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20 Abstract

It is important to understand how biodiversity, including that of rare species, affects ecosystem 21 22 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 23 across plant species, and typically find that pollination depends on a few common species. Here, 24 we used data from 11 plant-bee visitation networks in New Jersey, USA, to ask whether the 25 26 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 27 found the number of important bee species increased with the number of plant species. Overall, 28 2.5 to 7.6 times more bee species were important at the community scale, relative to the average 29 30 plant species in the same community. This effect did not asymptote in any of our datasets, suggesting that even greater bee diversity is needed in real world systems. Lastly, on average 31 32 across plant communities, 25% of bee species that were important at the community scale were 33 also numerically rare within their network, making this study one of the strongest empirical demonstrations to date of the functional importance of rare species. 34

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

37

38 <u>Main Text</u>

39 Introduction

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

Ecologists' understanding of biodiversity-ecosystem function (BEF) relationships has evolved as 44 study systems have increasingly resembled natural systems. In experiments, which often focus 45 on single functions within one trophic level, greater biodiversity (specifically, species richness) 46 47 increases ecosystem function, but function is often maximized at relatively low richness or is driven by high-functioning, dominant species [4–7]. Further work on BEF relationships, 48 however, has highlighted nuance that comes from real-world complexity. In particular, BEF 49 50 relationships can be mediated by spatiotemporal scale [8–10], the number of functions being considered (i.e., multifunctionality) [11–13], trophic interactions [14–17], and facilitation, 51 including plant-soil feedbacks [18–21]. In these contexts, diversity effects often appear stronger 52 than in simplified experiments (e.g. [8,11]), though this is not always the case [22–25]. 53

An important consequence of studying BEF for a single function, place or time is that these narrow lenses can obscure the functional roles of rare species. Often, common species appear to provide most of the function while rare species appear to contribute relatively little [23,26–29]. This is even true in natural systems; for example, regional-scale analyses show 1% of Amazonian tree species store 50% of the carbon [30], and 2% of bee species provide 80% of 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 ofdiverse, wild plant communities.

Considering the many dimensions of natural systems has revealed some ways that rare species 62 can be important to ecosystem functioning. For example, rare species can contribute 63 disproportionately to functional trait diversity [32–34], which may facilitate multifunctionality 64 [35,36] or maintain function across variable environments [37–39]. Additionally, rare species 65 can contribute disproportionately to invasion resistance and food web stability [40–43]. All of 66 67 these examples suggest that the (observed) importance of rare species can depend on which 68 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. 69

70 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 71 [45]. Most studies quantifying function within plant-pollinator networks have been simplified to 72 either focus narrowly on the pollination of a single plant species (typically of a crop 73 monoculture, e.g. [31,46,47]), or focus coarsely on average pollination across plant species (e.g. 74 [48]). In nature, however, even in one time and place, pollination must be provided to many 75 species simultaneously. Similarly, plant-pollinator interaction networks have been well-studied 76 in ecological contexts (e.g., with respect to community stability or species interactions [49–52]), 77 78 but network-level data have rarely been used in a BEF context. The relationship between 79 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 80 81 plant-pollinator networks broadly, the simple question of how many pollinator species are needed to pollinate natural plant communities has yet to be addressed. 82

The number of pollinator species needed to pollinate a plant community will depend on the 83 extent of differences among pollinator species in the plant species they visit (i.e., functional 84 redundancy versus complementarity) (Figure 1). On the one hand, most plant-pollinator 85 networks exhibit some degree of nestedness, such that rare or specialist pollinators tend to 86 interact with abundant, generalist plant species (and vice versa) [55,56]. The more nested a 87 88 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, 89 networks are not perfectly nested and some degree of functional complementarity among 90 91 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 92 (Figure 1c,d) [53]. 93

94 Complementarity within plant-pollinator networks can also create a functional role for pollinator 95 species that are rare within their network. Pollination of a single plant species, at least in one 96 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, 97 98 however, when function is considered for each species in a plant community. For example, a 99 pollinator species that is rare within the community could still be an important pollinator of a 100 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 101 102 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. 103

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

106 of stochasticity from those of complementarity among bee species, we used a randomization-

107 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

109 *important are rare bee species to pollination?*

110 Methods

111 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 119 120 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 121 (Tables S1-S3). This meant excluding a mean of 54% of plant species (range = 0 - 83% across 122 networks), but only 8.0% of bee species (range = 0 - 33%) and 9.5% of individual plant-bee 123 interactions (range = 0 - 27%). For the 11 datasets as analyzed, plant species richness varied 124 from 6 to 23, bee species richness varied from 22 to 86, and total individual plant-bee 125 interactions varied from 227 to 4513. In total, the analyzed datasets included 70 plant species and 126

127 173 bee species, with 20943 total observed interactions, and 1479 unique species-species pairs128 across networks.

