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### **Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks**

Simmons, BI; Vizentin-Bugoni, J; Maruyama, PK; Cotton, PA; Marín-Gómez, OH; Lara, C; Rosero-Lasprilla, L; Maglianesi, MA; Ortiz-Pulido, R; Rocca, MA; Rodrigues, LC; Tinoco, B; Vasconcelos, MF; Sazima, M; González, AMM; Sonne, J; Rahbek, C; Dicks, LV; Dalsgaard, B; Sutherland, WJ

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# 1 **Abundance drives broad patterns of generalisation in plant-**

## 2 **hummingbird pollination networks**

3  
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45 **Abstract**

46

47 Abundant pollinators are often more generalised than rare pollinators. This could be because  
48 abundant species have more chance encounters with potential interaction partners. On the other  
49 hand, generalised species could have a competitive advantage over specialists, leading to  
50 higher abundance. Determining the direction of the abundance-generalisation relationship is  
51 therefore a ‘chicken-and-egg’ dilemma. Here we determine the direction of the relationship  
52 between abundance and generalisation in plant-hummingbird pollination networks across the  
53 Americas. We find evidence that hummingbird pollinators are generalised because they are  
54 abundant, and little evidence that hummingbirds are abundant because they are generalised.  
55 Additionally, most patterns of species-level abundance and generalisation were well explained  
56 by a null model that assumed interaction neutrality (interaction probabilities defined by species  
57 relative abundances). These results suggest that neutral processes play a key role in driving  
58 broad patterns of generalisation in animal pollinators across large spatial scales.

59

60 **Keywords:** generalisation, hummingbirds, mutualism, mutualistic networks, plant-animal  
61 interactions, pollination, specialisation

## 62 **Declarations**

63

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86

## 87 **Introduction**

88

89 Pollination and other mutualistic associations are crucial for the functioning and maintenance  
90 of ecological communities (Heithaus 1974, Rech et al. 2016, Ollerton 2017, Ratto et al. 2018).

91 A common phenomenon in mutualistic communities is that more abundant species have more  
92 generalised interaction niches (Dupont et al. 2003, Vázquez and Aizen 2003, Olesen et al.

93 2008). However, the direction of the relationship between abundance and generalisation has  
94 been described as a ‘chicken-and-egg’ dilemma because there are valid *a priori* explanations

95 for both directions (Fort et al. 2016, Dormann et al. 2017). On the one hand, high abundance  
96 could lead to high generalisation. For example, abundant species are more likely to encounter

97 a greater number of potential interaction partners than rare species (Vázquez et al. 2007, 2009,  
98 Poisot et al. 2015). Additionally, in a given area, higher species abundance leads to greater

99 conspecific competition for available resources, resulting in increased generalization as  
100 predicted by optimal foraging theory (Fontaine et al. 2008, Tinoco et al. 2017). On the other

101 hand, generalisation can have a selective advantage over specialisation, leading to higher  
102 abundance (Batstone et al. 2018). For example, the wider diet breadth of generalist individuals

103 could allow them to receive a more stable benefit over time in communities with high levels of  
104 variability or species turnover; generalisation increases the likelihood that a given mutualist

105 will interact with the most beneficial partner; and generalists benefit from having diverse  
106 partners that occupy different niches but provide the same rewards via different mechanisms

107 (complementarity) (Waser et al. 1996, Albrecht et al. 2012, CaraDonna et al. 2017, Batstone  
108 et al. 2018). Generalisation can also provide a better nutrient balance (Tasei and Aupinel 2008,

109 Behmer 2009, Vaudo et al. 2015), improve species’ pathogen resistance (Alaux et al. 2010, Di  
110 Pasquale et al. 2013), entail a large resource base, and afford functional redundancy that buffers

111 against partner extinction (Biesmeijer et al. 2006).

112

113 Here we evaluate the direction of the abundance-generalisation relationship in plant-  
114 hummingbird pollination networks and use a null model to assess the extent to which observed  
115 patterns of species-level generalisation can be explained by neutral effects. Plant-hummingbird  
116 interactions are a particularly interesting model system to answer these questions as they  
117 involve species spanning the entire specialisation-generalisation spectrum (Bleiweiss 1998,  
118 Martín González et al. 2015, Dalsgaard et al. 2018, Maruyama et al. 2018). Additionally,  
119 pollination by vertebrates is important, especially in the tropics (Bawa 1990, Vizentin-Bugoni  
120 et al. 2018), and is on average responsible for 63% of fruit or seed production in vertebrate-  
121 pollinated plants (Ratto et al. 2018). Therefore, understanding the abundance-generalisation  
122 relationship in vertebrate pollinators such as hummingbirds has important implications for  
123 understanding the processes maintaining tropical plant and vertebrate communities.

