).

366   Nine potentially confounding variables were also included in the models: 1) plant

367   species richness ($\log_{10}$ transformed), included because species-rich communities are

368   expected to have greater specialization (Dalsgaard *et al.*, 2011; Martín González *et*

369   *al.*, 2015; but see Vázquez & Stevens, 2004; Schleuning *et al.*, 2012); 2) asymmetry

370   ($\log_{10}$ transformed), described as the ratio between bird and plant species richness and

371   included because connectance decreases when asymmetry increases (Blüthgen *et al.*,

372   2006); 3) absolute latitude, because several studies have found greater network

373   specialization towards the tropics (Olesen & Jordano, 2002; Dalsgaard *et al.*, 2011;

374   but see Vázquez & Stevens, 2004; Schleuning *et al.*, 2012); 4) insularity, where

375   mainland communities were classified as "0" and island communities as "1" and

376   included in the models because insular communities are expected to be more

377   generalized than mainland communities (Martín González *et al.*, 2015; Traveset *et al.*,

378   2015); 5) topography (square root transformed), defined as the elevational range of

379   the sampled localities calculated in 1×1 km grid cells within a concentric distance of

380   10 km from each sampled locality; 6) duration of each study ($\log_{10}$ transformed),

381   based on the number of sampling months; 7) the method used to record species

382   interactions, included because it may influence network structure (Ramírez-Burbano

383   *et al.*, 2017), where focal observations were classified as "0" and sampling pollen

384   loads on visiting birds as "1"; 8) sampling coverage, where "1" represents studies that

385   sampled the supposed entire communities of bird and plant species, and "0"

386   represents studies that sampled only a subset of the community (for example, studies

387   focusing on ornithophilous plant species or a given plant family); and 9) sampling

388   intensity ($\log_{10}$ transformed), calculated as the ratio between the square root of the

389   total number of interactions and the square root of the product of the number of bird

390   and plant species in the network (Schleuning *et al.*, 2012; Dalsgaard *et al.*, 2017). As

391   interaction frequency is required to quantify sampling intensity, we were only able to

392   estimate this variable on the weighted networks (Table S2).

393   Model selection was performed using the *dredge* function in *MuMIn* package

394   (Barton, 2016). We reported the standardized coefficients for an averaged model

395   (AVM) and the importance (Σw_i) of each predictor variable measured across all

396   models (Burnham & Anderson, 2002). We used an importance threshold value of $\geq$

397   0.80 to identify relevant predictor variables (Sebastián-González *et al.*, 2015). When

398   the bird-flower community variable was selected in the MAM, we used partial

399   regressions to detect the total and individual variation explained by this variable. The

400   differences between the three types of bird-flower communities were tested by Tukey

401   contrasts for general linear hypothesis, using the *glht* function in *multcomp* package

402   (Hothorn *et al.*, 2008). We considered multicollinearity to be absent when the

403   variance inflation factor (VIF) or the generalized variance inflation factor (GVIF) was

404   $\leq$ 10 (Hair *et al.*, 2009), both indices were measured using the *vif* function in *car*

405   package (Fox & Weisberg, 2011). We checked for positive spatial autocorrelation in

406   the residuals of the MAM with the lowest ΔAICc computing Moran's *I* in 14-equally

407   spaced distance classes and applying a permutation test with 10,000 iterations, using

408   the *correlog* function in *pgirmess* package (Giraudoux, 2016). Initial analyses found

409   that interaction specialization was associated with the method of recording

410   interactions (Tables 1–2). Therefore, we checked the consistency of our results by

411   repeating all analyses using networks sampled only through focal observations

412   (Tables S3–S4). Analyses were conducted using R (R Core Team, 2017).

413   To determine how our sample of networks spanned the global nectar-feeding

414   bird species richness gradient in each bird family, we compared the cumulative

415   frequency distribution of bird species richness in grid cells across the global

416   distribution and the richness in the grid cells containing the sampled networks.

