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

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

Keywords: mutualism, mutualistic networks, plant–animal interactions, specialisation

Introduction

Pollination and other mutualistic associations are crucial for the functioning and maintenance of ecological communities (Heithaus 1974, Rech et al. 2016, Ollerton 2017, Ratto et al. 2018). A common phenomenon in mutualistic communities is that more abundant species have more generalised interaction niches (Dupont et al. 2003, Vázquez and Aizen 2003, Olesen et al. 2008). However, the direction of the relationship between abundance and generalisation has been described as a 'chicken-and-egg' dilemma because there are valid a priori explanations for both directions (Fort et al. 2016, Dormann et al. 2017). On the one hand, high abundance could lead to high generalisation. For example, abundant species are more likely to encounter a greater number of potential interaction partners than rare species (Vázquez et al. 2007, 2009, Poisot et al. 2015). Additionally, in a given area, higher species abundance leads to greater conspecific competition for available resources, resulting in increased generalization as predicted by optimal foraging theory (Fontaine et al. 2008, Tinoco et al. 2017). On the other hand, generalisation can have a selective advantage over specialisation, leading to higher abundance (Batstone et al. 2018). For example, the wider diet breadth of generalist individuals could allow them to receive a more stable benefit over time in communities with high levels of variability or species turnover; generalisation increases the likelihood that a given mutualist will interact with the most beneficial partner; and generalists benefit from having diverse partners that occupy different niches but provide the same rewards via different mechanisms (complementarity) (Waser et al. 1996, Albrecht et al. 2012, CaraDonna et al. 2017, Batstone et al. 2018). Generalisation can also provide a better nutrient balance (Tasei and Aupinel 2008, Behmer 2009, Vaudo et al. 2015), improve species' pathogen resistance (Alaux et al. 2010, Di Pasquale et al. 2013), entail a large resource base, and afford functional redundancy that buffers against partner extinction (Biesmeijer et al. 2006).

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

Material and methods

Dataset

We assembled a database of plant–hummingbird pollination networks with complementary information on hummingbird and plant abundance. In total, we gathered 19 quantitative networks, where link weights represent the number of observed hummingbird visits to plants. The database contained 103 hummingbird species and 403 plant species. For each of the 19 networks, hummingbird abundances were quantified as the mean number of individuals per species either recorded along transect counts within the sampling plots or caught using mist nets (Supplementary material Appendix 1). For four networks where not all species were recorded within the sampling plots during transect counts or mist netting, we used frequency of occurrence (the proportion of days of fieldwork in which a given species was recorded) as a proxy for relative abundances, as both measures are strongly correlated and frequency of occurrence is still independent from the network data (Vizentin-Bugoni et al. 2014). To test whether these four networks affected our results, we repeated all analyses excluding these data (Supplementary material Appendix 2). Plant abundances were quantified along transect counts or inside plots within the study areas and summarized as the number of flowers per species recorded over the sampling period. Species abundances and interactions were quantified several times (typically, monthly) over at least a complete annual cycle in each community. Further details of each network are given in Supplementary material Appendix 1. The inclusion of independent abundance estimates is an important advance because all 35 pollination and seed dispersal networks analysed in a similar study by Fort et al. (2016) used estimates of animal abundance based on the interaction network data, and the authors had direct measures of plant abundance for only 29% of networks. Using species' interaction frequency as a proxy for animal abundance can lead to biased conclusions (Vizentin-Bugoni et al. 2014); by Fort et al.'s own admission, 'These animal abundance data are arguably limited, as they are not independent from the interactions; but these are the best data available to evaluate our question.' Conversely, our is the first study of the abundance–generalisation 'chicken-and-egg' dilemma where we have estimates of plant and animal abundance independent from the interaction observations for the majority of networks.