124

## 125 **Material and Methods**

126

### 127 **Dataset**

128

129 We assembled a database of plant-hummingbird pollination networks with complementary  
130 information on hummingbird and plant abundance. In total, we gathered 19 quantitative  
131 networks, where link weights represent the number of observed hummingbird visits to plants.  
132 The database contained 103 hummingbird species and 403 plant species. For each of the 19  
133 networks, hummingbird abundances were quantified as the mean number of individuals per  
134 species either recorded along transect counts within the sampling plots or caught using mist  
135 nets (Appendix 1). For four networks where not all species were recorded within the sampling  
136 plots during transect counts or mist netting, we used frequency of occurrence (the proportion

137 of days of fieldwork in which a given species was recorded) as a proxy for relative abundances,  
138 as both measures are strongly correlated and frequency of occurrence is still independent from  
139 the network data (Vizentin-Bugoni et al. 2014). To test whether these four networks affected  
140 our results, we repeated all analyses excluding these data (Appendix 2). Plant abundances were  
141 quantified along transect counts or inside plots within the study areas and summarized as the  
142 number of flowers per species recorded over the sampling period. Species abundances and  
143 interactions were quantified several times (typically, monthly) over at least a complete annual  
144 cycle in each community. Further details of each network are given in Appendix 1. The  
145 inclusion of independent abundance estimates is an important advance because all 35  
146 pollination and seed dispersal networks analysed by Fort et al (2016) used estimates of animal  
147 abundance based on the interaction network data, and the authors had direct measures of plant  
148 abundance for only 29% of networks. Using species' interaction frequency as a proxy for  
149 animal abundance can lead to biased conclusions (Vizentin-Bugoni et al. 2014); by Fort et al's  
150 own admission, "These animal abundance data are arguably limited, as they are not  
151 independent from the interactions; but these are the best data available to evaluate our  
152 question." Conversely, ours is the first study where we have estimates of plant and animal  
153 abundance independent from the interaction observations for the majority of networks.

154

### 155 **Measures of generalisation**

156

157 We calculated the level of generalisation of all hummingbird species in all networks. We focus  
158 on hummingbird species, rather than plants, as plants may have non-hummingbird partners not  
159 included in our data that could result in misleading estimates of generalisation (Dalsgaard et  
160 al. 2008). To assess the sensitivity of our results to the choice of generalisation metric, we  
161 measured generalisation in three ways. First, species degree, which is simply the number of



162 plant species a given hummingbird species interacts with. Second, normalised degree, which  
163 is equal to a species' degree divided by the total number of possible partners. Third, a  
164 generalisation index  $g$ , based on a widely used species-level measure of specialization ( $d'$ ) that  
165 quantifies the extent to which a species deviates from a random sampling of its available  
166 interaction partners (Blüthgen et al. 2006). We calculated  $d'$  using independent plant abundance  
167 data. To ensure that higher values of  $d'$  corresponded to higher levels of generalisation, we  
168 calculated the standardised generalisation index  $g$ , defined as  $1-d'/d'_{\max}$  where  $d'_{\max}$  is the  
169 maximum possible value of  $d'$  (Fort et al. 2016).  $d'$  and  $d'_{\max}$  were calculated using the 'dfun'  
170 function in the 'bipartite' R package (Dormann et al. 2009).

171

## 172 **General approach**

173

174 First, we tested whether there was a relationship between hummingbirds' abundance and their  
175 level of generalisation for each generalisation metric. The generalisation metric was the  
176 response variable, with log(abundance) and network identity as explanatory variables. A linear  
177 mixed effects model with a Gaussian distribution was used for the model with  $g$  as the response  
178 variable and network identity as a random effect. The model was fitted using the 'lme4' R  
179 package (Bates et al. 2015) and the significance of the fixed effect was calculated using Wald  
180  $\chi^2$  tests available in the 'Anova' function of the 'car' R package (Fox and Weisberg 2002). We  
181 calculated both the marginal pseudo- $R^2_{(G)LMM(m)}$ , which represents the variance explained by  
182 fixed effects, and the conditional pseudo- $R^2_{(G)LMM(c)}$ , which represents the variance explained  
183 by both fixed and random effects (Nakagawa and Schielzeth 2013, Emer et al. 2016, Kaiser-  
184 Bunbury et al. 2017, Bartoń 2018). A zero-truncated negative binomial distribution was used  
185 for the model with degree as the response variable and a beta distribution was used for the  
186 model with normalised degree as the response variable. We used the zero-truncated negative

187 binomial regression to account for overdispersion and zero-truncation in the degree data (no  
188 species had a degree of zero). A beta regression was used to model the normalised degree data  
189 because it accounts for overdispersion and is used for analysing continuous data greater than 0  
190 and less than 1 (necessary for our analyses because no species had a normalised degree of zero).  
191 One data point in our dataset had a value of 1 and so we applied the standard correction  
192 following Smithson and Verkuilen (2006). These distributions are not available for mixed  
193 effects models, therefore the zero-truncated negative binomial model was fitted using the  
194 ‘VGAM’ R package (Yee and Wild 1996, Yee 2015) and the beta regression was fitted using  
195 the ‘betareg’ R package (Cribari-Neto and Zeileis 2010).