129 Analysis

To start, we identified the most functionally important bee species for each plant species within 130 131 each network. We used interaction frequency (i.e., the number of individual bees of a species 132 that were collected from a given plant species) as a proxy for function, and defined 'functionally 133 important' bee species as those that contributed a threshold percent of visits to at least one plant 134 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 135 136 the analyses across thresholds from 2.5% to 10% (see Texts S2-S3 and Figures S2-S3 for further 137 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 138 depends also on its effectiveness (per-visit pollen deposition) and efficiency (essentially the 139 'quality' of pollination), and there are examples of frequent insect visitors being poor pollinators 140 [64,65]. However, plants' most frequent floral visitors are typically their most important 141 pollinators, and this relationship is especially pronounced for bees, which are the focus of this 142 study [31,64,66]. Also, on a practical level, it would not have been possible to measure per-visit 143 function for the 1479 unique plant-pollinator interactions in our data sets. Lastly, although plants 144 145 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 146 on existing biodiversity-ecosystem function literature [2], and also because it is more appropriate 147 148 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 beespecies important for pollinating them?

Within networks, we performed rarefaction to relate the number of important bee species to plant 152 153 species richness. More specifically, we subset the observations in each network to generate plant 154 communities of varying richness and counted the number of bee species important to at least one 155 plant species in that set. Thus, just as site-based rarefaction measures the accumulation of new 156 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 157 158 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 159 possible combinations. We then took the mean number of important bees across combinations of 160 plant identity for each level of plant richness. 161

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 177 species, but assigned interactions by random draw (with replacement) from the network-wide 178 179 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 180 181 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 182 these datasets, we estimated the mean number of important bee species for each level of plant 183 184 species richness.

In the Results, we report three metrics for each network. First, we calculate the change in the 185 number of important bee species recorded for the average single plant species versus for the 186 entire network (i.e., all plant species). This metric shows how the need for bee diversity increases 187 with the number of plant species considered, when both the stochastic and the biological 188 components of that increase are included. Second, we compare the observed number of 189 important bee species to the inner 95th percentile of what was predicted by the null model. 190 Observed values beyond the inner 95th percentile were considered significantly different than 191 192 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, 193

we calculate a standardized effect size (a Z-score) for each network that represents the magnitude 194 of any non-stochastic (i.e., biological) effects on the number of important bee species in that 195 network. Z-scores were calculated as the difference between the observed value and the null 196 prediction, divided by the standard deviation of the null (i.e. (observed - null)/sd_{null}), where all 197 three values are calculated at maximum plant species richness (i.e., using all the plant species in 198 199 the network). Thus, the Z-scores measure the strength of biological effects, such as niche partitioning and bee specialization, in driving the need for bee diversity, and express this effect 200 in units of standard deviations of the null distribution. 201

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

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

Here, we measured how many important bee species (i.e., functionally important to at least one 208 209 plant species) in each network were also rare within that network. While rarity can be defined in many ways (e.g. [70,71]), we focus simply on local rarity – i.e. species with low relative 210 abundance – which is how rarity has been typically considered in the BEF literature (e.g. 211 [36,42]). This means we do not treat rarity as an intrinsic trait of a species; by our definition, a 212 species could be rare in one community and common in another. In the main text, we focus on an 213 analysis in which rarity was defined as any bee species representing < 1% of all bee observations 214 in its network (sensu [72,73]). However, because any definition of rarity is arbitrary, we also 215

11

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.

All our analyses were performed in R (3.6.3), using packages *parallel* (3.6.3) and *pbapply* (1.4-

220 0). Data management was done with *tidyverse* (1.3.1) and *lubridate* (1.7.10). All data and stand-

alone code needed to re-create our analysis are available in the supplement.

