

Abundance drives broad patterns of generalisation in plant-hummingbird pollination networks

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44 **Abstract**

45

46 Abundant pollinators are often more generalised than rare pollinators. This could be because
47 abundance drives generalisation: neutral effects suggest that more abundant species will be
48 more generalised simply because they have more chance encounters with potential interaction
49 partners. On the other hand, generalisation could drive abundance, as generalised species could
50 have a competitive advantage over specialists, being able to exploit a wider range of resources
51 and gain a more balanced nutrient intake. Determining the direction of the abundance-
52 generalisation relationship is therefore a ‘chicken-and-egg’ dilemma. Here we determine the
53 direction of the relationship between abundance and generalisation in plant-hummingbird
54 pollination networks sampled from a variety of locations across the Americas. For the first time
55 we resolve the direction of the abundance-generalisation relationship using independent data
56 on animal abundance. We find evidence that hummingbird pollinators are generalised because
57 they are abundant, and little evidence that hummingbirds are abundant because they are
58 generalised. Additionally, a null model analysis suggests this pattern is due to neutral
59 processes: most patterns of species-level abundance and generalisation were well explained by
60 a null model that assumed interaction neutrality. These results suggest that neutral processes
61 play a key role in driving broad patterns of generalisation in animal pollinators across large
62 spatial scales.

63

64 **Keywords:** generalisation, hummingbirds, mutualism, mutualistic networks, plant-animal
65 interactions, pollination, specialisation

66 **Declarations**

67

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88 Introduction

89

90 Pollination and other mutualistic associations are crucial for the functioning and maintenance
91 of ecological communities (Heithaus 1974, Rech et al. 2016, Ollerton 2017, Ratto et al. 2018).
92 A common phenomenon in mutualistic communities is that more abundant species tend to have
93 more generalised interaction niches, interacting with a greater number of partners than rare
94 species (Dupont et al. 2003, Vázquez and Aizen 2003, Olesen et al. 2008). Thus, abundant
95 species are often ‘ecological’ generalists (Ollerton et al. 2007). However, the direction of the
96 relationship between abundance and generalisation has been described as a ‘chicken-and-egg’
97 dilemma as there are valid *a priori* explanations for both directions (Fort et al. 2016, Dormann
98 et al. 2017). For example, high abundance could lead to high generalisation simply due to
99 neutral effects: more abundant species have a higher likelihood of encountering a greater
100 number of potential interaction partners than rarer species (Vázquez et al. 2007, 2009, Poisot
101 et al. 2015). Additionally, pollinators have been observed to increase their generalisation when
102 at high densities: in a given area, higher species abundance leads to greater conspecific
103 competition for the available resources, resulting in increased generalization as predicted by
104 optimal foraging theory (Fontaine et al. 2008, Tinoco et al. 2017). Conversely, high
105 generalisation could lead to high abundance. For example, the wider diet breadth of generalist
106 individuals could be advantageous in communities with high levels of variability or species
107 turnover where flexibility is beneficial (Waser et al. 1996, CaraDonna et al. 2017). Such
108 ‘portfolio effects’ allow a mutualist to receive a more stable benefit over time despite having
109 partners with asynchronous dynamics or different performance trade-offs (Batstone et al.
110 2018). Generalisation can also provide a better nutrient balance (Tasei and Aupinel 2008,
111 Behmer 2009, Vaudo et al. 2015), improve species’ pathogen resistance (Alaux et al. 2010, Di
112 Pasquale et al. 2013) and afford functional redundancy that buffers against partner extinction
113 (Biesmeijer et al. 2006). In a recent review by Batstone et al. (2018), the authors argue that
114 generalisation in mutualisms can have a selective advantage over specialisation for many
115 reasons. These include sampling effects, where generalisation increases the likelihood that a
116 given mutualist will sample the most beneficial partner (for example, Albrecht et al. 2012), and
117 complementarity, where a given mutualist benefits from having diverse partners that occupy
118 different niches, but provide the same rewards via different mechanisms. Therefore,
119 generalization may confer advantages to specific pollinators, resulting in higher abundances.