Measures of generalisation

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

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

General approach

First, we tested whether there was a relationship between hummingbirds' abundance and their level of generalisation for each generalisation metric. The generalisation metric was the response variable, with log(abundance) and network identity as explanatory variables. A linear mixed effects model with a Gaussian distribution was used for the model with g as the response variable and network identity as a random effect. The model was fitted using the 'lme4' R package (Bates et al. 2015) and the significance of the fixed effect was calculated using Wald χ^2 tests available in the 'Anova' function of the 'car' R package (Fox and Weisberg 2002). We calculated both the marginal pseudo-$R^2_{(G)LMM(m)}$, which represents the variance explained by fixed effects, and the conditional pseudo-$R^2_{(G)LMM(c)}$, which represents the variance explained by both fixed and random effects (Nakagawa and Schielzeth 2013, Emer et al. 2016, Kaiser-Bunbury et al. 2017, Bartoń 2018). A zero-truncated negative binomial distribution was used for the model with degree as the response variable and a beta distribution was used for the model with normalised degree as the response variable. We used the zero-truncated negative binomial regression to account for overdispersion and zero-truncation in the degree data (no species had a degree of zero). A beta regression was used to model the normalised degree data because it accounts for overdispersion and is used for analysing continuous data greater than 0 and less than 1 (necessary for our analyses because no species had a normalised degree of zero). One data point in our dataset had a value of 1 and so we applied the standard correction following Smithson and Verkuilen (2006). These distributions are not available for mixed effects models, therefore the zero-truncated negative binomial model was fitted using the 'VGAM' R package (Yee and Wild 1996, Yee 2015) and the beta regression was fitted using the 'betareg' R package (Cribari-Neto and Zeileis 2010).

Having established that there is a relationship between abundance and generalisation, we used the approach of Fort et al. (2016) to determine whether abundance drives generalisation or generalisation drives abundance. This approach uses formal logic, specifically material implication, to derive expectations for broad species-level patterns of abundance and generalisation in ecological communities. To explain the approach, it is useful to consider a simple example. Consider the proposition, P, 'if it is a dodo, it is extinct'. P is made up of two statements: 1) 'it is a dodo' and 2) 'it is extinct'. Given that each of these statements can either be true or false, we can derive four possible outcomes, as shown in Table 1. Outcome A is a dodo that is extinct. Outcome B is a non-dodo that is not extinct, such as the hummingbird species *Amazilia versicolor*. Outcome C is a non-dodo that is extinct, such as the dinosaur species *Tyrannosaurus rex*. Finally, outcome D is a dodo that is not extinct. We can only refute the proposition 'if it is a dodo, it is extinct' when we observe outcome D to be true; that is, if we observe a living dodo. Conversely, observing an extinct dodo, an extant *Amazilia versicolor* individual, or an extinct *T. rex* specimen are all consistent with P.

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

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

Therefore, by calculating the proportion of hummingbird species in each of the four abundance–generalisation categories (rare specialists, abundant specialists, rare generalists and abundant generalists), it is possible to test these two hypotheses and determine whether the relationship between hummingbird abundance and generalisation is unidirectional (Fort et al. 2016). If hypothesis 1 is correct, the proportion of abundant specialists should be << the proportion of rare specialists, rare generalists and abundant generalists; if hypothesis 2 is correct, the proportion of rare generalists should be << rare specialists, abundant specialists and abundant generalists. We used contrasts within an ANOVA framework to test these hypotheses. To test hypothesis 1, we set abundant specialists as the reference contrast and tested whether it was significantly less than the other three categories. To test hypothesis 2, we set rare generalists as the reference contrast and tested whether it was significantly less than the other three categories.

