Title: Many bee species, including rare species, are important for function of entire plant-pollinator networks

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Abstract

It is important to understand how biodiversity, including that of rare species, affects ecosystem function. Here we consider this question with regard to pollination. Studies of pollination function have typically focused on pollination of single plant species, or average pollination across plants, and typically find that pollination depends on a few common species. Here, we used data from 11 plant-bee visitation networks in New Jersey, USA, to ask whether the number of functionally important bee species changes as we consider function separately for each plant species in increasingly diverse plant communities. Using rarefaction analysis, we found the number of important bee species increased with the number of plant species. Overall, 2.5 to 7.6 times more bee species were important at the community scale, relative to the average plant species in the same community. This effect did not asymptote in any of our datasets, suggesting that even greater bee biodiversity is needed in real world systems. Lastly, on average across plant communities, 24% of bee species that were important at the community scale were also numerically rare within their network, making this study is one of the strongest empirical demonstrations to date of the functional importance of rare species.

Keywords: biodiversity; ecosystem function; mutualism; bipartite networks; pollination; rare species

36 **Main Text**

37 **Introduction**

38 Given the rapid loss of global biodiversity [1], it is imperative to understand how decreased
39 biodiversity will affect functioning of natural systems [2]. In particular, ecologists need to
40 understand the role of rare species in ecosystem function, given that rare species are at highest
41 risk of extinction and are the primary focus of conservation [3].

42 Ecologists' understanding of biodiversity-ecosystem function (BEF) relationships has evolved as
43 studies have increasingly resembled natural systems. In experiments, which often focus on single
44 functions within one trophic level, greater biodiversity (specifically, species richness) increases
45 ecosystem function, but function is often maximized at relatively low richness or is driven by
46 high-functioning, dominant species [4–7]. Further work on BEF relationships, however, has
47 highlighted nuance that comes from real-world complexity. In particular, BEF relationships can
48 be mediated by spatiotemporal scale [8–10], the number of functions being considered (i.e.,
49 multifunctionality) [11–13], trophic interactions [14–17], and facilitation, including plant-soil
50 feedbacks [18–21]. In these contexts, diversity effects often appear stronger than in simplified
51 experiments (e.g. [8,11]), though this is not always the case [22–25].

52 An important consequence of studying BEF for a single function, place or time is that these
53 narrow lenses can obscure the functional roles of rare species. Often, common species appear to
54 provide most of the function while rare species appear to contribute relatively little [23,26–29].
55 This is even true in natural systems; for example, regional-scale analyses show 1% of
56 Amazonian tree species store 50% of the carbon [30], and 2% of bee species provide 80% of
57 crop pollination [31]. However, these examples focus only on carbon storage while omitting

myriad other ecosystem processes, or only on crop pollination, while omitting the pollination of diverse, wild plant communities.

Considering the many dimensions of natural systems has revealed some ways that rare species can be important to ecosystem functioning. For example, rare species can contribute disproportionately to functional trait diversity [32–34], which may facilitate multifunctionality [35,36] or maintain function across variable environments [37–39]. Additionally, rare species can contribute disproportionately to invasion resistance and food web stability [40–43]. All of these examples suggest that the (observed) importance of rare species can depend on which function(s) are measured and at which scale(s). Thus, it is important that BEF relationships be studied in their most relevant, real-world contexts.

Animal-mediated pollination is used by ~88% of plant species [44] and is one of the model systems for BEF research [2], but the study of plant communities in this context has been limited [45]. Most studies quantifying function within plant-pollinator networks have been simplified to either focus narrowly on the pollination of a single plant species (typically of a crop monoculture, e.g. [31,46,47]), or focus coarsely on average pollination across plant species (e.g. [48]). In nature, however, even in one time and place, pollination must be provided to many species simultaneously. Similarly, plant-pollinator interaction networks have been well-studied in ecological contexts (e.g., with respect to community stability or species interactions [49–52]), but network-level data have rarely been used in a BEF context. The relationship between network structure and ecosystem function has been explored theoretically [45,53], but empirical studies are rare (see [6,54]), especially in natural communities. Thus, despite the attention paid to plant-pollinator networks broadly, the simple question of how many pollinator species are needed to pollinate natural plant communities has yet to be addressed.