120

121 Here we evaluate the direction of the abundance-generalisation relationship in plant-
122 hummingbird pollination networks and use a null model to assess the extent to which observed
123 patterns of species-level generalisation can be explained by neutral effects. We focus on
124 hummingbird species, rather than plants, as plants may have non-hummingbird mutualistic
125 partners not included in our data that could result in misleading estimates of generalisation
126 (Dalsgaard et al. 2008). Plant-hummingbird interactions are a particularly interesting model
127 system to answer these questions as they involve species spanning the entire specialisation-
128 generalisation spectrum (Bleiweiss 1998, Martín González et al. 2015, Dalsgaard et al. 2018)
129 and recent studies suggest that abundance has little influence on network structure compared
130 to morphological trait matching (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, 2016,
131 Weinstein and Graham 2017, though see Bergamo et al. 2017 and Dalsgaard et al. 2018).
132 Understanding the processes governing specialisation and generalisation can also contribute to
133 explaining the high diversity of sympatric hummingbird species as niche partitioning can play
134 a role in species coexistence, thus it may also add to the explanation why there are so many
135 species in the tropics (Dalsgaard et al. 2011). Additionally, pollination by vertebrates is
136 important, especially in the tropics (Bawa 1990, Vizentin-Bugoni et al. 2018), and is on average
137 responsible for 63% of fruit or seed production in vertebrate-pollinated plants (Ratto et al.

138 2018). Therefore, understanding the abundance-generalisation relationship in vertebrate
139 pollinators such as hummingbirds has important implications for understanding the processes
140 maintaining tropical plant and vertebrate communities. While previous attempts to resolve the
141 abundance-generalisation chicken-and-egg dilemma have used species' interaction frequency
142 as a proxy for animal abundance (Fort et al. 2016), which can lead to biased conclusions
143 (Vizentin-Bugoni et al. 2014), here we use independent animal abundance estimates. This is
144 an important advance because all 35 pollination and seed dispersal networks analysed by Fort
145 et al (2016) used estimates of animal abundance based on the interaction network data, and the
146 authors had direct measures of plant abundance for only 29% of networks. By their own
147 admission, "These animal abundance data are arguably limited, as they are not independent
148 from the interactions; but these are the best data available to evaluate our question."
149 Conversely, ours is the first study where we have estimates of plant and animal abundance
150 independent from the interaction observations for the majority of networks. This study also
151 represents a significant methodological advance for resolving the chicken-and-egg dilemma.
152 While Fort et al (2016) classified species' abundance and generalisation using either strict
153 thresholds or parametric fuzzy logic methods which assume linearity, our approach makes no
154 such assumptions about the distributions of the data and uses the data's full continuous range
155 without the use of thresholds. We find evidence of a unidirectional relationship with
156 hummingbird abundance driving hummingbird generalisation. Importantly, a null model
157 assuming neutrality of interactions closely matched most empirical results. This suggests that
158 neutral effects have an important role in structuring broad patterns of species-level
159 generalisation, even in a system such as plant-hummingbird pollination networks where
160 phenotypical matching has a strong influence on the occurrence of pairwise interactions among
161 species.

162

163 **Material and Methods**

164

165 **Dataset**

166

167 We assembled a database of plant-hummingbird pollination networks with complementary
168 information on hummingbird and plant abundance. In total we gathered 19 quantitative
169 networks, where link weights represent the number of observed hummingbird visits to plants.
170 In total, the database contained 103 hummingbird species and 403 plant species. For each of
171 the 19 networks, hummingbird abundances were quantified as the mean number of individuals
172 per species either recorded along transect counts within the sampling plots or caught using mist
173 nets (Appendix 1). For four networks where species were not recorded within the sampling
174 plots during transect counts or mist netting, we used frequency of occurrence (the proportion
175 of days of fieldwork in which a given species was recorded) as a proxy for relative abundances,
176 as both measures are strongly correlated and frequency of occurrence is still independent from
177 the network data (Vizentin-Bugoni et al. 2014). To test whether these four networks affected
178 our results, we repeated all analyses excluding these data (Appendix 2). Plant abundances were
179 quantified along transect counts or inside plots within the study areas and summarized as the
180 number of flowers per species recorded over the sampling period. Species abundances and
181 interactions were quantified several times (typically, monthly) over at least a complete annual
182 cycle in each community. Further details of each network are given in Appendix 1.