Abundance and generalisation classification

To calculate the proportion of hummingbird species in each abundance–generalisation category, we developed a novel methodology to classify each species in a community as either rare or abundant and as either specialist or generalist. For each

Table 1. Truth table listing all possible outcomes for the propositions 'if it is a dodo, it is 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

network, we first rescaled the abundance and generalisation values of all hummingbird species to range between 0 and 1 according to $(x - x_{min})/(x_{max} - x_{min})$, where x_{min} and x_{max} are the minimum and maximum values of abundance or generalisation (Aizen et al. 2012). We then conducted two Bernoulli trials for each species: 1) to classify a species as 'Abundant' or 'Rare' and 2) to classify a species as 'Generalist or 'Specialist'. The probability of being classified as 'Abundant' in trial 1) was equal to the species' rescaled abundance; the probability of being classified as 'Generalist' in trial 2) was equal to the species' rescaled generalisation. Therefore, a species with a rescaled abundance of 0.2 would have a 20% probability of being classified as abundant in a given iteration. Similarly, a species with a rescaled abundance of 0.8 would have an 80% probability of being classified as abundant. This was repeated 1000 times. The mean proportion of species in each of the four abundance–generalisation categories for each network was then calculated. This was repeated for each of the three generalisation metrics.

Our method offers a number of improvements over that used by Fort et al. (2016), who used two methods to classify species. First, they classified species in a network as abundant or rare based on whether their abundance was greater than or less than the mean network abundance, respectively. Similarly, species were classified as generalised if their generalisation was greater than the mean network generalisation, and specialist otherwise. Delineating categories using a strict threshold such as this is problematic because it ignores the continuous nature of abundance and generalisation data: all values below the mean are treated as equivalent, as are all values above the mean. Consider a set of species with the following rescaled abundance 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. Therefore, using Fort et al's method, species with abundances of 0.01, 0.02, 0.03, 0.04 and 0.499 will always be classified as rare, while species with abundances of 0.501, 0.96, 0.97, 0.98 and 0.99 will always be classified as abundant. This is problematic because a species with 0.499 abundance is classified as rare, while one with 0.501 abundance is classified as abundant, despite there being a very small difference in the abundances of these two species. Conversely, species with very low or high abundances are treated as equal to those with medium abundances. For example, species with abundances between 0.01 and 0.04 are treated as equally rare to a species with an abundance of 0.499. Our method avoids these issues by using the full continuous range of the data to determine probabilities in the classification. For example,

the species with an abundance of 0.499 and the species with an abundance of 0.501 both have similar probabilities of being classified as abundant. Similarly, the species with an abundance of 0.499 is 0.498 more likely to be classified as abundant than the species with an abundance of 0.01, thus more accurately accounting for abundance differences between these two species. Furthermore, given the highly-skewed nature of abundance and generalisation distributions, the mean threshold used by Fort et al. could be misleading. Our method builds on this work to make no assumptions about the skewness of the data.

To remedy the problems with using the mean as a threshold, Fort et al also used a fuzzy logic classification, where species were classified as abundant or generalist if the value of abundance or generalisation was above the mean abundance or generalisation plus one standard deviation. Species were classified as rare or specialist if the value of abundance or generalisation was below the mean abundance or generalisation minus one standard deviation. Species with measures between these values were given a linear class membership function, interpolated between 0 and 1. While this method overcomes some of the issues associated with categorisation based on a strict mean threshold, it still ignores continuous variation in abundance and generalisation values that are greater or less than one standard deviation from the mean. Conversely, our method considers the full range of the data, because the rescaled values simply determine probabilities of success in the Bernoulli trial. Additionally, the standard deviation could be a misleading measure given the highly-skewed distributions of abundance and generalisation. Our method makes no assumptions about skewness and works equally well for all distributions regardless of skewness. Finally, Fort et al's method assumes that a linear class membership function between the mean minus one standard deviation and the mean plus one standard deviation is appropriate, while our method requires no such assumptions.