The number of pollinator species needed to pollinate a plant community will depend on the extent of differences among pollinator species in the plant species they visit (i.e. functional redundancy versus complementarity) (Figure 1). On the one hand, most plant-pollinator networks exhibit some degree of nestedness, such that rare or specialist pollinators tend to interact with abundant, generalist plant species (and vice versa) [55,56]. The more nested a network is, the more redundant pollinator species will tend to be, because a few abundant generalists will dominate pollination across plant species (Figure 1b,d). On the other hand, networks are not perfectly nested and some degree of functional complementarity among pollinators is also common [57]. The more complementary pollinator species are in their plant use, the greater need there will be for pollinator diversity at the scale of the entire network (Figure 1c,d) [53].

Complementarity within plant-pollinator networks can also create a functional role for pollinator species that are rare within their network. Pollination of a single plant species, at least in one time and place, tends to be dominated by a few abundant pollinator species, while locally rare species contribute relatively little [58,59] (but see [60]). The situation might be very different, however, when function is considered for each species in a plant community. For example, a pollinator species that is rare within the community could still be an important pollinator of a particular plant species if it is among the most frequent visitors to that plant (Figure 1c). In this situation, locally rare pollinator species could still be important for pollination of the entire plant community, but this effect would be missed in studies in which function is measured for only a single plant species or is averaged across plant species.

Here, we use data from 11 plant-bee networks to ask how many pollinator species are needed to pollinate all of the plants in each network. To control for sampling effects and distinguish effects

of stochasticity from those of complementarity among bee species, we used a randomization-based null model. Specifically, we ask 1) *What is the relationship between the number of plant species in a network and the number of bee species important for pollinating them?* And 2) *How important are rare bee species to pollination?*

Methods

Network data

We used 11 quantitative plant-bee network datasets collected by our lab in New Jersey, USA [61–63] (Text S1; Figure S1; Table S1). Each dataset quantifies bee visitation to each species of a plant community, as observed in a single site in a single year. We chose datasets collected in one site and year so that differences in plant use by bees could not be driven by spatial or annual turnover in the bee community. Ten of these datasets were collected in natural or semi-natural meadows, while one was a planted field experiment in which each plant species was maintained at equal abundance.

Most of these networks include plant species on which few individual bees were observed. To limit our analyses to plant species for which we could be relatively confident of the visiting bee community, we excluded plant species with fewer than 20 observed plant-bee interactions (Tables S1-S3). This meant excluding a mean of 54% of plant species (range = 0 – 83% across networks), but only 8.0% of bee species (range = 0 – 33%) and 9.5% of individual plant-bee interactions (range = 0 – 27%). For the 11 datasets as analyzed, plant species richness varied from 6 to 23, bee species richness varied from 22 to 86, and total individual plant-bee interactions varied from 227 to 4513. In total, the analyzed datasets included 70 plant species and

173 bee species, with 20943 total observed interactions, and 1479 unique species-species pairs across networks.

Analysis

To start, we identified the most functionally important bee species for each plant species within each network. We used interaction frequency (i.e., the number of individual bees of a species that were collected from a given plant species) as a proxy for function, and defined 'functionally important' bee species as those that contributed a threshold percent of visits to at least one plant species in their network [31]. We focus on results based on using a 5% threshold (as used by Kleijn *et al.* 2015) but, to test the sensitivity of our results to our choice in threshold, we repeat the analyses across thresholds from 2.5% to 10% (see Texts S2-S3 and Figures S2-S3 for further discussion). Although visitation frequency can be an incomplete proxy for pollination function, we believe it is adequate in this case. Technically, a pollinator's contribution to function also depends also on their effectiveness (per-visit pollen deposition) and efficiency (essentially the 'quality' of pollination), and there are examples of frequent insect visitors being poor pollinators [64,65]. However, plants' most frequent floral visitors are typically their most important pollinators, and this relationship is especially pronounced for bees, which are the focus of this study [31,64,66]. Also, on a practical level, it would not have been possible to measure per-visit function for the 1496 unique plant-pollinator interactions in our data sets. Lastly, although plants and bees are mutually dependent, we chose to focus on the role of bee diversity in providing pollination, rather than the role of plant diversity in supporting bees. This was in part to expand on existing biodiversity-ecosystem function literature [2], and also because it is more appropriate given our data, which represent the bees that visit a given plant community.