183

184 **Measures of generalisation**

185

186 We calculated the level of generalisation of all hummingbird species in all networks. To assess
187 the sensitivity of our results to the choice of generalisation metric, we measured generalisation

188 in three ways. First, species degree, which is simply the number of plant species a given
189 hummingbird species interacts with. Second, normalised degree, which is equal to a species'
190 degree divided by the total number of possible partners. Third, a generalisation index g , based
191 on a widely used species-level measure of specialization (d') that quantifies the extent to which
192 a species deviates from a random sampling of its available interaction partners (Blüthgen et al.
193 2006). We calculated d' using independent abundance data. To ensure that higher values of d'
194 corresponded to higher levels of generalisation, we calculated the standardised generalisation
195 index g , defined as $1-d'/d'_{\max}$ where d'_{\max} is the maximum possible value of d' (Fort et al. 2016).
196 d' and d'_{\max} were calculated using the 'dfun' function in the 'bipartite' R package (Dormann et
197 al. 2009).

198

199 **General approach**

200

201 First, we tested whether there was a relationship between hummingbirds' abundance and their
202 level of generalisation using three linear mixed effects models, one for each generalisation
203 metric. The generalisation metric was the response variable, with $\log(\text{abundance})$ as a fixed
204 effect and species and network identity as random effects. A Poisson distribution was used for
205 the model with degree as the response variable, a binomial distribution was used for the model
206 with normalised degree as the response variable (with weights equal to the maximum degree
207 of each species) and a Gaussian distribution was used for the model with g as the response
208 variable. Mixed effects models were fitted using the 'lme4' R package (Bates et al. 2015) and
209 the significance of fixed effects was calculated using Wald χ^2 tests available in the 'Anova'
210 function of the 'car' R package (Fox and Weisberg 2002). We calculated both the marginal
211 $R^2_{(G)LMM(m)}$, which represents the variance explained by fixed effects, and the conditional
212 $R^2_{(G)LMM(c)}$, which represents the variance explained by both fixed and random effects
213 (Nakagawa and Schielzeth 2013, Emer et al. 2016, Kaiser-Bunbury et al. 2017, Bartoń 2018).

214

215 Having established that there is a relationship between abundance and generalisation, we used
216 the approach of Fort *et al.* (2016) to determine whether abundance drives generalisation or
217 generalisation drives abundance. This approach uses formal logic, specifically material
218 implication, to derive expectations for broad species-level patterns of abundance and
219 generalisation in ecological communities. To explain the approach, it is useful to consider a
220 simple example. Consider the proposition, P , "if it is a dodo, it is extinct". P is made up of two
221 statements: (i) "it is a dodo" and (ii) "it is extinct". Given that each of these statements can
222 either be true or false, we can derive four possible outcomes, as shown in Table 1. Outcome A
223 is a dodo that is extinct. Outcome B is a non-dodo that is not extinct, such as the hummingbird
224 species *Amazilia versicolor*. Outcome C is a non-dodo that is extinct, such as the dinosaur
225 species *Tyrannosaurus rex*. Finally, outcome D is a dodo that is not extinct. We can only refute
226 the proposition "if it is a dodo, it is extinct" when we observe outcome D to be true; that is, if
227 we observe a living dodo. Conversely, observing an extinct dodo, an extant *Amazilia versicolor*
228 individual, or an extinct *T. Rex* specimen are all consistent with P .

229

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

233

- 234 1. If abundance implies generalisation, there should be no species which are abundant and
235 specialist (outcome D: living dodos); we would only expect to observe abundant
236 generalists (outcome A: extinct dodos), rare specialists (outcome B: a living *Amazilia*
237 *versicolor*) and rare generalists (outcome C: extinct *T. Rex*).

238 2. If generalisation implies abundance, there should be no generalist species that are rare;
239 we would only expect to observe rare specialists, abundant specialists and abundant
240 generalists.

241
242 Therefore, by calculating the proportion of hummingbird species in each of the four abundance-
243 generalisation categories (rare specialists, abundant specialists, rare generalists and abundant
244 generalists), it is possible to test these two hypotheses and determine whether the relationship
245 between hummingbird abundance and generalisation is unidirectional (Fort et al. 2016).
246 Particularly it is important to look at the proportion of rare generalists and abundant specialists:
247 if hypothesis 1 is correct, there should be few abundant specialists; if hypothesis 2 is correct,
248 there should be few rare generalists.