Null model analysis

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

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

Data deposition

Results

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

Only a small proportion of species were abundant and specialist for all three generalisation metrics, while the proportion of species that were rare and generalist was consistently larger, particularly for the g generalisation metric (Fig. 1). These differences were significant. We found that abundant specialists were significantly less common than rare specialists, rare generalists and abundant generalists for all generalisation metrics (Table 2). Conversely, for the degree and normalised degree metrics, we found that rare generalists were significantly less common than rare specialists, significantly more common than abundant specialists, and not significantly different to abundant generalists (Table 2). For the generalisation index (g), we found that rare generalists were not significantly different to rare specialists, and were significantly more common than abundant specialists and abundant generalists (Table 2).

Overall, these findings support hypothesis 1, that abundance drives generalisation, and do not support hypothesis 2, that generalisation drives abundance.

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

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

Discussion

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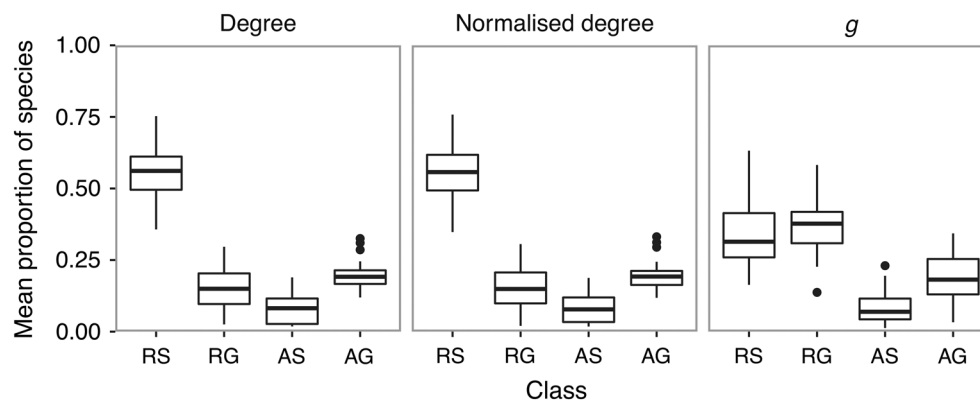

Figure 1. The mean proportion of hummingbird species classified as rare specialists ('RS'), rare generalists ('RG'), abundant specialists ('AS') and abundant generalists ('AG') across all networks, for three generalisation metrics: degree, normalised degree and g. The bold centre line in each box is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

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

Metric	Class	Estimate	t-value	p	Significance
Hypothesis 1: Abundant specialist << rare specialist, rare generalist, abundant generalist					
Reference contrast = abundant specialist					
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	***
g	(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	***
Hypothesis 2: Rare generalist << rare specialist, abundant generalist, abundant specialist					
Reference contrast = rare generalist					
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
g	(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	***