222 **Results**

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

225 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 226 respective communities (i.e., comparing the starting and ending points of the accumulation 227 curves), the number of important bee species increased 2.5 to 7.6-fold (Figure 2a). The 228 accumulation curves of functionally important species were mostly non-saturating and rose 229 beyond the inner 95th percentile of the null in all but two of the smallest networks (Figures 2a-b, 230 S5). Z-scores, which measure the effect of complementarity on the number of important bee 231 species relative to the expectation under random foraging, ranged from 1.1 to 12.2 (Figure 2c). 232 Across networks, these results were each associated with plant species richness (Figure 2). There 233 was a strong correlation between the total number of plant species in a network and i) the 234 235 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 < 100236

237 0.001), and iii) the Z-score (r = 0.95, p < 0.001). These results were also robust to our choice of 238 threshold for defining functional importance. While the absolute number of important bee 239 species decreased under a higher, less inclusive threshold, the factor-differences between single 240 plant species and their respective communities, and the associated Z-scores (i.e., the relative 241 effect sizes), actually increased under higher thresholds (Text S3; Figure S5, S6).

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

243 Of the bee species that are functionally important to at least one plant species in a given network, 244 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 245 246 significantly greater than the null expectation in all but the smallest networks. As would have to 247 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) 248 (Figures S9, S10). Even with the most conservative combination of thresholds, though, a mean of 249 7.8% and as many as 25.0% of the important bee species were rare within their network. 250

251 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 266 bee species were frequently important to function. Regardless of the exact thresholds we used to 267 define importance and rarity, a substantial portion of the functionally important bee species in 268 269 our analyses were also rare within their community (means of 8-45%, across thresholds; Figures 270 3, S10). This result extends previous work that has suggested rare species could be important, but 271 measured their functional role less directly. For example, rare species have been valued because 272 they contribute to functional trait diversity [32,33,75] and because they could become abundant, 273 and thus functionally important, at other places or times (i.e. insurance effects) [10,37,38]. In 274 contrast, we demonstrated a direct and immediate contribution of locally rare species. This 275 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 276 be important. Instead, we found rare bees to be important because they filled distinct functional 277 278 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 279 functions (i.e. 'multifunctionality'), where it has likewise been found that locally rare species can 280 provide functions not provided by other, more common species [35]. Both types of findings 281

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 285 obvious that more plant species would require more pollinator species. Findings from network 286 ecology, however, might predict the opposite. In particular, because plant-pollinator networks 287 are typically nested [55,56], one might expect that abundant generalist pollinators would be 288 289 responsible for most of the pollination across plant species, with rare or specialist species being 290 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 291 292 important to more plant species (Figure S8). Yet, if we were to only consider bee species' 293 average contributions across plant species, we would be ignoring the needs of those plant species 294 that were visited primarily by less abundant bees (Figure S8). Our contribution in this paper is to 295 consider the pollinators needed by the whole plant community, rather than just single plant 296 species or the average plant species, and thereby to reveal the important role played by bee 297 species that are rare at the community scale. Of course, this assumes the function of pollination is 298 simply to support the plant community, and that plant species are equally important. If the greater function of interest is, for example, plant biomass, then these interactions between rarer 299 plant and bee species may be of less consequence. 300

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. seeddispersal 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 310 species were lost from our networks. In particular, we do not know the pollen limitation status of 311 the plants in our networks, which means we cannot predict how their reproduction would be 312 313 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 314 315 so following loss of a dominant pollinator. On the other hand, pollinator species' preferences are 316 often dynamic [79,80], which should lend resilience to species loss [81]. That is, following the 317 loss of a plant's dominant pollinator species, other pollinators might shift or expand their diets, 318 which could compensate for the loss [82]. However, increased pollinator generalization 319 following the loss of a competitor can also decrease pollination quality due to increased 320 interspecific pollen transfer [79,83,84]. Future research should work to determine which of these 321 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 322 require understanding the extent to which interactions are fixed or plastic, and whether changes 323 324 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