249

250 **Abundance and generalisation classification**

251

252 To calculate the proportion of hummingbird species in each abundance-generalisation
253 category, we developed a novel methodology to classify each species in a community as either
254 rare or abundant and as either specialist or generalist. As mentioned above, this improves on
255 Fort et al's (2016) methodology by making no assumptions about the distributions of the data
256 and by using the data's full continuous range without the use of thresholds. For each network,
257 we first rescaled the abundance and generalisation values of all hummingbird species to range
258 between 0 and 1 according to $(x - x_{\min}) / (x_{\max} - x_{\min})$, where x_{\min} and x_{\max} are the minimum and
259 maximum values of abundance or generalisation (Aizen et al. 2012). These values represent
260 the probability with which a species would be classified as abundant or generalist. Next, we
261 sampled a random value from a uniform distribution between 0 and 1. If a species' rescaled
262 abundance or generalisation was greater than or equal to this value, it was classified as
263 abundant or generalist, respectively. If it was less than this value, it was classified as rare or
264 specialist, respectively. Therefore, a species with a rescaled abundance of 0.2 would have a
265 20% probability of being classified as abundant in a given iteration. Similarly, a species with
266 a rescaled abundance of 0.8 would have an 80% probability of being classified as abundant.
267 This was repeated 1000 times. The mean proportion of species in each of the four abundance-
268 generalisation categories was then calculated. This was repeated for each of the three
269 generalisation metrics.

270

271 **Null model analysis**

272

273 To assess the extent to which our results could be explained purely by neutral effects, we used
274 a null model to generate 1000 randomised versions of each empirical network. The null model
275 assumed interaction neutrality by assigning interactions according to a probability matrix, \mathbf{A} ,
276 where element a_{ij} was the relative abundance of hummingbird species i multiplied by the
277 relative abundance of plant species j (Vázquez et al. 2007, Maruyama et al. 2014, Vizentin-
278 Bugoni et al. 2014, 2016). Therefore, the model assumes that two species with high abundance
279 have a greater likelihood of interacting than two species with low abundance. The model
280 constrained the number of links and ensured that each species had at least one interaction
281 (Vázquez et al. 2007). We used independent plant and hummingbird abundance data to create
282 the null networks, rather than relying on species marginal totals as a proxy for abundance. For
283 each of the 1000 null versions of each of the 19 empirical networks, we repeated the
284 permutational analysis described above ('Abundance and generalisation classification') to
285 calculate the mean proportion of species in each of the four abundance-generalisation
286 categories predicted by the neutral model. We then compared these proportions based on
287 neutrality to the empirical proportions: if the empirical proportions were within the 95%

288 confidence intervals of the null model proportions then there were no significant differences
289 between the null model and the observed values.

290

291 **Results**

292

293 We confirmed the positive relationship between abundance and generalisation in our dataset,
294 finding a significant correlation between abundance and generalisation for degree (Wald test:
295 $\chi^2 = 216.44$; $df = 1$; $P = < 0.001$; $R^2_{\text{GLMM}(m)} = 0.55$; $R^2_{\text{GLMM}(c)} = 0.79$), normalised degree (Wald
296 test: $\chi^2 = 232.1$; $df = 1$; $P = < 0.001$; $R^2_{\text{GLMM}(m)} = 0.26$; $R^2_{\text{GLMM}(c)} = 0.37$) and the generalisation
297 index g (Wald test: $\chi^2 = 10.7$; $df = 1$; $P = 0.001$; $R^2_{\text{LMM}(m)} = 0.06$; $R^2_{\text{LMM}(c)} = 0.44$).

298

299 Only a small proportion of species were abundant and specialist for all three generalisation
300 metrics (Figure 1). Conversely, the proportion of species that were rare and generalist was
301 consistently larger, particularly for the g generalisation metric. These differences were
302 significant: the proportion of species that were rare and generalist was significantly higher than
303 the proportion which were abundant and specialist for degree ($t = 2.92$, $df = 18$, $p = 0.009$),
304 normalised degree ($t = 2.91$, $df = 18$, $p = 0.009$) and g ($t = 10.34$, $df = 18$, $p = < 0.001$) (Figure
305 1). Overall, these findings support hypothesis 1, that abundance drives generalisation, and do
306 not support hypothesis 2, that generalisation drives abundance.