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

In all ecological studies it is worth asking whether sampling effort may impact the results. This is also the case for studies of species interaction networks, as sampling effects can influence the observed network structure (Fründ et al. 2016, Jordano 2016, Vizentin-Bugoni et al. 2016, Dalsgaard et al. 2017). Sampling is likely to result in missed detections of interactions for rare species, resulting in an underestimation of how generalised rare species are (Blüthgen 2010, Dorado et al. 2011). For this reason, Dormann et al. (2017) described sampling rare species with high generalisation as 'impossible'. This means that our results are unlikely to be a function of sampling effects, as the proportion of rare generalist species we observe is likely less than the true proportion: under theoretical perfect sampling, we would likely observe a larger proportion of species which are rare generalists, reinforcing our results (Dorado et al. 2011). Furthermore, sampling effects are likely to overestimate the proportion of species that are rare specialists as, even when rare species are observed, they are unlikely to be observed on all the plants they visit. This suggests that sampling effects will cause the generalisation level of rare species to be underestimated, and that consequently some species classified as rare specialists may actually be rare generalists (Blüthgen 2010, Dorado et al. 2011). Sampling effects are therefore not likely to impact our conclusions, because with perfect sampling we would expect the proportion of rare generalists to increase and the proportion of rare specialists to decrease, further increasing support for hypothesis 1 (many rare generalists, few abundant specialists) and refuting hypothesis 2 (few rare generalists, many abundant specialists). Additionally, we would not expect sampling artefacts to explain the low proportion of species which were abundant specialists because sampling effects tend to come from missing links for rare species rather
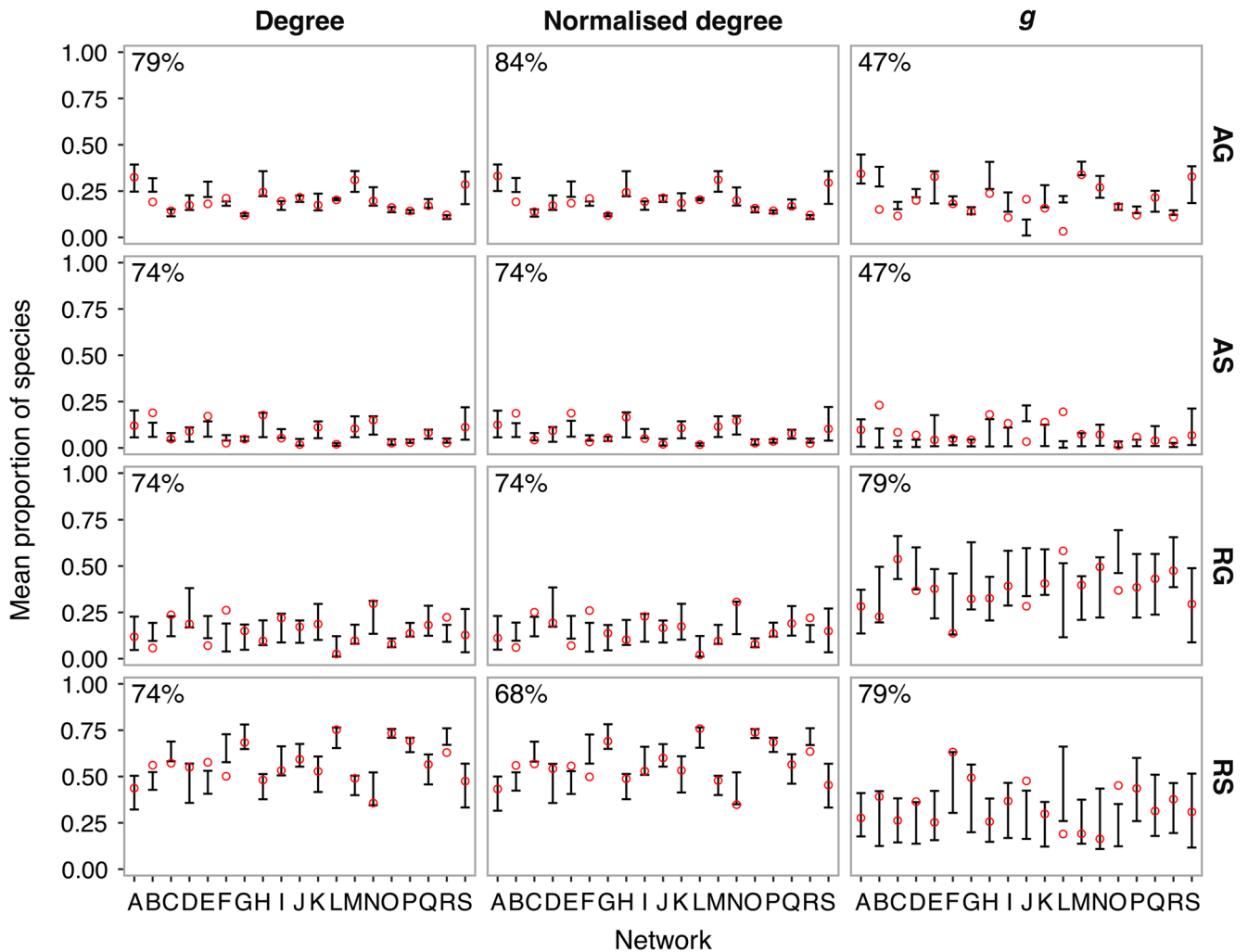
Figure 2. Comparisons between empirical networks (A–S) and null model networks in the proportions of species in each of the abundance–generalisation categories 'RS' (rare specialists), 'RG' (rare generalists), 'AS' (abundant specialists) and 'AG' (abundant generalists). Error bars represent the 95% confidence intervals of the mean proportion of hummingbird species in each abundance–generalisation category as predicted by 1000 null networks. Red circles show the empirically observed mean proportion of hummingbird species in each category. If the red circle is within the error bars, there were no significant differences between the observed proportions and the neutrality null model proportions. Percentages in the top left of each panel give the proportion of networks where empirical proportions were not significantly different from the null model proportions. Results are shown for each network (A–S) and for each generalisation metric (degree, normalised degree, g).

