Abundance drives generalisation in hummingbird-plant pollination networks

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Abstract

Abundant pollinators are often more generalised than rare pollinators. This could be because abundance drives generalisation: neutral effects suggest that more abundant species will be more generalised simply because they have more chance encounters with potential partners. On the other hand, generalisation could drive abundance, as generalised species could have a competitive advantage over specialists, being able to exploit a wider range of resources and gain a more balanced nutrient intake. 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 hummingbird-plant pollination networks sampled from a variety of locations across the Americas. We find evidence that hummingbirds are generalised because they are abundant, and little evidence that hummingbirds are abundant because they are generalised. Additionally, a null model analysis suggests this pattern is due to neutral processes: most patterns of species-level abundance and generalisation were well explained by a null model that assumed interaction neutrality. These results suggest that neutral processes play a key role in driving broad patterns of generalisation in hummingbird pollinators.

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

Declarations

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Introduction

Pollination and other mutualistic associations are crucial for the functioning and maintenance of most ecological communities (Rech et al. 2016, Ollerton 2017, Ratto et al. 2018). A common phenomenon in mutualistic communities is that more abundant species tend to have more generalised interaction niches, interacting with a greater number of partners than rare species (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' as there are valid *a priori* explanations for both directions (Fort et al. 2016, Dormann et al. 2017). For example, high abundance could lead to high generalisation simply due to neutral effects: more abundant species have a higher likelihood of encountering a greater number of potential interaction partners than rarer species (Vázquez et al. 2007, 2009, Poisot et al. 2015). Additionally, pollinators have been observed to increase their generalisation at high densities, suggesting that generalisation can vary with resource availability (Fontaine et al. 2008). Conversely, high generalisation could lead to high abundance. For example, the wider diet breadth of generalist individuals could be advantageous in communities with high levels of variability or species turnover where flexibility is beneficial (Waser et al. 1996, CaraDonna et al. 2017). 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) and afford functional redundancy that buffers against partner extinction (Biesmeijer et al. 2006), though these benefits are accompanied by lower foraging efficiency (Maldonado et al. 2013).

Here we evaluate the direction of the abundance-generalisation relationship in hummingbird-plant pollination networks and use a null model to assess the extent to which observed patterns of generalisation can be explained by neutral effects. Hummingbird-plant 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) and recent studies suggest that abundance has little influence on network structure compared to morphological trait matching (Maruyama et al. 2014, Vizentin-Bugoni et al. 2014, 2016, Weinstein and Graham 2017, though see Dalsgaard et al. 2018). Additionally, pollination by vertebrates is important for plant reproductive success, especially in the tropics (Vizentin-Bugoni et al. 2018), 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 has hummingbirds could also have important implications for understanding the processes maintaining tropical plant communities. Importantly, while previous attempts to resolve the abundance-generalisation chicken-and-egg dilemma in mutualistic networks have used species' total interaction frequency as a proxy for animal abundance (Fort et al. 2016), which can lead to biased conclusions (Vizentin-Bugoni et al. 2014), here we are able to resolve the abundance-generalisation chicken-and-egg dilemma using independent animal abundance estimates. We find evidence of a unidirectional relationship with abundance driving generalisation. Importantly, a null model assuming neutrality of interactions closely matched most empirical results. This suggests that neutral effects have an important role in structuring broad, species-level patterns of generalisation in hummingbird-plant communities.

Material and Methods

Dataset

We assembled a database of hummingbird-plant 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 or, for network *E*, the frequency the pollen of a plant was found on animals' bodies. The database contained 75 hummingbird species and 283 plant species. For each of these 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 (Appendix 1). If species were not 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 (Vizentin-Bugoni et al. 2014). 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. 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 Appendix 1.