417   Comparisons were done using a two-sample Kolmogorov-Smirnov test in GraphPad

418   Prism 6.0 (Morgan, 1998). The global richness dataset was based on presence-absence

419   data for Trochilidae, Nectariniidae and Meliphagidae at the spatial resolution of 1×1

420   latitudinal-longitudinal degree grid following Rahbek & Graves (2001). This global

421   richness dataset was also used to build the richness maps in ArcMap 9.2 (ESRI, 2009;

422   Figs. 2–3).

423   RESULTS

424   Hummingbird-flower networks had lower connectance than sunbird- and honeyeater-

425   flower networks. Furthermore, hummingbird-flower networks had greater

426   complementary specialization and modularity than honeyeater-flower networks.

427   However, no differences were found between the complementary specialization and

428   modularity of hummingbird- and sunbird-flower networks, and neither between

429   sunbird- and honeyeater-flower networks. Likewise, using null-model corrected

430   values, a similar pattern of interaction specialization was observed (Fig. 1).

431   Additionally, when potentially confounding variables were included in the linear

432   models, hummingbird-flower networks still had lower connectance than sunbird- and

433   honeyeater-flower networks and greater complementary specialization and null-model

434   corrected binary modularity than honeyeater-flower networks. Moreover, no

435   differences were found between complementary specialization and binary modularity

436   of hummingbird- and sunbird-flower networks, and neither between sunbird- and

437   honeyeater-flower networks. Only weighted modularity did not differ between the

438   networks of these bird-flower communities when including potentially confounding

439   variables (Tables 1–2). Hummingbird communities visited more plant species than

440   sunbird and honeyeater communities (Kruskal-Wallis test: K = 28.32, p < 0.001;

441   Dunn's multiple comparison tests: hummingbirds > sunbirds = honeyeaters).

442   Several of the confounding variables were associated with estimates of

443   interaction specialization (Tables 1–2). Notably, specialization increased with plant

444   species richness for both observed and null-model corrected metrics (Fig. S1).

445   Moreover, communities with greater bird than plant species richness exhibited greater

446   specialization, with lower observed connectance, but not in null-model corrected

447   connectance, where the pattern was reversed. On islands, networks were less

448   specialized, with lower observed and null-model corrected weighted modularity.

449   Sampling also influenced specialization, with greater specialization detected in

450   networks sampled by focal observations (Tables 1–2). Nonetheless, restricting the

451   analysis to networks sampled through focal observations, the most important predictor

452   variables ($\Sigma w_i \geq 0.80$) were the same as in the complete dataset, with the same pattern

453   described above for interaction specialization between the bird-flower communities

454   (Tables S3–S4). Intensity of sampling affected interaction specialization, with

455   decreased null-model corrected connectance and weighted modularity when sampling

456   intensity was high (Tables 1–2).

457   Hummingbird-flower networks were geographically widely distributed, but

458   with some parts of North America and the Amazon region being poorly sampled.

459   Also, when the cumulative frequency distribution of nectar-feeding bird species

460   richness was compared between the global and the sampled localities, we found that

461   species-poor communities were disproportionately less sampled than species-rich

462   hummingbird communities (Fig. S2). In the Old World, in contrast, network

463   distributions were more restricted and some species-rich regions, especially in Central

464   Africa, India, Southeast Asia and Southeast Australia, had few or no studies of bird-

465   flower interactions at the community-level (Figs. 2–3). Nonetheless, the included

466   networks encompassed well the global bird species richness gradient in sunbird and

467   honeyeater communities (Fig. S2).

468   DISCUSSION

469   We found that New World (NW) hummingbird-flower interaction networks are more

470   specialized than Old World (OW) honeyeater-flower networks, as predicted. Notably,

471   hummingbird-flower networks have fewer realized interactions, lower niche overlap

472   and greater binary modularity, as compared to honeyeater-flower networks.

473   Interaction specialization of sunbird-flower networks, however, was similar to both

474   hummingbird- and honeyeater-flower networks, contrarily to the prediction that they

475   would have intermediate values (see below).