than abundant species (Blüthgen 2010, Dorado et al. 2011, Fort et al. 2016). We also note that we do not consider the phylogenetic dependence of the hummingbird species within communities, which could cause an increase in type I errors. While currently there are not ways to incorporate phylogenetic effects into our novel methodological framework, this is an important area for future research.

A frequent interpretation of the abundance–generalisation relationship is that abundant species are more generalised due to neutral effects; that is, they are more likely to encounter a greater number of interaction partners than less abundant species by chance alone (Vázquez et al. 2007). Our null model analysis supports this interpretation, particularly for degree and normalised degree: we found that the numbers of rare

specialists, abundant specialists, rare generalists and abundant generalists were well predicted for the majority of networks by a null model that assumed interactions were formed entirely from neutral processes. This finding complements other recent studies of plant–hummingbird pollination networks showing the importance of morphological trait matching in predicting pairwise interactions at the network level (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, 2016, Weinstein and Graham 2017), while here we show that abundance predicts broad patterns of generalisation at the species level. Among Antillean hummingbirds, it was recently shown that local environmental conditions and floral richness, not hummingbirds' morphological traits, determined species level nectar-feeding specialization (Dalsgaard et al. 2018).

Combined with our findings, this might suggest a hierarchy of mechanisms structuring plant–hummingbird interactions, and more broadly whole pollination networks (Junker et al. 2013, Bartomeus et al. 2016, Vizentin-Bugoni et al. 2018): neutrality and local conditions govern broad patterns of generalisation, such as the number of plant partners, while morphological matching operates at a lower level to determine the identity of these plant partners. For the generalisation index g, the null model performed less well, predicting the proportion of abundant specialists and abundant generalists correctly in only 47% of networks. For the remaining 53% of networks, the model generally over predicted the number of abundant generalists and under predicted the number of abundant specialists. This may be due the nature of the g index itself: by accounting for the abundance of plants, g does not necessarily correlate with species degree (number of plant partners). For example, a hummingbird which visits one abundant plant could receive a higher value of g than a hummingbird that visits three rare plants. This means the null model may overestimate the number of abundant generalists and underestimate the number of abundant specialists as, in the model, an abundant hummingbird will have a higher probability of interacting with all plants, while in the empirical network it may be able to gain sufficient resources by only interacting with the most abundant plants.

Taken together, our study confirms that abundance is a sufficient, but not necessary, condition for generalisation in plant–hummingbird pollination networks; it is the first study to test this hypothesis in animals using independent data on species abundance encompassing a wide array of communities. Remarkably, our result corroborates the findings of Fort et al. (2016), giving further support that this may be a general phenomenon in mutualistic systems. Further research should investigate whether the relationships found here hold for other types of ecological systems, especially given evidence of the importance of neutral effects in structuring antagonistic host–parasite communities (Vázquez et al. 2005). We also find evidence that neutral effects are good predictors of coarse species-level patterns of generalisation, even in a system in which interactions are widely recognized to be constrained by species traits. This might suggest a hierarchy of mechanisms structuring plant–hummingbird interactions, with neutral effects operating at a 'high level' to determine coarse patterns of generalisation, such as the number of partners, while niche-based processes act at a lower level to determine the identity of these partners.