307

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

315

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

319

320 **Discussion**

321

322 Our analysis of numerous plant-hummingbird communities sampled widely across the
323 Americas support the hypothesis that abundance drives species-level generalisation, and
324 provide little evidence that generalisation drives species abundance. These results can be
325 discussed in the context of *sufficient* and *necessary* conditions from formal logic. If we say that
326 P is a *necessary* condition for Q , then in the absence of P there is also an absence of Q . For
327 example, sitting the exam is a *necessary* condition for getting an A grade. If a student does not
328 sit the exam, they will not get an A grade. Similarly, if a student is awarded an A grade, they
329 must have sat the exam. However, if P is a *sufficient* condition for Q , then if we have P , Q must
330 follow. For example, obtaining full marks on every exam question is a *sufficient* condition for
331 getting an A grade in the exam. Therefore, if a student gets full marks on every question, they
332 will get an A grade. However, getting full marks on every question is not a *necessary* condition
333 for getting an A grade: it is possible to get an A without achieving full marks on all questions.
334 Similarly, sitting the exam is not a *sufficient* condition for getting an A grade: it is possible to
335 sit the exam and not get an A. Our results suggest abundance is a *sufficient* condition for
336 generalisation as, if a species is abundant, it tends to also be a generalist. However, it is not a
337 *necessary* condition as species can be generalist without being abundant. Conversely, our

338 results suggest generalisation is a *necessary* condition for abundance as, if a species is a
339 specialist, it tends to be rare. However, it is not a *sufficient* condition for abundance as, if a
340 species is a generalist, this does not mean it is abundant. Therefore, our results agree with those
341 of Fort *et al.* (2016) using pollination and seed dispersal networks, suggesting that abundance
342 driving generalisation may be a general phenomenon that can be observed in mutualistic
343 systems.

344

345 In all ecological studies it is worth asking whether sampling effort may impact the results. This
346 is also the case for studies of species interaction networks, as sampling effects can influence
347 the observed network structure (Fründ *et al.* 2016, Jordano 2016, Vizentin-Bugoni *et al.* 2016,
348 Dalsgaard *et al.* 2017). Sampling is likely to result in missed detections of interactions for rare
349 species, resulting in an underestimation of how generalised rare species are (Blüthgen 2010,
350 Dorado *et al.* 2011). For this reason, Dormann *et al.* (2017) described sampling rare species
351 with high generalisation as “impossible”. This means that our results are unlikely to be a
352 function of sampling effects, as the proportion of rare generalist species we observe is likely
353 less than the true proportion: under theoretical perfect sampling, we would likely observe a
354 larger proportion of species which are rare generalists, reinforcing our results (Dorado *et al.*
355 2011). Furthermore, sampling effects are likely to overestimate the proportion of species that
356 are rare specialists as, even when rare species are observed, they are unlikely to be observed
357 on all the plants they visit. This suggests that sampling effects will cause the generalisation
358 level of rare species to be underestimated, and that consequently some species classified as rare
359 specialists may actually be rare generalists (Blüthgen 2010, Dorado *et al.* 2011). Sampling
360 effects are therefore not likely to impact our conclusions, because with perfect sampling we
361 would expect the proportion of rare generalists to increase and the proportion of rare specialists
362 to decrease, further increasing support for hypothesis 1 (many rare generalists, few abundant
363 specialists) and refuting hypothesis 2 (few rare generalists, many abundant specialists).
364 Additionally, we would not expect sampling artefacts to explain the low proportion of species
365 which were abundant specialists because sampling effects tend to come from missing links for
366 rare species rather than abundant species (Blüthgen 2010, Dorado *et al.* 2011, Fort *et al.* 2016).

367

368 A frequent interpretation of the abundance-generalisation relationship is that abundant species
369 are more generalised due to neutral effects; that is, they are more likely to encounter a greater
370 number of interaction partners than less abundant species by chance alone (Vázquez *et al.*
371 2007). Our null model analysis supports this interpretation, particularly for degree and
372 normalised degree: we found that the numbers of rare specialists, abundant specialists, rare
373 generalists and abundant generalists were well predicted for the majority of networks by a null
374 model that assumed interactions were formed entirely from neutral processes. This finding
375 complements other recent studies of plant-hummingbird pollination networks showing the
376 importance of morphological trait matching in predicting pairwise interactions at the network
377 level (Maruyama *et al.* 2014, Vizentin-Bugoni *et al.* 2014, 2016, Weinstein and Graham 2017),
378 while here we show that abundance predicts broad patterns of generalisation at the species
379 level. Among Antillean hummingbirds, it was recently shown that local environmental
380 conditions and floral richness, not hummingbirds’ morphological traits, determined species
381 level nectar-feeding specialization (Dalsgaard *et al.* 2018). Combined with our findings, this
382 might suggest a hierarchy of mechanisms structuring plant-hummingbird interactions, and
383 more broadly whole pollination networks (Junker *et al.* 2013, Bartomeus *et al.* 2016, Vizentin-
384 Bugoni *et al.* 2018): neutrality and local conditions govern broad patterns of generalisation,
385 such as the number of plant partners, while morphological matching operates at a lower level
386 to determine the identity of these plant partners. For the generalisation index g , the null model
387 performed less well, predicting the proportion of abundant specialists and abundant generalists