What is the relationship between the number of plant species in a network and the number of bee species important for pollinating them?

Within networks, we performed rarefaction to relate the number of important bee species to plant species richness. More specifically, we subset the observations in each network to generate plant communities of varying richness and counted the number of bee species important to at least one plant species in that set. Thus, just as site-based rarefaction measures the accumulation of new species with additional sites, we measured the accumulation of important bee species with additional plant species. We included every possible level of richness for the network (i.e from 1 to *n* species) and up to 1000 unique (and random) combinations of plant species per richness level. In instances in which there were ≤ 1000 combinations of plant species, we included all possible combinations. We then took the mean number of important bees across combinations of plant identity for each level of plant richness.

We represent results from this analysis as accumulation curves in which the mean number of bee species important to at least one plant species is plotted against the number of plant species in the community (sensu [8,9,67,68]; Figure 1d). Greater complementarity among bee species should result in lower values for single plant species (indicating higher specialization by bees at the plant species level) and/or steeper slopes (indicating greater turnover of important bee species among plants).

The slopes observed in these curves will also be due, at least in part, to stochasticity. That is, even if there were no biological differences among bee species in terms of the plants they visit, they will visit plant species at different frequencies due to chance (i.e. sampling error) [51].

Similarly, we will observe differences in visitation rates due to human sampling error. As a result, any observed complementarity effect should be a combination of biology and stochasticity. To account for these stochastic effects, we created a randomization-based null model to define an expectation under a scenario of no biological complementarity. This null model assumes that there are no underlying differences among bee species, but rather that individual bees forage randomly across all the plant species in their network.

To generate the null expectation, we maintained the total number of observations of each plant species, but assigned interactions by random draw (with replacement) from the network-wide bee-species abundance distribution. Said another way, the model maintained the empirical number of bee visits to each plant species (row sums of the plant-bee matrix), but resampled individual bee interactions with probabilities proportional to each bee species' relative abundance (column sums). We generated 999 null datasets per network [69] and then, for each of these datasets, we estimated the mean number of important bee species for each level of plant species richness.

In the Results, we report three metrics for each network. First, we calculate the change in the number of important bee species recorded for the average single plant species versus for the entire network (i.e., all plant species). This metric shows how the need for bee diversity increases with the number of plant species considered, when both the stochastic and the biological components of that increase are included. Second, we compare the observed number of important bee species to the inner 95th percentile of what was predicted by the null model. Observed values beyond the inner 95th percentile were considered significantly different than what would be expected under random foraging, suggesting that biological effects increase the functional complementarity among bee species and contribute to the need for biodiversity. Third,

192 we calculate a standardized effect size (a Z-score) for each network that represents the magnitude
193 of any non-stochastic (i.e., biological) effects on the number of important bee species in that
194 network. Z-scores were calculated as the difference between the observed value and the null
195 prediction, divided by the standard deviation of the null (i.e. (observed – null)/sd_{null}), where all
196 three values are calculated at maximum plant species richness (i.e., using all the plant species in
197 the network). Thus, the Z-scores measure the strength of biological effects, such as niche
198 partitioning and bee specialization, in driving the need for bee diversity, and express this effect
199 in units of standard deviations of the null distribution.

200 Lastly, because our 11 networks varied in the number of plant species they contained, we also
201 examined the role of plant species richness across (rather than within) networks. Specifically, we
202 looked at Pearson's correlation between the number of plant species in a network and each of the
203 measures above, as well as simply the total number of bee species that were important to at least
204 one plant species in that network.