References

Aizen, M. A. et al. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. – Science 335: 1486–1489.

Alaux, C. et al. 2010. Diet effects on honeybee immunocompetence. – Biol. Lett. 6: 562–565.

Albrecht, M. et al. 2012. Diverse pollinator communities enhance plant reproductive success. – Proc. R. Soc. B 279: 4845–4852.

Bartomeus, I. et al. 2016. A common framework for identifying linkage rules across different types of interactions. – Funct. Ecol. 30: 1894–1903.

Bartoń, K. 2018. MuMIn: multi-model inference. Ver. 1.40.4. – <https://CRAN.R-project.org/package=MuMIn>

Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Batstone, R. T. et al. 2018. Using niche breadth theory to explain generalization in mutualisms. – Ecology 99: 1039–1050.

Bawa, K. S. 1990. Plant–pollinator interactions in tropical rain forests. – Annu. Rev. Ecol. Syst. 21: 399–422.

Behmer, S. T. 2009. Insect herbivore nutrient regulation. – Annu. Rev. Entomol. 54: 165–187.

Biesmeijer, J. C. et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. – Science 313: 351–354.

Bleiweiss, R. 1998. Origin of hummingbird faunas. – Biol. J. Linn. Soc. 65: 77–97.

Blüthgen, N. 2010. Why network analysis is often disconnected from community ecology: a critique and an ecologist's guide. – Basic Appl. Ecol. 11: 185–195.

Blüthgen, N. et al. 2006. Measuring specialization in species interaction networks. – BMC Ecol. 6: 9.

CaraDonna, P. J. et al. 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. – Ecol. Lett. 20: 385–394.

Cribari-Neto, F. and Zeileis, A. 2010. Beta regression in R. – J. Stat. Softw. 34: 1–24.

Dalsgaard, B. et al. 2008. Pollination networks and functional specialization: a test using Lesser Antillean plant–hummingbird assemblages. – Oikos 117: 789–793.

Dalsgaard, B. et al. 2017. Opposed latitudinal patterns of network-derived and dietary specialization in avian plant–frugivore interaction systems. – Ecography 40: 1395–1401.

Dalsgaard, B. et al. 2018. Trait evolution, resource specialization and vulnerability to plant extinctions among antillean hummingbirds. – Proc. R. Soc. B 285: 20172754.

Di Pasquale, G. et al. 2013. Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? – PLoS One 8: e72016.

Dorado, J. et al. 2011. Rareness and specialization in plant–pollinator networks. – Ecology 92: 19–25.

Dormann, C. F. et al. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. – Open Ecol. J. 2: 7–24.

Dormann, C. F. et al. 2017. Identifying causes of patterns in ecological networks: opportunities and limitations. – Annu. Rev. Ecol. Evol. Syst. 48: 559–584.

Dupont, Y. L. et al. 2003. Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. – Ecography 26: 301–310.

Emer, C. et al. 2016. Species roles in plant–pollinator communities are conserved across native and alien ranges. – Divers. Distrib. 22: 841–852.

Fontaine, C. et al. 2008. Generalist foraging of pollinators: diet expansion at high density. – J. Ecol. 96: 1002–1010.

Fort, H. et al. 2016. Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma. – Ecol. Lett. 19: 4–11.

Fox, J. and Weisberg, S. 2002. An R companion to applied regression. – Sage.

Fründ, J. et al. 2016. Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. – Oikos 125: 502–513.

Heithaus, E. R. 1974. The role of plant–pollinator interactions in determining community structure. – Ann. Miss. Bot. Gard. 61: 675–691.