388 correctly in only 47% of networks. For the remaining 53% of networks, the model generally
389 over predicted the number of abundant generalists and under predicted the number of abundant
390 specialists. This may be due the nature of the g index itself: by accounting for the abundance
391 of plants, g does not necessarily correlate with species degree (number of plant partners). For
392 example, a hummingbird which visits one abundant plant could receive a higher value of g than
393 a hummingbird that visits three rare plants. This means the null model may overestimate the
394 number of abundant generalists and underestimate the number of abundant specialists as, in the
395 model, an abundant hummingbird will have a higher probability of interacting with all plants,
396 while in the empirical network it may be able to gain sufficient resources by only interacting
397 with the most abundant plants.

398
399 Taken together, our study confirms that abundance is a sufficient, but not necessary, condition
400 for generalisation in plant-hummingbird pollination networks; it is the first study to test this
401 hypothesis in animals using independent data on species abundance encompassing a wide array
402 of communities. Remarkably, our result corroborates the findings of Fort et al. (2016), giving
403 further support that this may be a general phenomenon in mutualistic systems. Further research
404 should investigate whether the relationships found here hold for other types of ecological
405 systems. We also find evidence that neutral effects are good predictors of coarse species-level
406 patterns of generalisation, even in a system in which interactions are widely recognized to be
407 constrained by species traits. This might suggest a hierarchy of mechanisms structuring plant-
408 hummingbird interactions, with neutral effects operating at a ‘high level’ to determine coarse
409 patterns of generalisation, such as the number of partners, while niche-based processes act at a
410 lower level to determine the identity of these partners.

411

412 **Data accessibility**

413

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

416

417 **References**

418

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- 533

534 **Tables**

535

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

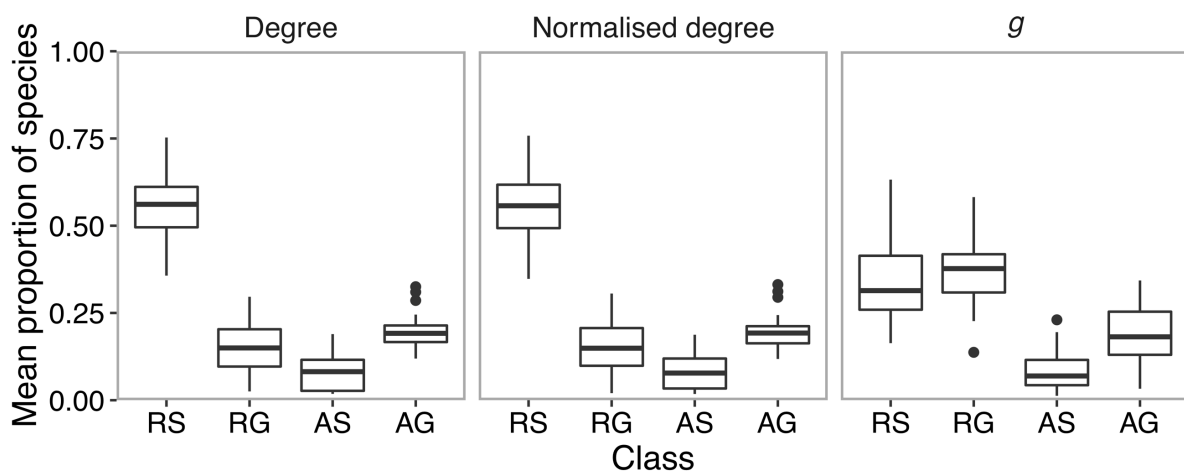
Outcome	Dodo/Abundant	Extinct/Generalist
A	T	T
B	F	F
C	F	T
D	T	F