196

197 Having established that there is a relationship between abundance and generalisation, we used  
198 the approach of Fort *et al.* (2016) to determine whether abundance drives generalisation or  
199 generalisation drives abundance. This approach uses formal logic, specifically material  
200 implication, to derive expectations for broad species-level patterns of abundance and  
201 generalisation in ecological communities. To explain the approach, it is useful to consider a  
202 simple example. Consider the proposition,  $P$ , “if it is a dodo, it is extinct”.  $P$  is made up of two  
203 statements: (i) “it is a dodo” and (ii) “it is extinct”. Given that each of these statements can  
204 either be true or false, we can derive four possible outcomes, as shown in Table 1. Outcome A  
205 is a dodo that is extinct. Outcome B is a non-dodo that is not extinct, such as the hummingbird  
206 species *Amazilia versicolor*. Outcome C is a non-dodo that is extinct, such as the dinosaur  
207 species *Tyrannosaurus rex*. Finally, outcome D is a dodo that is not extinct. We can only refute  
208 the proposition “if it is a dodo, it is extinct” when we observe outcome D to be true; that is, if  
209 we observe a living dodo. Conversely, observing an extinct dodo, an extant *Amazilia versicolor*  
210 individual, or an extinct *T. rex* specimen are all consistent with  $P$ .

211

212 There are four possible outcomes when applying this to the abundance-generalisation chicken-  
213 and-egg dilemma: abundant generalists, rare generalists, abundant specialists and rare  
214 specialists (Table 1). We can therefore derive two hypotheses:

215

- 216 1. If abundance implies generalisation, there should be no species which are abundant and  
217 specialist (outcome D: living dodos); we would only expect to observe abundant  
218 generalists (outcome A: extinct dodos), rare specialists (outcome B: a living *Amazilia*  
219 *versicolor*) and rare generalists (outcome C: extinct *T. rex*).
- 220 2. If generalisation implies abundance, there should be no generalist species that are rare;  
221 we would only expect to observe rare specialists, abundant specialists and abundant  
222 generalists.

223

224 Therefore, by calculating the proportion of hummingbird species in each of the four abundance-  
225 generalisation categories (rare specialists, abundant specialists, rare generalists and abundant  
226 generalists; see below), it is possible to test these two hypotheses and determine whether the  
227 relationship between hummingbird abundance and generalisation is unidirectional (Fort et al.  
228 2016). If hypothesis 1 is correct, the proportion of abundant specialists should be  $\ll$  the  
229 proportion of rare specialists, rare generalists, and abundant generalists; if hypothesis 2 is  
230 correct, the proportion of rare generalists should be  $\ll$  rare specialists, abundant specialists,  
231 and abundant generalists. We used contrasts within an ANOVA framework to test these  
232 hypotheses. To test hypothesis 1, we set abundant specialists as the reference contrast and  
233 tested whether it was significantly less than the other three categories. To test hypothesis 2, we  
234 set rare generalists as the reference contrast and tested whether it was significantly less than  
235 the other three categories.

236 **Abundance and generalisation classification**

237

238 To calculate the proportion of hummingbird species in each abundance-generalisation  
239 category, we developed a novel methodology to classify each species in a community as either  
240 rare or abundant and as either specialist or generalist. For each network, we first rescaled the  
241 abundance and generalisation values of all hummingbird species to range between 0 and 1  
242 according to  $(x - x_{\min}) / (x_{\max} - x_{\min})$ , where  $x_{\min}$  and  $x_{\max}$  are the minimum and maximum values  
243 of abundance or generalisation (Aizen et al. 2012). We then conducted two Bernoulli trials for  
244 each species: (i) to classify a species as ‘Abundant’ or ‘Rare’ and (ii) to classify a species as  
245 ‘Generalist’ or ‘Specialist’. The probability of being classified as ‘Abundant’ in trial (i) was  
246 equal to the species’ rescaled abundance; the probability of being classified as ‘Generalist’ in  
247 trial (ii) was equal to the species’ rescaled generalisation. Therefore, a species with a rescaled  
248 abundance of 0.2 would have a 20% probability of being classified as abundant in a given  
249 iteration. Similarly, a species with a rescaled abundance of 0.8 would have an 80% probability  
250 of being classified as abundant. This was repeated 1000 times. The mean proportion of species  
251 in each of the four abundance-generalisation categories for each network was then calculated.  
252 This was repeated for each of the three generalisation metrics.