205 *How important are rare bee species to pollination?*

206 Here, we measured how many important bee species (i.e. functionally important to at least one
207 plant species) in each network were also rare within that network. While rarity can be defined in
208 many ways (e.g. [70,71]), we focus simply on local rarity – i.e. species with low relative
209 abundance – which is how rarity has been typically considered in the BEF literature (e.g.
210 [36,42]). This means we do not treat rarity as an intrinsic trait of a species; by our definition, a
211 species could be rare in one community and common in another. In the main text, we focus on an
212 analysis in which rarity was defined as any bee species representing < 1% of all bee observations
213 in its network (sensu [72,73]). However, because any definition of rarity is arbitrary, we also

repeat the analysis across rarity thresholds of 0.5% to 1.5%. Finally, because rare species may occasionally appear important just due to sampling effects, we use our null model to compare our observed results to the null expectation under random foraging.

Results

What is the relationship between the number of plant species in a network and the number of bee species important for pollinating them?

Within networks, the number of functionally important bee species increased rapidly with plant species richness (Figures 2, S4). Comparing the average single plant species with their respective communities (i.e., comparing the starting and ending points of the accumulation curves), the number of important bee species increased 2.5 to 7.6-fold (Figure 2a). The accumulation curves of functionally important species were mostly non-saturating and rose beyond the inner 95th percentile of the null in all but two of the smallest networks (Figures 2a-b, S5). Z-scores, which measure the effect of complementarity on the number of important bee species relative to the expectation under random foraging, ranged from 1.1 to 12.2 (Figure 2c).

Across networks, these results were each associated with plant species richness (Figure 2). There was a strong correlation between the total number of plant species in a network and i) the observed number of important bee species in that network ($r = 0.92$, $p < 0.001$), ii) the factor increases in the number of important bee species, relative to a single plant species ($r = 0.95$, $p < 0.001$), and iii) the Z-score ($r = 0.95$, $p < 0.001$). These results were also robust to our choice of threshold for defining functional importance. While the absolute number of important bee species decreased under a higher, less inclusive threshold, the factor-differences between single

plant species and their respective communities, and the associated Z-scores (i.e. the relative effect sizes), actually increased under higher thresholds (Text S3; Figure S5, S6).

How important are rare bee species to pollination?

Of the bee species that are functionally important to at least one plant species in a given network, a mean of 25% (range = 0-52%) were rare within that network (Figures 3, S7, S8). More rare bees were important in more plant-rich networks ($r = 0.97$, $p < 0.001$), and this number was significantly greater than the null expectation in all but the smallest networks. As would have to be the case, the proportion of important bee species that are rare decreases with more conservative thresholds (higher thresholds for importance, and lower thresholds for rarity) (Figures S9, S10). Even with the most conservative combination of thresholds, though, a mean of 7.8% and as many as 25.0% of the important bee species were rare within their network.

Discussion

By focusing on the pollination of individual plant species rather than plant communities, ecologists have likely underestimated the importance of pollinator diversity to pollination function in nature. Here, we show that the number of functionally important bee species increases rapidly as we expand from considering one to many plant species (Figure 2). Up to seven times more bee species made important contributions at the community scale, as compared with any single plant species. The number of important bee species increased with the number of plant species in a community and did not asymptote in any of our datasets (Figure 2), suggesting that even more bees are important in nature. This increased role of biodiversity results from complementary floral use among bee species. Complementarity in resource use among species is a well-known mechanism through which biodiversity increases ecosystem function in

experiments [74], yet the primary way species partition resources within a mutualist network – partitioning the partners with which they interact – is invisible when function is measured for only a single partner species or averaged across species. Thus, it has largely been overlooked up to now.