Measures of generalisation

We calculated the level of generalisation of all hummingbird species in all networks. 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). Rather than calculate *g* using d' itself, which uses species' total interaction frequency as a proxy for abundance, we used s' which conceptually is identical to d' but uses independent abundance data rather than total interaction frequency. To ensure that higher values of s' corresponded to higher levels of generalisation, we calculated the standardised generalisation index *g*, defined as $1\text{-}s'/s'_{max}$ where s'_{max} is the maximum possible value of s' (Fort et al. 2016). s' and s'_{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 abundance and generalisation using three linear mixed effects models, one for each generalisation metric. The generalisation metric was the response variable, with log(abundance) as a fixed effect and species and network identity as random effects. A Poisson distribution was used for the model with degree as the response variable, a binomial distribution was used for the model with normalised degree as the response variable (with weights equal to the maximum degree of each species) and a Gaussian distribution was used for the model with *g* as the response variable. Mixed effects models were fitted using the 'lme4' R package (Bates et al. 2015) and the significance of fixed effects was calculated using Wald χ^2 tests available in the 'Anova' function of the 'car' R package (Fox and Weisberg 2002).

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. The 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 bear, it can swim". *P* is made up of two statements: (i) "it is a bear" and (ii) "it can swim". 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 bear that can swim. Outcome B is a non-bear than cannot swim, such as a cactus. Outcome C is a non-bear that can swim, such as a whale. Finally, outcome D is a bear that cannot swim. *P* can only be refuted if we observe outcome D to be true; that is, if we observe a bear that cannot swim. Conversely, observing a swimming bear, a drowning cactus or a swimming whale are all consistent with *P*.

Table 1: Truth table listing all possible outcomes for the proposition "if it is a bear, it can swim". 'T' is 'True' and 'F' is 'FALSE'.

Outcome	Bear	Swim
A	T	T
B	F	F
C	F	T
D	T	F

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. We can therefore derive two hypotheses:

1. If abundance implies generalisation, there should be no species which are abundant and specialist (bears that cannot swim); we would only expect to observe abundant generalists (bears that can swim), rare generalists (whales that can swim) and rare specialists (cacti that cannot swim).
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 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 abundance and generalisation is unidirectional (Fort et al. 2016). Here we focus on hummingbird species, rather than plants, as plants may have non-hummingbird mutualistic partners not included in our data that could result in misleading estimates of generalisation (Dalsgaard et al. 2008).

Abundance and generalisation classification

To calculate the proportion of 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 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). These values represented the probability

with which a species would be classified as abundant or generalist. Next, we sampled a random value between 0 and 1. If a species' rescaled abundance or generalisation was greater than or equal to this value, it was classified as abundant or generalist, respectively. If it was less than this value, it was classified as rare or specialist, respectively. This was repeated 1000 times, resulting in an ensemble of classifications where species with higher abundance and generalisation were classified as abundant and generalist, respectively, in a higher proportion of permutations than species with lower abundance and generalisation. For example, a species with a rescaled abundance of 0.2 would, on average, be classified as abundant in 20% of simulations because 0.2 would only be greater than the randomly chosen value in ~20% of iterations. Similarly, a species with a rescaled abundance of 0.8 would be classified as abundant in 80% of simulations as 0.8 would, on average, be greater than the randomly chosen value in ~80% of iterations. The species with the maximum abundance or generalisation in a given network were always classified as abundant or generalist, respectively, while those with the minimum abundance or generalisation were always classified as rare or specialist, respectively. The mean proportion of species in each of the four abundance-generalisation categories was then calculated. This was repeated for each of the three generalisation metrics.

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, **M**, where element m_{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.

Results

We first confirmed the positive relationship between abundance and generalisation in our dataset, finding a significantly positive correlation between abundance and generalisation for degree (Wald test: $\chi^2 = 217.9$; df = 1; $P = < 0.001$; $R^2_{GLMM(m)} = 0.55$; $R^2_{GLMM(c)} = 0.79$), normalised degree (Wald test: $\chi^2 = 234.4$; df = 1; $P = < 0.001$; $R^2_{GLMM(m)} = 0.26$; $R^2_{GLMM(c)} = 0.37$) and the generalisation index g (Wald test: $\chi^2 = 10.7$; df = 1; $P = 0.001$; $R^2_{LMM(m)} = 0.06$; $R^2_{LMM(c)} = 0.44$). $R^2_{(G)LMM(m)}$ is the marginal R^2 which represents the variance explained by fixed effects; $R^2_{(G)LMM(c)}$ is the conditional R^2 which represents the variance explained by both fixed and random effects (Emer et al. 2016, Kaiser-Bunbury et al. 2017, Bartoń 2018).