328 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 329 needed for function in nature. For instance, despite positive biodiversity effects [46,74,86], 330 function at local scales often relies on relatively few species because of dominance [4,7,23,29]. 331 Yet, because of species turnover, far more species are needed to maintain function across broader 332 spatiotemporal scales [8,10,37,87,88]. Similarly, more species are needed to maintain multiple 333 functions simultaneously than for any function alone because of functional complementarity 334 [9,13,89,90]. Here, we demonstrate an analogous role of biodiversity in mutualist networks: even 335 336 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 337 on many functions operating across broad spatiotemporal scales [85] and, like pollination, many 338 of these functions are realized through mutualist interactions [91]. In light of this, our results 339 suggest that biodiversity may be even more important for real-world function than previously 340 341 supposed.

342

343	Data	and code: The analysis in this paper uses 11 plant-bee network datasets collected by our	
344	lab group. For convenience, these data, along with code to reproduce our analysis and figures,		
345	are in	cluded here as electronic supplementary material. Any use of these data, however, should	
346	cite th	e original papers.	
347	Auth	or contributions: DTS and RW conceived of study in collaboration with LW and MG.	
348	DTS o	developed and performed analyses. DTS drafted the manuscript with input from RW, and	
349	all aut	hors contributed to revision. MR and MM contributed data.	
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351	versio	n of this manuscript.	
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586

587 **Figure legends**

Figure 1 Hypothetical pollinator abundance distributions illustrating how complementarity
among pollinator species should affect the number of functionally important species. (a) The

abundance of pollinators visiting the entire plant community. The two most abundant pollinators

- 591 contribute 80% of floral visits. (b) In a community with low complementarity, the same
- 592 generalist pollinator species dominate function for every plant species. (c) In a plant community
- 593 with high complementarity, different pollinator species dominate visits to different plant species.
- (d) If pollinator species are perfectly redundant (as in b), the number of important pollinator

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

Figure 2 The number of important pollinator species increases with the number of plant species. 599 600 (a) Accumulation curves for each of the 11 networks. Points represent the number of pollinator species important to at least one plant species in the full community, and lines represent the 601 accumulation of important pollinator species across levels of plant species richness (i.e., means 602 603 of rarefied plant communities) where the left end represents the average single plant species, and the right end represents the full plant community. (b) An example of one network's accumulation 604 curve, now shown together with its null model and 95% CIs. The null model curve represents the 605 606 expectation if individual pollinators forage randomly across the available plant species, while the observed curve includes biological effects, such as species-specific preferences, morphology, or 607 phenology that led to non-random foraging. (c) Z-scores for each network, representing the 608 strength of the biological effects (complementarity) on the number of pollinator species found to 609 be functionally important in a network, relative to the expectation under random foraging, Z-610 611 scores were calculated as the difference between observed and null expectation (large, red vertical bar in b) divided by the standard deviation of the null (small, blue vertical bar in b) at 612 maximum plant richness for each network (i.e., at the endpoints of the curves in a and b). In (a) 613 614 and (c), the blue line and points (light grey in black and white) represent the experimental garden. 615

Figure 3 Many rare species are functionally important as pollinators. (a) Pollinator rank
abundance distribution for a single network, with pollinator species that were important to at

618 least one plant species highlighted in red (appearing darker in black and white). The dotted line represents 1% of total pollinator abundance in the network, which is our definition of rarity. In 619 this community, 13 of 25 important pollinator species are rare. Similar plots for the rest of our 620 621 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 = 622 0.95, p <0.001). When datasets were large enough to include more plant species, more rare 623 pollinator species were found to be important. This increase was only weakly reflected in the null 624 model. The network shown in (a) is circled. 625



Pollinator individuals

Number plant species







Supplemental Text

Text S1: Information on datasets

Ten of our 11 datasets were collected from natural or semi-natural meadows of New Jersey. In these, workers walked transects and collected all bee individuals observed visiting flowers along that transect.

Six of the meadow datasets were collected by MR and are described in detail in published papers (Roswell *et al.* 2019, 2020). In brief, the sites in this study were old fields ranging in size from 0.8 to 2.2 ha, and transects were walked to cover the entire field. Each field was visited multiple times from June through August, and observations from all visits were combined. These datasets are large in terms of the number of individual bees collected (mean = 2894.5, sd = 1091.1) and the number of plant species included (mean = 17.7, sd = 4.3).