253

254 Our method offers a number of improvements over that used by Fort et al (2016), who used  
255 two methods to classify species. First, they classified species in a network as abundant or rare  
256 based on whether their abundance was greater than or less than the mean network abundance,  
257 respectively. Similarly, species were classified as generalised if their generalisation was greater  
258 than the mean network generalisation, and specialist otherwise. Delineating categories using a  
259 strict threshold such as this is problematic because it ignores the continuous nature of  
260 abundance and generalisation data: all values below the mean are treated as equivalent, as are  
261 all values above the mean. Consider a set of species with the following rescaled abundance

262 values: 0.01, 0.02, 0.03, 0.04, 0.499, 0.501, 0.96, 0.97, 0.98, 0.99. Here the mean is 0.5.  
263 Therefore, using Fort et al's method, species with abundances of 0.01, 0.02, 0.03, 0.04 and  
264 0.499 will always be classified as rare, while species with abundances of 0.501, 0.96, 0.97,  
265 0.98 and 0.99 will always be classified as abundant. This is problematic because a species with  
266 0.499 abundance is classified as rare, while one with 0.501 abundance is classified as abundant,  
267 despite there being a very small difference in the abundances of these two species. Conversely,  
268 species with very low or high abundances are treated as equal to those with medium  
269 abundances. For example, species with abundances between 0.01 and 0.04 are treated as  
270 equally rare to a species with an abundance of 0.499. Our method avoids these issues by using  
271 the full continuous range of the data to determine probabilities in the classification. For  
272 example, the species with an abundance of 0.499 and the species with an abundance of 0.501  
273 both have similar probabilities of being classified as abundant. Similarly, the species with an  
274 abundance of 0.499 is 0.498 more likely to be classified as abundant than the species with an  
275 abundance of 0.01, thus more accurately accounting for abundance differences between these  
276 two species. Furthermore, given the highly-skewed nature of abundance and generalisation  
277 distributions, the mean threshold used by Fort et al could be misleading. Our method builds on  
278 this work to make no assumptions about the skewness of the data.

279

280 To remedy the problems with using the mean as a threshold, Fort et al also used a fuzzy logic  
281 classification, where species were classified as abundant or generalist if the value of abundance  
282 or generalisation was above the mean abundance or generalisation plus one standard deviation.  
283 Species were classified as rare or specialist if the value of abundance or generalisation was  
284 below the mean abundance or generalisation minus one standard deviation. Species with  
285 measures between these values were given a linear class membership function, interpolated  
286 between 0 and 1. While this method overcomes some of the issues associated with

287 categorisation based on a strict mean threshold, it still ignores continuous variation in  
288 abundance and generalisation values that are greater or less than one standard deviation from  
289 the mean. Conversely, our method considers the full range of the data, because the rescaled  
290 values simply determine probabilities of success in the Bernoulli trial. Additionally, the  
291 standard deviation could be a misleading measure given the highly-skewed distributions of  
292 abundance and generalisation. Our method makes no assumptions about skewness and works  
293 equally well for all distributions regardless of skewness. Finally, Fort et al's method assumes  
294 that a linear class membership function between the mean minus one standard deviation and  
295 the mean plus one standard deviation is appropriate, while our method requires no such  
296 assumptions.

297

#### 298 **Null model analysis**

299

300 To assess the extent to which our results could be explained purely by neutral effects, we used  
301 a null model to generate 1000 randomised versions of each empirical network. The null model  
302 assumed interaction neutrality by assigning interactions according to a probability matrix,  $\mathbf{A}$ ,  
303 where element  $a_{ij}$  was the relative abundance of hummingbird species  $i$  multiplied by the  
304 relative abundance of plant species  $j$  (Vázquez et al. 2007, Maruyama et al. 2014, Vizentin-  
305 Bugoni et al. 2014, 2016). Therefore, the model assumes that two species with high abundance  
306 have a greater likelihood of interacting than two species with low abundance. The model  
307 constrained the number of links and ensured that each species had at least one interaction  
308 (Vázquez et al. 2007). We used independent plant and hummingbird abundance data to create  
309 the null networks, rather than relying on species marginal totals as a proxy for abundance. For  
310 each of the 1000 null versions of each of the 19 empirical networks, we repeated the  
311 permutational analysis described above ('Abundance and generalisation classification') to

312 calculate the mean proportion of species in each of the four abundance-generalisation  
313 categories predicted by the neutral model. We then compared these proportions based on  
314 neutrality to the empirical proportions: if the empirical proportions were within the 95%  
315 confidence intervals of the null model proportions then there were no significant differences  
316 between the null model and the observed values.