Perhaps our most striking finding is that, when the whole plant community was considered, rare bee species were frequently important to function. Regardless of the exact thresholds we used to define importance and rarity, a substantial portion of the functionally important bee species in our analyses were also rare within their community (means of 8-45%, across thresholds; Figures 3, S10). This result extends previous work that has suggested rare species could be important, but measured their functional role less directly. For example, rare species have been valued because they contribute to functional trait diversity [32,33,75] and because they could become abundant, and thus functionally important, at other places or times (i.e. insurance effects) [10,37,38]. In contrast, we demonstrated a direct and immediate contribution of locally rare species. This contribution did not depend on rare species making disproportionately large contributions to function (i.e. keystone effects [76,77]), which is another commonly cited way for rare species to be important. Instead, we found rare bees to be important because they filled distinct functional roles [35,77], in this case pollinating different plant species. Mechanistically, our approach of considering the pollination of many plant species is akin to measuring multiple ecosystem functions (i.e. 'multifunctionality'), where it has likewise been found that locally rare species can provide functions not provided by other, more common species [35]. Both types of findings suggest that many more species are important to ecosystem function in complex natural communities, where the number of plant species and ecosystem functions greatly exceed what can be measured by researchers.

Floral specialization by pollinators is a well-described phenomenon [57,78], and so it may seem obvious that more plant species would require more pollinator species. Findings from network ecology, however, might predict the opposite. In particular, because plant-pollinator networks are typically nested [55,56], one might expect that abundant generalist pollinators would be responsible for most of the pollination across plant species, with rare or specialist species being largely redundant (Figure 1b,d). Indeed, abundant bees in our study did provide more flower visits than rare bees (by definition), and so did have higher average contributions and were important to more plant species (Figure S8). Yet, if we were to only consider bee species' average contributions across plant species, we would be ignoring the needs of those plant species that were visited primarily by less abundant bees (Figure S8). Our contribution in this paper is to consider the pollinators needed by the whole plant community, rather than just single plant species or the average plant species, and thereby to reveal the important role played by bee species that are rare at the community scale.

The extent to which our results extend to mutualist systems other than pollination networks likely depends on the extent of complementarity in those systems. Pollination networks tend to be relatively specialized (i.e. high complementarity). Other systems with similarly high levels of specialization (e.g., ant-myrmecophyte networks) might behave similarly, while the importance of partner-species diversity may be lower in systems with relatively low specialization (e.g. seed-dispersal networks) [57]. There is also already evidence that interaction complementarity in plant-mycorrhizal networks lends an effect of fungal diversity on plant growth [20]. Thus, our study is neither the first nor final word, but is further evidence that we should consider biodiversity-ecosystem function relationships in the context of real-world interaction networks.

Because our study was observational, we cannot know what would happen if particular bee species were lost from our networks. In particular, we do not know the pollen limitation status of the plants in our networks, which means we cannot predict how their reproduction would be impacted by some level of pollinator loss. Nor can we predict how the network might restructure after species loss. On the one hand, even a plant that is not currently pollen limited could become so following loss of a dominant pollinator. On the other hand, pollinator species' preferences are often dynamic [79,80], which should lend resilience to species loss [81]. That is, following the loss of a plant's dominant pollinator species, other pollinators might shift or expand their diets, which could compensate for the loss [82]. However, increased pollinator generalization following the loss of a competitor can also decrease pollination quality due to increased interspecific pollen transfer [79,83,84]. Future research should work to determine which of these processes are dominant in determining pollination function (i.e. plant reproductive success) in the face of species loss. More broadly, understanding function within mutualistic networks will require understanding the extent to which interactions are fixed or plastic, and whether changes to network structure following species loss affect function for the remaining species.