Four meadow datasets are published for the first time here. These data were collected in natural or semi-natural meadows of New Jersey, USA, in 2011, 2013, and 2014, as part of a larger, unpublished study. Each study site included paired, adjacent fields, one of which was unmanipulated and one of which had been seeded with wild flowers. In each of the four study sites included here, eight 40x2 m transects (four in each field) were positioned within 250 m of one another. Bees were collected along transects in 10-min sampling bouts in which a data collector slowly walked the transect (10 m per 2.5 min) and collected all bees observed on flowers within 1 m of the transect. Each site was visited four to seven times from May through August or September, and each site visit included 2-4 sampling bouts. Due to less intensive sampling effort, these datasets are smaller in terms of the number of individual bees collected (302.3, sd = 64.1) and the number of plant species included (mean = 6.25, sd = 0.5).

The final dataset included in this analysis is wild bee visits to an outdoor experimental garden, which is described in detail in a published paper (MacLeod et al 2016). The garden was planted in a 6 x 17 block design, in which 17 plant species were planted in 1 m² monoculture plots, randomly arranged in each of 6 blocks (i.e. 6 rows), such that each plant species was replicated six times. Total garden area was ~1600 m². Bees were collected during repeated, timed observations of each plot. Thus, the abundance of each plant species was standardized by area, and sampling effort was standardized across plant species. This dataset was relatively large, including 2367 individual bees, and 17 plant species.

Text S2: Identifying "functionally important bee species"

In this study, we define "important" bee species as those providing some threshold proportion of visits to a given plant species. In doing so, our aim is to identify the bee species that account for a substantial proportion of all bee visits to a given plant species. We acknowledge that any choice of threshold is to some extent arbitrary; we are collapsing a continuous measure to a binary measure. In the analysis of real-world ecosystem functions, however, it is often necessary to use some method to distinguish the more functionally important species, to avoid counting all species, including those that may have been observed only once or twice in a large study, as essential to function. Similarly, real-world datasets will always be subject to sampling effects (e.g., increases in the number of species recorded with increased sampling effort) because it is not possible to sample natural communities completely. Focusing on those species that account for a large(r) proportion of individuals collected will mitigate the impact of sampling effects on

the analysis, because the more common species are better sampled than the rare ones for a given level of sampling effort.

In the main text, we use a 5% threshold, such that any bee species contributing at least 5% of the visits to a given plant species is considered important. We believe this captures 'functionally important' species in a biologically reasonable way. When using the 5% threshold, the important species provide 81% of the bee visits per plant species on average (sd = 8.9%), while representing only 35% of the bee species per plant species (sd = 18%). Fig. S2 shows what the 5% threshold means graphically by plotting example rank-abundance distributions of bees per plant species, with the functionally important bee species shaded. Fig. S3 shows how the proportion of species considered important and the visits they provide changes with the choice of threshold.

Text S3: Sensitivity analyses

We re-ran each of our analyses using a range of thresholds to define bee importance, from bees providing at least 2.5% of a plant's visits to those providing at least 10% of visits, by increments of 0.1% (76 total runs). Because the null model takes hours to run, however, we only ran the null model four times, for thresholds of 2.5, 5, 7.5, and 10%. For plant species with few observations, low importance thresholds can mean that *every* bee species is considered important, even bee species with only one visit. To avoid this, we included a condition that a bee must meet the threshold for importance *and* be represented by >1 individual.

A lower, more inclusive threshold would mean that more bee species would be considered functionally important to each plant, raising the intercepts of the accumulation curves. A higher, less inclusive threshold should result in the opposite. Having a larger number of important species also creates more opportunity for turnover of important species, so we might also expect the lower, more inclusive thresholds to result in steeper accumulation curves. Indeed, the absolute number of important bee species varied with the choice of threshold as expected (Figs S5a, S6). Yet, the factor-increase in the total number of functionally important bees between a single plant species and its community varied little, ranging from 4.3 to 5.2, and actually increasing with the threshold used (Figs S5b, S6). Z-scores also increased with higher thresholds, from an average of 5.7 at the more inclusive threshold of 2.5%, to 8.1 at the less inclusive threshold of 10% (Fig S6). This also meant that, at higher thresholds, more networks were significantly different than the null; at the 2.5% threshold, none of the four smallest networks significantly differed from the null, while at the 10% threshold all networks significantly differed from the null. This is because the null models were flatter and less variable under higher thresholds, accentuating differences between the observed results and null expectation. In turn, this is likely because of the skewed bee species abundance distributions; at higher thresholds, when only highly dominant bee species are considered important, it is more difficult for less abundant bees to appear important by chance. As a result, there is less turnover of important bees across plants, and less variation in results between runs of the null model. In sum, while the number of bee species defined as 'important' changed with the threshold used (as would have to be the case), the main results of the study (the factor increase across the species accumulation curve, and the Z score representing the biological component of the increase) were qualitatively similar across thresholds.