476   The greater overall specialization between hummingbirds and their floral

477   resources indicates that their interactions are more species-restricted than the

478   interactions of honeyeaters with their flowers (Blüthgen, 2010). This greater

479   interaction partitioning in hummingbird networks may be a consequence of the

480   greater variation in bill length among hummingbirds than honeyeaters, as well as the

481   greater richness of bird-pollinated plant species in the NW (Fleming, 2005;

482   Abrahamczyk & Kessler, 2015; Higgins *et al.*, 2016). Hummingbird bill morphology

483   in combination with corolla morphology may play a key role in constraining

484   interactions via morphological mismatching (Cotton, 1998a; Temeles *et al.*, 2002;

485   Vizentin-Bugoni *et al.*, 2014). Indeed, in most hummingbird-flower communities,

486   there is a subset of flowers with long, curved corollas visited by one or few long and

487   curve-billed birds (Feinsinger & Colwell, 1978; Maglianesi *et al.*, 2014). Thus,

488   increased range of bill and corolla lengths in hummingbird-flower networks may

489   contribute to reduced niche overlap and increased community-level specialization

490   (Cotton, 1998b; Abrahamczyk & Kessler, 2010; Maruyama *et al.*, 2014; Maglianesi *et*

491   *al.*, 2015). A greater specialization in hummingbird-flower networks could also be

492   due to a greater spatio-temporal floral resource predictability (Fleming & Muchhala,

493   2008). NW annual flowering cycles tend to be more predictable (Bawa *et al.*, 2003)

494   than, for instance, the supra-annual mass flowering in South Asian forests (Sakai,

495   2002). Additionally, flowers are more diverse and abundant in the understory of NW

496   in comparison to OW forests (LaFrankie *et al.*, 2006). This greater diversity may

497   create new interaction opportunities for hummingbirds, resulting in greater niche

498   partitioning in the NW than in the OW networks. Conversely, the lower specialization

499   of honeyeater communities, compared to hummingbird communities, is likely to be

500   due to the much less variable bill length and corolla shapes in those communities

501   (Ford & Paton, 1977), particularly in northern Australia where most of the flowers

502   visited by honeyeaters have an open or cup-shaped corolla that is morphologically

503   accessible to several bird species (Ford *et al.*, 1979; Franklin & Noske, 2000). Hence,

504   more uniform bill lengths and more generalized corolla shapes among honeyeater-

505   flower communities may result in lower interaction specialization, when compared to

506   hummingbird-flower networks. Honeyeaters also tend to have broader dietary

507   preferences in general, feeding on other resources, such as fruits, insects and lerp

508   more frequently than hummingbirds do (Pyke, 1980; Higgins *et al.*, 2016). Although

509   hummingbirds also forage for insects as a source of protein (Stiles, 1995). These

510   diversified feeding habits of honeyeaters may decrease competition for nectar

511   resources, producing the more generalized interactions with flowers demonstrated

512   here (though see Dalsgaard *et al.*, 2017 for an opposed example on frugivorous birds

513   networks). The greatest overall specialization in hummingbird networks implies in

514   narrower niche overlaps of interactions. If combined to species turnover across

515   continental scales, this greater specialization may imply in a larger spatial variability

516   of interactions, resulting in a larger spatial β-diversity of interactions (Trojelsgaard *et*

517   *al.*, 2015) for hummingbird networks. Additionally, temporal variation of resources

518   spanning across the entire year in NW communities (Bawa *et al.*, 2003) may also

519   cause a temporal variation in interactions, resulting in a larger temporal β-diversity of

520   interactions.

521   The similarity between sunbird-flower networks and the other two bird-flower

522   communities is likely to be due two reasons: First, relatively few sunbird-flower

523   networks were available, resulting in wider confidence intervals (Fig. 1). Perhaps

524   more networks would have reduced that variability and made it possible to detect

525   differences between sunbird-flower networks and hummingbird- and honeyeater-

526   flower networks, respectively. Second, sunbird-flower communities are ecologically

527   similar to both hummingbird- and honeyeater-flower communities, and indeed have

528   intermediate interaction specialization levels (Fig. 1). For instance, although sunbirds

529   are considered less phenotypically specialized for nectar-feeding than hummingbirds