317

## 318 **Results**

319

320 We confirmed the positive relationship between abundance and generalisation in our dataset,  
321 finding a significant correlation between abundance and generalisation for degree ( $P = < 0.001$ ;  
322 pseudo- $R^2 = 0.69$ ), normalised degree ( $P = < 0.001$ ; pseudo- $R^2 = 0.63$ ) and the generalisation  
323 index  $g$  (Wald test:  $\chi^2 = 10.7$ ;  $df = 1$ ;  $P = 0.001$ ;  $R^2_{LMM(m)} = 0.06$ ;  $R^2_{LMM(c)} = 0.44$ ).

324

325 Only a small proportion of species were abundant and specialist for all three generalisation  
326 metrics, while the proportion of species that were rare and generalist was consistently larger,  
327 particularly for the  $g$  generalisation metric (Figure 1). These differences were significant. We  
328 found that abundant specialists were significantly less common than rare specialists, rare  
329 generalists and abundant generalists for all generalisation metrics (Table 2). Conversely, for  
330 the degree and normalised degree metrics, we found that rare generalists were significantly less  
331 common than rare specialists, significantly more common than abundant specialists, and not  
332 significantly different to abundant generalists (Table 2). For the generalisation index ( $g$ ), we  
333 found that rare generalists were not significantly different to rare specialists, and were  
334 significantly more common than abundant specialists and abundant generalists (Table 2).  
335 Overall, these findings support hypothesis 1, that abundance drives generalisation, and do not  
336 support hypothesis 2, that generalisation drives abundance.

337

338 The proportion of species in each of the four abundance-generalisation categories predicted by  
339 the neutrality null model closely matched the empirical proportions, particularly for degree and  
340 normalised degree where there were no significant differences between observed and predicted  
341 proportions for the majority of networks (68–84% of networks; Figure 2). For  $g$ , the model  
342 correctly predicted the proportion of rare specialists and generalists for 79% of networks, but  
343 performed less well in predicting the proportion of abundant specialists and generalists, with  
344 predictions matching observed values for only 47% of networks (Figure 2).

345

346 All results were qualitatively the same and conclusions identical after the exclusion of the four  
347 networks where we used frequency of occurrence (the proportion of days of fieldwork in which  
348 a given species was recorded) as a proxy for relative abundances (Appendix 2).

349

## 350 **Discussion**

351

352 The abundance-generalisation ‘chicken and egg’ dilemma concerns whether the widely  
353 observed positive relationship between abundance and generalisation is a consequence of  
354 abundance driving generalisation or generalisation driving abundance. Our analysis of plant-  
355 hummingbird communities sampled widely across the Americas provides evidence of a  
356 unidirectional relationship, with hummingbird abundance driving hummingbird generalisation.  
357 Importantly, a null model assuming neutrality of interactions closely matched most empirical  
358 observations. This suggests that neutral effects have an important role in structuring broad  
359 patterns of species-level generalisation, even in a system such as plant-hummingbird  
360 pollination networks where phenotypical matching has a strong influence on the occurrence of  
361 pairwise interactions among species. Our results can be discussed in the context of *sufficient*



362 and *necessary* conditions from formal logic. If we say that *P* is a *necessary* condition for *Q*,  
363 then in the absence of *P* there is also an absence of *Q*. However, if *P* is a *sufficient* condition  
364 for *Q*, then if we have *P*, *Q* must follow. For example, obtaining full marks on every question  
365 in an exam is a *sufficient*, but not *necessary*, condition for getting the top grade. Our results  
366 suggest abundance is a *sufficient* condition for generalisation as, if a species is abundant, it  
367 tends to also be a generalist. However, it is not a *necessary* condition as species can be  
368 generalist without being abundant. Conversely, our results suggest generalisation is a *necessary*  
369 condition for abundance as, if a species is a specialist, it tends to be rare. However, it is not a  
370 *sufficient* condition for abundance as, if a species is a generalist, this does not mean it is  
371 abundant. Therefore, our results agree with those of Fort *et al.* (2016) using pollination and  
372 seed dispersal networks, suggesting that abundance driving generalisation may be a general  
373 phenomenon that can be observed in mutualistic systems.

374

375 In all ecological studies it is worth asking whether sampling effort may impact the results. This  
376 is also the case for studies of species interaction networks, as sampling effects can influence  
377 the observed network structure (Fründ *et al.* 2016, Jordano 2016, Vizentin-Bugoni *et al.* 2016,  
378 Dalsgaard *et al.* 2017). Sampling is likely to result in missed detections of interactions for rare  
379 species, resulting in an underestimation of how generalised rare species are (Blüthgen 2010,  
380 Dorado *et al.* 2011). For this reason, Dormann *et al.* (2017) described sampling rare species  
381 with high generalisation as “impossible”. This means that our results are unlikely to be a  
382 function of sampling effects, as the proportion of rare generalist species we observe is likely  
383 less than the true proportion: under theoretical perfect sampling, we would likely observe a  
384 larger proportion of species which are rare generalists, reinforcing our results (Dorado *et al.*  
385 2011). Furthermore, sampling effects are likely to overestimate the proportion of species that  
386 are rare specialists as, even when rare species are observed, they are unlikely to be observed