Altogether, our results highlight the many dimensions of ecosystem function, and the importance of considering real-world complexity for understanding biodiversity-ecosystem function relationships in nature. In particular, mechanisms governing BEF relationships in nature may be invisible in small-scale or simplified study systems [16,85]. As a result, studying function at too small a scale or in too simple a system may lead us to underestimate the number of species needed for function in nature. For instance, despite positive biodiversity effects [46,74,86], function at local scales often relies on relatively few species because of dominance [4,7,23,29]. Yet, because of species turnover, far more species are needed to maintain function across broader

spatiotemporal scales [8,10,37,87,88]. Similarly, more species are needed to maintain multiple functions simultaneously than for any function alone because of functional complementarity [9,13,89,90]. Here, we demonstrate an analogous role of biodiversity in mutualist networks: even for a single function in a single place and time, many more species are needed to maintain function across a network than for any one partner species alone. Real-world ecosystems depend on many functions operating across broad spatiotemporal scales [85] and, like pollination, many of these functions are realized through mutualist interactions [91]. In light of this, our results suggest that biodiversity may be even more important for real-world function than previously supposed.

Data and code: The analysis in this paper uses 11 plant-bee network datasets collected by our lab group. For convenience, these data, along with code to reproduce our analysis and figures, are included here as supplemental material. Any use of these data, however, should cite the original papers.

Author contributions: DTS and RW conceived of study in collaboration with LW and MG. DTS developed and performed analyses. DTS drafted the manuscript with input from RW, and all authors contributed to revision. MR and MM contributed data.

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578

579 **Figure legends**

580 **Figure 1** Hypothetical pollinator abundance distributions illustrating how complementarity
581 among pollinator species should affect the number of functionally important species. (a) The
582 abundance of pollinators visiting the entire plant community. The two most abundant pollinators
583 contribute 80% of floral visits. (b) In a community with low complementarity, the same
584 generalist pollinator species dominate function for every plant species. (c) In a plant community
585 with high complementarity, different pollinator species dominate visits to different plant species.
586 (d) If pollinator species are perfectly redundant (as in b), the number of important pollinator

587 species would not change with the number of plant species. If pollinator species are perfectly
588 complementary (similar to c), there would be a positive linear relationship between the number
589 of plants and important pollinators. The real world is likely in between, leading to a positive but
590 saturating relationship.

591 **Figure 2** The number of important pollinator species increases with the number of plant species.
592 (a) Accumulation curves for each of the 11 networks. Points represent the number of pollinator
593 species important to at least one plant species in the full community, and lines represent the
594 accumulation of important pollinator species across levels of plant species richness (i.e., means
595 of rarefied plant communities) where the left end represents the average single plant species, and
596 the right end represents the full plant community. (b) An example of one network's accumulation
597 curve, now shown together with its null model and 95% CIs. The null model curve represents the
598 expectation if individual pollinators forage randomly across the available plant species, while the
599 observed curve includes biological effects, such as species-specific preferences, morphology, or
600 phenology that lead to non-random foraging. (c) Z-scores for each network, representing the
601 strength of the biological effects (complementarity) on the number of pollinator species found to
602 be functionally important in a network, relative to the expectation under random foraging. Z-
603 scores were calculated as the difference between observed and null expectation (red bar in b)
604 divided by the standard deviation of the null (blue bar in b) at maximum plant richness for each
605 network (i.e. at the endpoints of the curves in a and b). In (a) and (c), the blue line and points
606 represent the experimental garden.

607 **Figure 3** Many rare species are functionally important as pollinators. (a) Pollinator rank
608 abundance distribution for a single network, with pollinator species that were important to at
609 least one plant species highlighted in red. The dotted line represents 1% of total pollinator

abundance in the network, which is our definition of rarity. In this community, 13 of 25 important pollinator species are rare. Similar plots for the rest of our communities can be found in the supplement (Figure S7). (b) The proportion of important species that were rare correlated with the number of plant species included in the analysis ($r = 0.95$, $p < 0.001$). When datasets were large enough to include more plant species, more rare pollinator species were found to be important. This increase was only weakly reflected in the null model. The network shown in (a) is circled in red.