Supplemental figures



Fig S1 Map of our study plots in New Jersey, USA. The experimental garden is the southernmost plot.


Fig S2 Example rank abundance distributions of bee species visiting four different plant species, with important bees (those contributing \geq 5% of visits) shown in red. These distributions demonstrate the range of what the 5% importance thresholds look like in practice. Most plant species' distributions look like (a) or (b), in which relatively few bee species are considered important. For some plants, however, quirks of small sample sizes or more even bee abundance distributions led to a high proportion bee species being considered important, as in (c) and (d).



Fig. S3 Effect of the threshold used to define importance on the proportion of bee species considered important and the proportion of visits provided by those important species. (a-b) The proportion of species considered important declines with higher importance thresholds; (a) shows the mean, across networks, and (b) shows the distribution of values across networks. (c-d) Because fewer species are considered important with higher thresholds, the proportion of visits contributed by those species also decreases. However, across all thresholds we considered (2.5-10% of visits), important bee species account for a high proportion of total flower visits (ca. 70-90%).



Figure S4. Observed and null accumulation curves for each network. Text in the upper left of each panel refers to the network (see Table S1); 'cm13' is the experimental garden and the rest are natural / semi-natural meadow communities. Each curve describes the mean number of important bee species, taken across combinations of plant species. The ribbon around the observed accumulation curve shows the inner 95th percentile (i.e., 2.5th to 97.5th percentile) at each rarefied value of plant richness, and thus describes variation in the number of important bee species that is due to plant identity. The vertical bars on the null accumulation curve were similarly calculated, but represent the inner 95th percentile of *means* across iterations of the null model. This variation comes from stochastic sampling effects under an assumption of no true differences among bee species in the plant species they visit. Thus, these vertical bars represent 95% confidence intervals around the mean expectation and its CI (grey curve and vertical bars) asks whether, on average, more bee species are important than expected due to sampling effects alone. In 9 of our 11 networks, the answer is yes.



Fig S5a (cont'd next page)



Number plant species

Figure S5 Sensitivity analysis showing the accumulation of important bee species with increasing plant species richness under varying thresholds of importance. Text in the upper left of each panel refers to the network/dataset (see Table S1); 'cm13' is the experimental garden and the rest are natural / semi-natural meadow communities. We re-ran our analysis while defining important bees as those contributing 2.5% to 10% of visits to at least one plant species, using increments of 0.1%. (a) Increasing the threshold of importance lowers the absolute number of important species. (b) However, the proportional change in the number important bee species, relative to a single plant species, was very robust to changes in threshold definition, and actually tended to increase with higher thresholds.



Fig S6 Effect of the threshold of importance on our main results. Each column is analogous to the main text Fig. 2. The first row shows the accumulation curves for each network. Points represent the number of bee species important to at least one plant species in the full community, and grey lines represent the accumulation of important species across rarefied levels of plant species richness (i.e., means of across rarefied plant communities). The r value refers to the correlation between plant species richness and the number of important bees in the whole network (i.e. the black points). The second row shows the accumulation curve of a typical network together with its null model. The third row shows Z-scores for the number of important bees in each network, and r values refer to the correlation between these Z-scores and plant species richness. Although the absolute number of important bees and plant richness remains largely unchanged. In fact, the average Z-score goes up under higher thresholds because the null models get flatter and less variable.