Only a small proportion of species were abundant and specialist for all three generalisation metrics (Figure 1). Conversely, the proportion of species that were rare and generalist was

consistently larger, particularly for the *g* generalisation metric. These differences were significant: the proportion of species that were rare and generalist was significantly higher than the proportion which were abundant and specialist for degree (t = 2.91, df = 18, p = 0.009), normalised degree (t = 2.91, df = 18, p = 0.009) and *g* (t = 10.34, df = 18, p = < 0.001) (Figure 1). Overall, these findings support hypothesis 1, that abundance drives generalisation, and do not support hypothesis 2, that generalisation drives abundance.

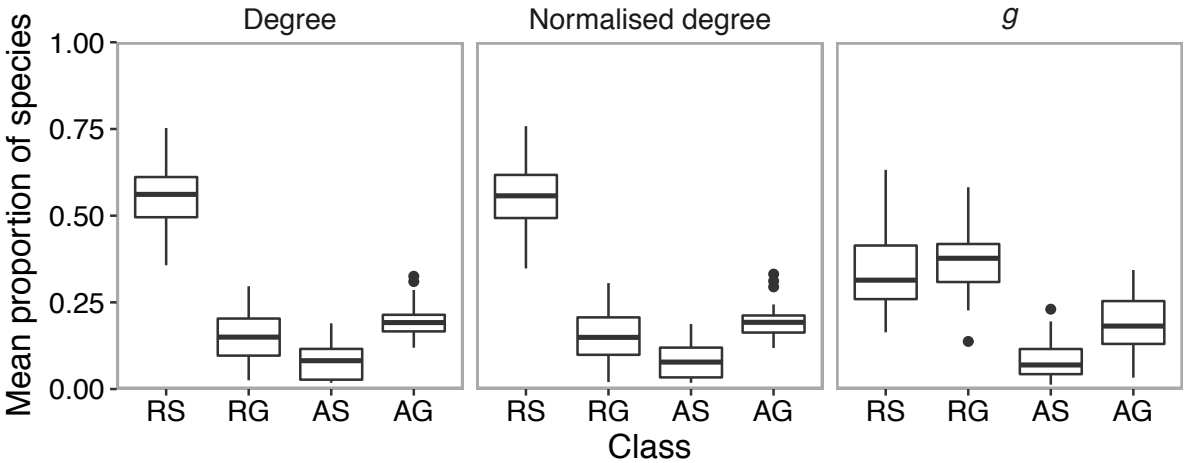

Figure 1: The mean proportion of hummingbird species classified as rare specialists ('RS'), rare generalists ('RG'), abundant specialists ('AS') and abundant generalists ('AG') across all networks, for three generalisation metrics: degree, normalised degree and *g*. The bold centre line in each box is the mean; 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.

The proportion of species in each of the four abundance-generalisation categories predicted by the 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; Figure 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 (Figure 2).