Figure 1

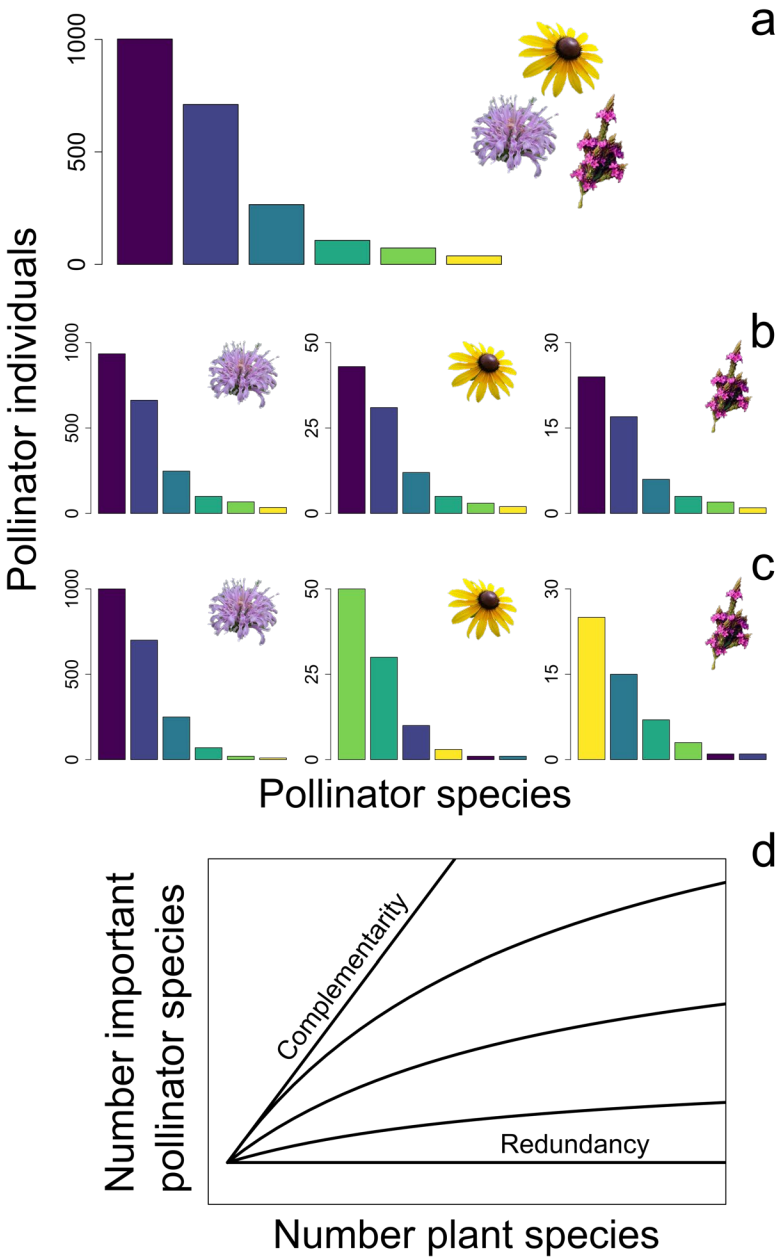
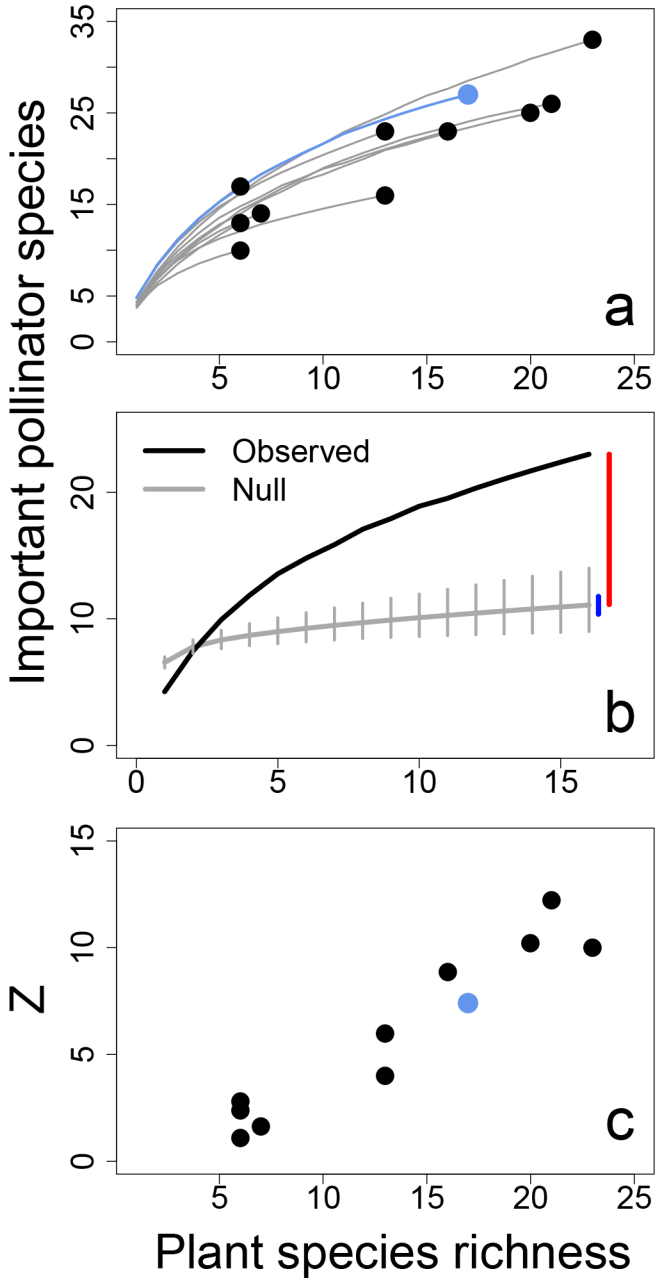
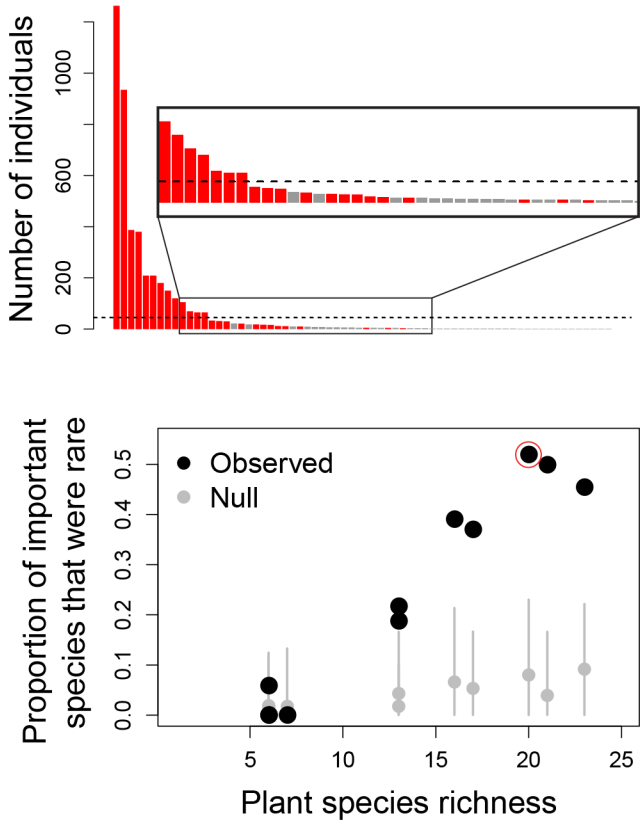

a
b
c
d
Pollinator individuals
Pollinator species
Number important pollinator species
Number plant species
Complementarity
Redundancy
0
500
1000
25
50
15
30

Figure 2


Important pollinator species
Plant species richness
Z
a
b
c
Observed
Null
0
5
10
15
20
25
35

623 **Figure 3**


Number of individuals
0
200
600
1000
Proportion of important species that were rare
0.0
0.1
0.2
0.3
0.4
0.5
Observed
Null
5
10
15
20
25
Plant species richness