387 on all the plants they visit. This suggests that sampling effects will cause the generalisation  
388 level of rare species to be underestimated, and that consequently some species classified as rare  
389 specialists may actually be rare generalists (Blüthgen 2010, Dorado et al. 2011). Sampling  
390 effects are therefore not likely to impact our conclusions, because with perfect sampling we  
391 would expect the proportion of rare generalists to increase and the proportion of rare specialists  
392 to decrease, further increasing support for hypothesis 1 (many rare generalists, few abundant  
393 specialists) and refuting hypothesis 2 (few rare generalists, many abundant specialists).  
394 Additionally, we would not expect sampling artefacts to explain the low proportion of species  
395 which were abundant specialists because sampling effects tend to come from missing links for  
396 rare species rather than abundant species (Blüthgen 2010, Dorado et al. 2011, Fort et al. 2016).  
397 We also note that we do not consider the phylogenetic dependence of the hummingbird species  
398 within communities, which could cause an increase in Type I errors. While currently there are  
399 not ways to incorporate phylogenetic effects into our novel methodological framework, this is  
400 an important area for future research.

401

402 A frequent interpretation of the abundance-generalisation relationship is that abundant species  
403 are more generalised due to neutral effects; that is, they are more likely to encounter a greater  
404 number of interaction partners than less abundant species by chance alone (Vázquez et al.  
405 2007). Our null model analysis supports this interpretation, particularly for degree and  
406 normalised degree: we found that the numbers of rare specialists, abundant specialists, rare  
407 generalists and abundant generalists were well predicted for the majority of networks by a null  
408 model that assumed interactions were formed entirely from neutral processes. This finding  
409 complements other recent studies of plant-hummingbird pollination networks showing the  
410 importance of morphological trait matching in predicting pairwise interactions at the network  
411 level (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, 2016, Weinstein and Graham 2017),

412 while here we show that abundance predicts broad patterns of generalisation at the species  
413 level. Among Antillean hummingbirds, it was recently shown that local environmental  
414 conditions and floral richness, not hummingbirds' morphological traits, determined species  
415 level nectar-feeding specialization (Dalsgaard et al. 2018). Combined with our findings, this  
416 might suggest a hierarchy of mechanisms structuring plant-hummingbird interactions, and  
417 more broadly whole pollination networks (Junker et al. 2013, Bartomeus et al. 2016, Vizentin-  
418 Bugoni et al. 2018): neutrality and local conditions govern broad patterns of generalisation,  
419 such as the number of plant partners, while morphological matching operates at a lower level  
420 to determine the identity of these plant partners. For the generalisation index  $g$ , the null model  
421 performed less well, predicting the proportion of abundant specialists and abundant generalists  
422 correctly in only 47% of networks. For the remaining 53% of networks, the model generally  
423 over predicted the number of abundant generalists and under predicted the number of abundant  
424 specialists. This may be due the nature of the  $g$  index itself: by accounting for the abundance  
425 of plants,  $g$  does not necessarily correlate with species degree (number of plant partners). For  
426 example, a hummingbird which visits one abundant plant could receive a higher value of  $g$  than  
427 a hummingbird that visits three rare plants. This means the null model may overestimate the  
428 number of abundant generalists and underestimate the number of abundant specialists as, in the  
429 model, an abundant hummingbird will have a higher probability of interacting with all plants,  
430 while in the empirical network it may be able to gain sufficient resources by only interacting  
431 with the most abundant plants.

432

433 Taken together, our study confirms that abundance is a sufficient, but not necessary, condition  
434 for generalisation in plant-hummingbird pollination networks; it is the first study to test this  
435 hypothesis in animals using independent data on species abundance encompassing a wide array  
436 of communities. Remarkably, our result corroborates the findings of Fort et al. (2016), giving

437 further support that this may be a general phenomenon in mutualistic systems. Further research  
438 should investigate whether the relationships found here hold for other types of ecological  
439 systems, especially given evidence of the importance of neutral effects in structuring  
440 antagonistic host-parasite communities (Vázquez et al. 2005). We also find evidence that  
441 neutral effects are good predictors of coarse species-level patterns of generalisation, even in a  
442 system in which interactions are widely recognized to be constrained by species traits. This  
443 might suggest a hierarchy of mechanisms structuring plant-hummingbird interactions, with  
444 neutral effects operating at a ‘high level’ to determine coarse patterns of generalisation, such  
445 as the number of partners, while niche-based processes act at a lower level to determine the  
446 identity of these partners.