538

539

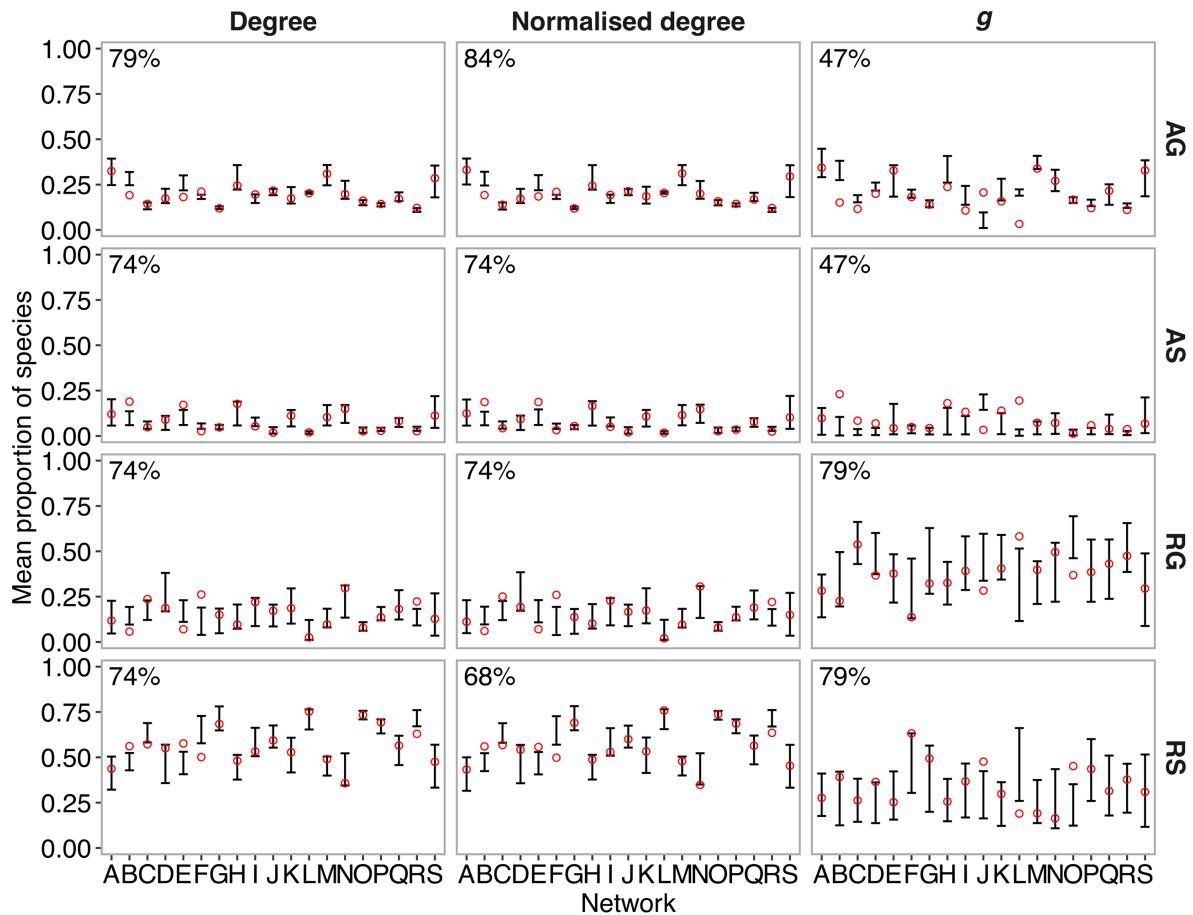
540 **Figures**

541



542

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



550
551 **Figure 2:** Comparisons between empirical networks (A-S) and null model networks in the
552 proportions of species in each of the abundance-generalisation categories ‘RS’ (rare
553 specialists), ‘RG’ (rare generalists), ‘AS’ (abundant specialists) and ‘AG’ (abundant
554 generalists). Error bars represent the 95% confidence intervals of the mean proportion of
555 hummingbird species in each abundance-generalisation category as predicted by 1000 null
556 networks. Red circles show the empirically observed mean proportion of hummingbird species
557 in each category. If the red circle is within the error bars, there were no significant differences
558 between the observed proportions and the neutrality null model proportions. Percentages in the
559 top left of each panel give the proportion of networks where empirical proportions were not
560 significantly different from the null model proportions. Results are shown for each network
561 (A-S) and for each generalisation metric (Degree, Normalised degree, g).
562