530   (Stiles, 1981), the flowers they visit may have rather restrictive morphologies, with

531   tubular and gullet shapes, similar to those of hummingbird-pollinated flowers

532   (Fleming & Muchhala, 2008). This greater morphological restriction of flowers may

533   decrease niche overlap among species, as tubular and gullet corolla shapes may be

534   inaccessible to some species of the nectar-feeding bird community (Pettet, 1977;

535   Temeles *et al.*, 2002). This morphological mismatch in both communities may

536   produce the similar interaction specialization of sunbird- and hummingbird-flower

537   networks that we detected in this study. Additionally, some sunbirds may have

538   specialized feeding behaviours, similar to hummingbirds, of hovering and traplining

539   while visiting flowers (Padyšáková & Janeček, 2016). However, this is not consistent

540   with the observation that interaction specialization was also similar between sunbird-

541   and honeyeater-flower communities. The specialization similarity of honeyeater and

542   sunbird communities may be related to their lower floral resource richness in

543   comparison to hummingbird communities, as demonstrated in this study. This lower

544   resource diversity may increase niche overlap, producing the more generalized

545   feeding-niches found in OW networks. However, we suggest that it is likely that a

546   larger sample size of sunbird-flower networks would have resolved these possibilities

547   in favour of our first explanation because the sunbird interaction specialization tends

548   to be intermediate between those of hummingbirds and honeyeaters (Fig. 1).

549   The correlation between plant species richness and interaction specialization

550   may be because niche availability is greater in species-rich than species-poor

551   communities, thereby promoting greater niche partitioning among species (Dalsgaard

552   *et al.*, 2011; Martín González *et al.*, 2015; Sebastián-González *et al.*, 2015; but see

553   Schleuning *et al.*, 2012). The greater generalization of interactions of insular

554   compared to mainland networks may be a consequence of their species-poor

555   communities (MacArthur & Wilson, 1963; Dalsgaard *et al.*, 2009; Abrahamczyk *et*

556   *al.*, 2015), but may also be due to the tendency of generalist species having greater

557   establishment success on islands than specialist species (Olesen *et al.*, 2002;

558   Maldonado *et al.*, 2013; Traveset *et al.*, 2015). Moreover, at least for hummingbirds,

559   generalized interactions on islands may have been influenced by their rather recent

560   colonization (McGuire *et al.*, 2014; Abrahamczyk *et al.*, 2015) and a greater level of

561 strong and periodic disturbances in islands in comparison to mainland communities,

562 which may favour generalized over specialized bird species (Dalsgaard *et al.*, 2009).

563 In conclusion, we confirmed that interactions are more specialized in

564 hummingbird- than in honeyeater-flower networks, but we were unable to show that

565 sunbird-flower networks differ from those of hummingbirds and honeyeaters. The

566 increased interaction specialization in the hummingbird-flower networks may be a

567 consequence of their greater floral resource richness and phenotypic specialization, in

568 contrast to honeyeater-flower communities (Stiles, 1981; Fleming & Muchhala,

569 2008). These results suggest that there is a potential link between phenotypic

570 specialization and floral resource richness with interaction specialization among

571 nectarivorous bird-flower communities across global scales.

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824   SUPPORTING INFORMATION

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

826   Appendix S1 – Data source (Table S1), geographical and sampling details of each

827   study used to build the interaction networks of bird-flower communities (Table S2).

828   Appendix S2 – Multiple linear regression models of bird-flower interaction networks

829   sampled through focal observation (Table S3–S4).

830   Appendix S3 – Linear regressions between network metrics and the plant species

831   richness (Fig. S1) and two-sample Kolmogorov-Smirnov test comparing the global

832   and sampled cumulative species richness frequency of the three bird families (Fig.