447

#### 448 **Data accessibility**

449

450 Data will be deposited in Data Dryad before we submit a revised version of the manuscript  
451 prior to acceptance.

452

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571

572

573 **Tables**

574

575 **Table 1:** Truth table listing all possible outcomes for the propositions “if it is a dodo, it is  
576 extinct” and “if it is abundant, it is generalist”. ‘T’ is ‘True’ and ‘F’ is ‘False’.

Outcome	Dodo/Abundant	Extinct/Generalist
A	T	T
B	F	F
C	F	T
D	T	F

577

578

579 **Table 2:** Testing hypotheses 1 and 2 in an ANOVA framework, using abundant specialists  
580 and rare generalists as the reference contrast respectively. RS = rare specialist; RG = rare  
581 generalist; AS = abundant specialist; AG = abundant generalist. Significance codes: 0 ‘\*\*\*’  
582 0.001 ‘\*\*’, not significant ‘ns’

<b>Metric</b>	<b>Class</b>	<b>Estimate</b>	<b>t value</b>	<b>P</b>	<b>Significance</b>
<i>Hypothesis 1: Abundant specialist &lt;&lt; rare specialist, rare generalist, abundant generalist</i>					
<i>Reference contrast = abundant specialist</i>					
Degree	(Intercept)	0.08	4.88	0.00	***
	RS	0.48	19.70	0.00	***
	RG	0.07	2.87	0.01	**
	AG	0.11	4.70	0.00	***
Normalised degree	(Intercept)	0.08	4.77	0.00	***
	RS	0.48	19.00	0.00	***
	RG	0.07	2.81	0.01	**
	AG	0.11	4.57	0.00	***
<i>g</i>	(Intercept)	0.09	3.92	0.00	***
	RS	0.26	8.11	0.00	***
	RG	0.29	9.08	0.00	***
	AG	0.11	3.50	0.00	***
<i>Hypothesis 2: Rare generalist &lt;&lt; rare specialist, abundant generalist, abundant specialist</i>					
<i>Reference contrast = rare generalist</i>					
Degree	(Intercept)	0.15	8.93	0.00	***
	RS	0.41	16.83	0.00	***
	AS	-0.07	-2.87	0.01	**
	AG	0.04	1.83	0.07	ns
Normalised degree	(Intercept)	0.16	8.75	0.00	***
	RS	0.41	16.19	0.00	***
	AS	-0.07	-2.81	0.01	**
	AG	0.04	1.76	0.08	ns
<i>g</i>	(Intercept)	0.37	16.77	0.00	***
	RS	-0.03	-0.97	0.33	ns
	AS	-0.29	-9.08	0.00	***
	AG	-0.18	-5.58	0.00	***

583

584

585 **Figure captions**

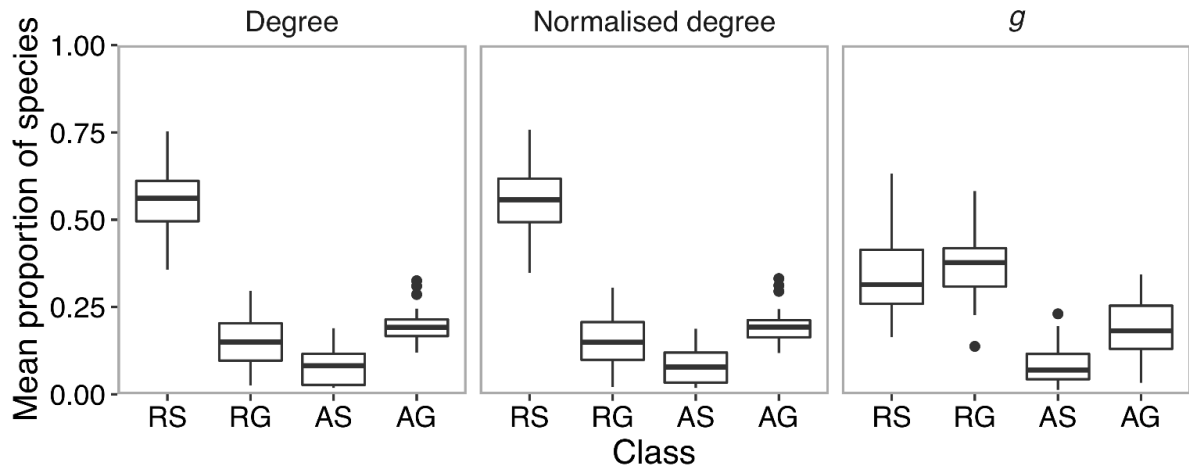
586

587 **Figure 1:** The mean proportion of hummingbird species classified as rare specialists ('RS'),  
588 rare generalists ('RG'), abundant specialists ('AS') and abundant generalists ('AG') across all  
589 networks, for three generalisation metrics: degree, normalised degree and  $g$ . The bold centre  
590 line in each box is the median; the lower and upper hinges are the first and third quartiles,  
591 respectively. The lower whisker indicates the smallest value no less than 1.5 times the inter-  
592 quartile range; the upper whisker indicates the largest value no greater than 1.5 times the inter-  
593 quartile range. Data outside the whiskers are outlying points plotted as solid black circles.