Jordano, P. 2016. Sampling networks of ecological interactions. – Funct. Ecol. 30: 1883–1893.

Junker, R. R. et al. 2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. – Funct. Ecol. 27: 329–341.

Kaiser-Bunbury, C. N. et al. 2017. Ecosystem restoration strengthens pollination network resilience and function. – Nature 542: 223–227.

Martín González, A. M. et al. 2015. The macroecology of phylogenetically structured hummingbird–plant networks. – Global Ecol. Biogeogr. 24: 1212–1224.

Maruyama, P. K. et al. 2014. Morphological and spatio-temporal mismatches shape a neotropical savanna plant–hummingbird network. – Biotropica 46: 740–747.

Maruyama, P. K. et al. 2018. Functional diversity mediates macroecological variation in plant–hummingbird interaction networks. – Global Ecol. Biogeogr. 27: 1186–1199.

Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. – Methods Ecol. Evol. 4: 133–142.

Olesen, J. M. et al. 2008. Temporal dynamics in a pollination network. – Ecology 89: 1573–1582.

Ollerton, J. 2017. Pollinator diversity: distribution, ecological function and conservation. – Annu. Rev. Ecol. Evol. Syst. 48: 353–376.

Poisot, T. et al. 2015. Beyond species: why ecological interaction networks vary through space and time. – Oikos 124: 243–251.

Ratto, F. et al. 2018. Global importance of vertebrate pollinators for plant reproductive success: a meta-analysis. – Front. Ecol. Environ. 16: 82–90.

Rech, A. R. et al. 2016. The macroecology of animal versus wind pollination: ecological factors are more important than historical climate stability. – Plant Ecol. Divers. 9: 253–262.

Simmons, B. I. et al. 2019. Data from: abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.c270ft8>.

Smithson, M. and Verkuilen, J. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. – Psychol. Methods 11: 54–71.

Tasei, J.-N. and Aupinel, P. 2008. Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). – Apidologie 39: 397–409.

Tinoco, B. A. et al. 2017. Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. – Oikos 126: 52–60.

Vaudo, A. D. et al. 2015. Bee nutrition and floral resource restoration. – Curr. Opin. Insect Sci. 10: 133–141.

Vázquez, D. P. and Aizen, M. A. 2003. Null model analyses of specialization in plant–pollinator interactions. – Ecology 84: 2493–2501.

Vázquez, D. P. et al. 2005. Species abundance and the distribution of specialization in host–parasite interaction networks. – J. Anim. Ecol. 74: 946–955.

Vázquez, D. P. et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. – Oikos 116: 1120–1127.

Vázquez, D. P. et al. 2009. Uniting pattern and process in plant–animal mutualistic networks: a review. – Ann. Bot. 103: 1445–1457.

Vizentin-Bugoni, J. et al. 2014. Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. – Proc. R. Soc. B 281: 20132397.

Vizentin-Bugoni, J. et al. 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant–hummingbird network. – J. Anim. Ecol. 85: 262–272.

Vizentin-Bugoni, J. et al. 2018. Plant–pollinator networks in the tropics: a review. – In: Dáttilo, W. and Rico-Gray, V. (eds), Ecological networks in the tropics: an integrative overview of species interactions from some of the most species-rich habitats on earth. Springer, pp. 73–91.

Waser, N. M. et al. 1996. Generalization in pollination systems, and why it matters. – Ecology 77: 1043–1060.

Weinstein, B. G. and Graham, C. H. 2017. Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird–plant interactions. – Ecol. Lett. 20: 326–335.

Yee, T. W. 2015. Vector generalized linear and additive models: with an implementation in R. – Springer.

Yee, T. W. and Wild, C. J. 1996. Vector generalized additive models. – J. R. Stat. Soc. Ser. B 58: 481–493.

Supplementary material (available online as Appendix oik-06104 at <www.oikosjournal.org/appendix/oik-06104>). Appendix 1–2.