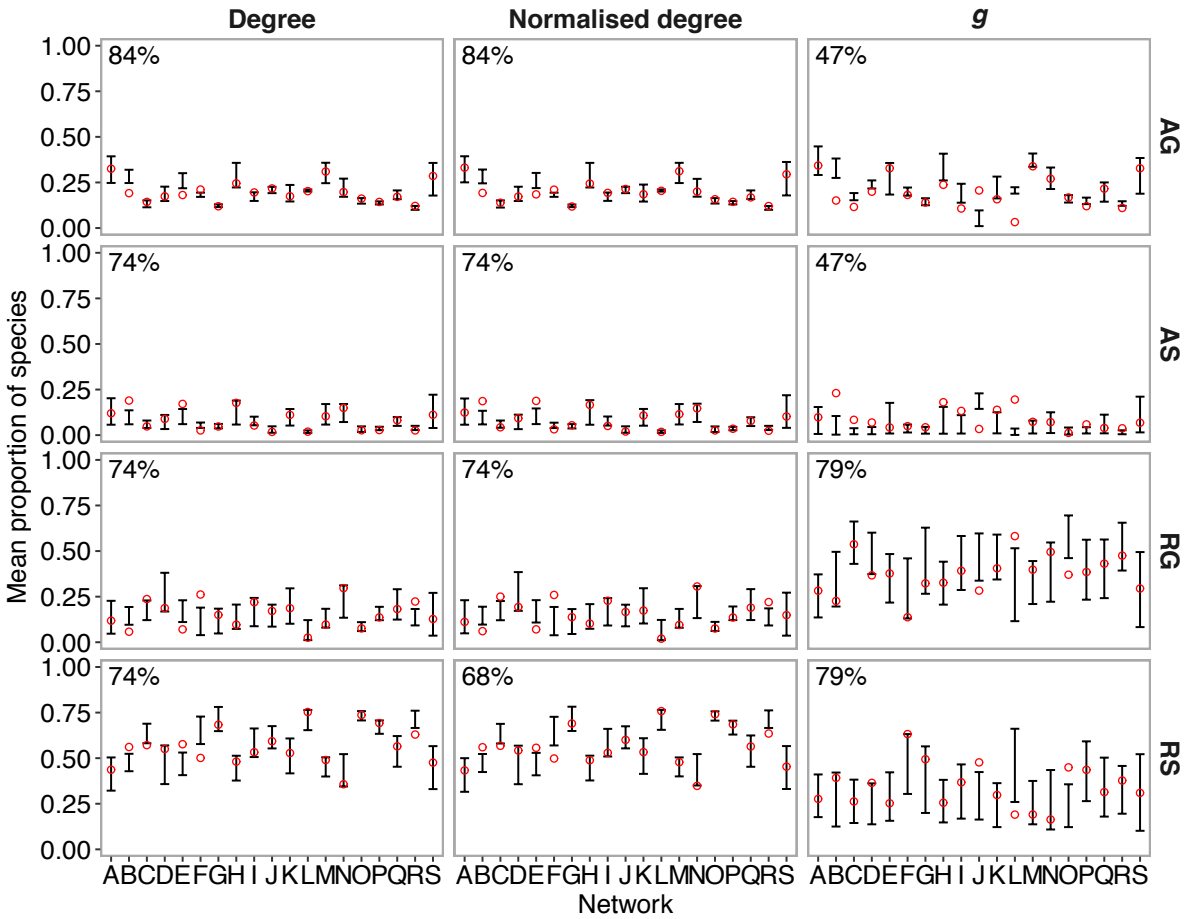

Figure 2: Comparisons between empirical networks (A-S) and null model networks in the proportions of species in each of the abundance-generalisation categories 'RS' (rare specialists), 'RG' (rare generalists), 'AS' (abundant specialists) and 'AG' (abundant generalists). Error bars represent the 95% confidence 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 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*).

Discussion

Hummingbird-plant communities across the Americas support the hypothesis that abundance drives generalisation, and provide little evidence that generalisation drives abundance. These results can be 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*. For example, sitting the exam is a *necessary* condition for getting an A grade. If a student does not sit the exam, they will not get an A grade. Similarly, if a student is awarded an A grade, they sat the exam. However, if *P* is a *sufficient* condition for *Q*, then if we have *P*, *Q* must follow. For example, obtaining full marks on every exam question is a *sufficient* condition for getting an A grade in the exam. Therefore, if a student gets full marks on every question, they will get an A grade. However, getting full marks on every question is not a *necessary*

condition for getting an A grade: it is possible to get an A without achieving full marks on all questions. Similarly, sitting the exam is not a *sufficient* condition for getting an A grade: it is possible to sit the exam and not get an A. 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), suggesting that abundance driving generalisation is 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 structure of species interaction networks (Jordano 2016, Vizentin-Bugoni et al. 2016, Dalsgaard et al. 2017). However, sampling is likely to result in missed detections of rarer species and interactions, resulting in an underestimation of both the number of rare species and their level of generalisation. It is for this reason that sampling rare species with high generalisation was described as "impossible" (Dormann et al. 2017). 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. 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 of rare species to be underestimated. Consequently, some species classified as rare specialists may actually be rare generalists. Therefore under 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. Sampling effects are therefore not likely to impact our conclusions.

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 hummingbird-plant communities 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 coarse 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, this might suggest a hierarchy of mechanisms structuring hummingbird-plant communities, 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 *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. 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 across Americas. Remarkably, our result corroborates the findings of Fort et al. (2016), giving further support that this may be a general phenomenon in mutualistic systems. 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. Further research should investigate whether the relationships found here hold for other types of systems.

Data accessibility

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

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