594

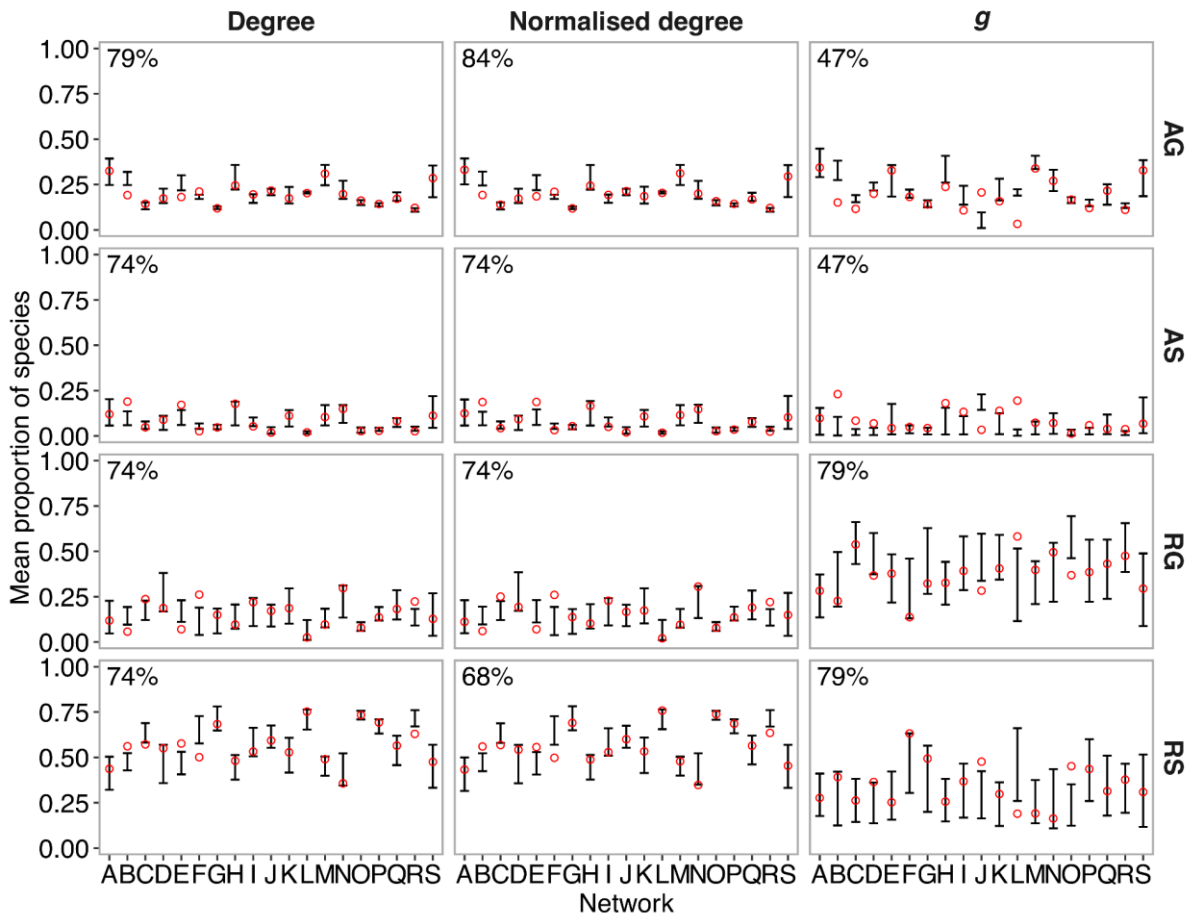
595 **Figure 2:** Comparisons between empirical networks (A-S) and null model networks in the  
596 proportions of species in each of the abundance-generalisation categories 'RS' (rare  
597 specialists), 'RG' (rare generalists), 'AS' (abundant specialists) and 'AG' (abundant  
598 generalists). Error bars represent the 95% confidence intervals of the mean proportion of  
599 hummingbird species in each abundance-generalisation category as predicted by 1000 null  
600 networks. Red circles show the empirically observed mean proportion of hummingbird species  
601 in each category. If the red circle is within the error bars, there were no significant differences  
602 between the observed proportions and the neutrality null model proportions. Percentages in the  
603 top left of each panel give the proportion of networks where empirical proportions were not  
604 significantly different from the null model proportions. Results are shown for each network  
605 (A-S) and for each generalisation metric (Degree, Normalised degree,  $g$ ).

606



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609