833   S2).

834   BIOSKETCH

835   Thais B. Zanata is an ecologist interested in mutualistic interactions, specifically in

836   the effects of morphology, evolution and climate on interaction patterns across broad

837   geographical scales. This working group, a collaboration among researchers that study

838   bird-flower interactions in different continents, was established to test the ideas

839   proposed by Fleming & Muchhala (2008). Authors contributions: TBZ, BD and IGV

840   conceived the ideas; BD, PAC, JJR, PKM, EF, MSc, AMMG, JVB, DCF, SA, RA,

841   ACA, FPA, SMAJ, ACB, KBG, DWC, HC, AGC, RRF, DH, TTI, SJ, GK, CL,

842   FMGLC, AVL, AOM, CMG, ICM, MAM, TSM, JMA, ACM, GMO, PEO, JFO, JR,

843   LCR, LRL, AMR, MSa, BS, OS, AT, MGRV, ZW, SW, CR and IGV collected the

844   data and helped with discussion; TBZ analysed the data; and TBZ, BD, FCP, PAC,

845   JJR, PKM, EF, MSc, AMMG, JVB, DCF and IGV led the writing. All authors read

846   and approved the final version of the manuscript.

847   Editor: Holger Kreft

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) | | | ΔH_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 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			$\leq0.04^{NS}$			$\leq0.13^{NS}$			$\leq0.06^{NS}$			$\leq0.08^{NS}$

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 only Bird-flower community – adjusted unique variation explained by the difference between the three types of bird-

flower communities; R^2 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 ≥ 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]
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

Predictor variables

	AVM	MAM		AVM	MAM		AVM	MAM		AVM	MAM	
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 total Bird-flower community			0.23			0.34			–			–
R^2 only Bird-flower community			0.06			0.09			–			–
Moran´s I			$\leq 0.06^{NS}$			$\leq 0.17^{NS}$			$\leq 0.07^{NS}$			$\leq 0.06^{NS}$

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 only Bird-flower community – adjusted unique variation explained by the difference between the three types of bird-flower communities; R^2 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) ≤ 1.60 and in weighted modularity models, as variance inflation factor (VIF) $\leq$ 2.30.

848   Figure legends

849   Fig. 1 – Comparison of the observed (OBS, first column) and null-model corrected

850   (Δ, second column) metrics of bird-flower interaction networks of the three types of

851   bird communities (hummingbirds, sunbirds and honeyeaters). Connectance (C) is the

852   realized proportion of possible interactions in a community, complementary

853   specialization (H_2') measures niche overlap among species and modularity (Q_B and Q)

854   detects preferentially interacting subsets of species within the community. Observed

855   connectance and binary modularity have a sample size of 121 networks, while the

856   other metrics have a sample size of 94 networks. Dots represent each network and

857   lines indicate mean and confidence interval at 95% confidence level. Letters represent

858   the group that each bird-flower community belongs, based on Tukey's or Dunn's

859   multiple comparison tests.

860   Fig. 2 – Specialization of bird-flower interaction networks in hummingbird, sunbird

861   and honeyeater communities, measured by observed connectance (C_{OBS}), which

862   describes the realized proportion of possible interactions in a community, and

863   observed complementary specialization (H_2'$_{OBS}$), which calculates the niche overlap

864   among species. Observed connectance has a sample size of 121 networks, while

865   complementary specialization has a sample size of 94 networks. The species richness

866   of hummingbirds, sunbirds and honeyeaters are represented in grey shades,

867   intensifying with an increase in species richness. Points were moved slightly to

868   improve visualization.

869   Fig. 3 – Specialization of bird-flower interaction networks in in hummingbird, sunbird

870   and honeyeater communities, measured by observed binary (Q_{B-OBS}) and weighted

871   modularity (Q_{OBS}). Modularity is a network metric that detects preferentially

872   interacting subsets of species within the community. Observed binary modularity has

873   a sample size of 121 networks, while weighted modularity has a sample size of 94

874   networks. The species richness of hummingbirds, sunbirds and honeyeaters are

875   represented in grey shades, intensifying with an increase in species richness. Points

876   were moved slightly to improve visualization.

Hummingbirds

Sunbirds

Honeyeaters

C_{OBS}

1.00

0.78

0.56

0.34

0.12

Specialization

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

New World nectarivorous bird richness

Old World nectarivorous bird richness