Figure S7 Log-transformed rank abundance distributions for each of the networks in our analysis with the important bee species (those contributing at least 5% of total bee visits to at least one plant species) shown in red. The horizontal dashed line represents 1% of the total bee community; bee species below this line are considered locally rare. Text in the upper right of each panel refers to the network/dataset (see Table S1); 'cm13' is the experimental garden and the rest are natural / semi-natural meadow communities. In most plant communities, many rare bees are also important to function of at least one plant species.



Fig S8 (cont'd next page)



Fig S8 (cont'd next page)



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Bee species

Fig S8 (cont'd next page)



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Bee species

Fig S8 (cont'd next page)



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Bee species

Figure S8. Bee abundances by rank in each of our networks (large insets at the top of each page) and on each plant species in each network (small insets). These plots are analogous to Figure 1 a-c. In the network-wide abundance distributions (large insets), dotted horizontal lines denote 5% and 1% of the total bee community. In the plant-level abundance distributions (small insets), horizontal line denotes 5% of the individuals visiting that plant species. The insets for each plant species are arranged in descending order (left to right, top to bottom) by the number of observations on each plant species. These figures are interpreted as in Figure 1: if bee species are mostly redundant, the same dominant bee species (in blue) will tend to dominate visits to individual plant species. Complementarity among bee species, on the other hand, will lead to subdominant or even rare species (in grey and red) to dominate visits to some plant species.



Figure S9 Sensitivity analysis showing the proportion of important bee species that are rare, across networks, using different rarity thresholds. In this figure, we held the threshold of importance at 5% of visits and used rarity thresholds of 0.5% to 1.5%, by increments of 0.01%. Raising the rarity threshold means more important bee species are considered rare, and vice versa. In the main text, we used a threshold of 1%. However, regardless of the threshold, our conclusion remains the same: across networks, a substantial proportion of important bee species are also locally rare.



Figure S10 Sensitivity analysis showing the proportion of important bees that were rare using different thresholds of both bee importance and rarity. The value shown is the mean proportion across all 11 networks. The proportion of important bees that are rare increases with lower thresholds of importance and higher thresholds of rarity. Within this parameter space, the mean (across networks) proportion of important bees that are considered rare ranges from 7.8% in the bottom right to 44.8% in the top left. In the main text, we used thresholds of 5% for importance and 1.0% for rarity, resulting in a mean of 25.0% of important bees being considered rare (shown as white). Although this value is dependent on the thresholds used, our general conclusion holds across networks: it is common for important bees to also be rare, even under strict definitions of importance and rarity.

Supplemental tables

Table S1. Datasets, or networks, included in our analysis. Each network was collected at one site in one year. Cape May (cm13) is the experimental garden, in which plant abundance was standardized (by area) ad sampling effort was standardized across plant species. The column Unique Sampling Days refers to the number of different days during the focal year on which sampling occurred. Total Sample Effort refers to the total number of minutes spent netting, summed across days and data collectors. In the remaining columns, we include values for the entire dataset as collected, and the subset of the data we analyzed here (by including only plant species with ≥ 20 observed interactions).

		Unique	Total sample				Unique
		sample	effort	Plant sp	Bee sp	Observations	interactions
Network	Citation	dates	(minutes)	(original/subset)	(original/subset)	(original/subset)	(original/subset)
Cm13	MacLeod et al 2016	30	5280	17/17	54/54	2346/2346	243/243
Baldpate	Roswell et al 2019	14	2400	47/21	69/68	4629/4513	383/313
Cold Soil	Roswell et al 2019	13	2580	52/23	84/83	2637/2498	447/375
Fox Hill	Roswell et al 2019	16	3690	37/20	74/70	3714/3582	363/306
IAS	Roswell et al 2019	16	3810	36/16	88/86	3342/3209	380/310
Lord Stirling	Roswell et al 2019	14	3690	26/13	65/64	2098/2039	268/232
URWA	Roswell et al 2019	16	4020	26/13	74/71	1594/1526	254/211
BW_2014	This paper	4	80	14/6	35/30	334/271	91/59
HP_2011	This paper	7	250	21/7	33/29	415/353	109/66
MU_2013	This paper	6	160	36/6	42/37	488/358	133/62
RO 2014	This paper	4	80	22/6	33/22	289/227	80/40

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Table S2. Plant species and the number of individual bees observed on that species, for each network as analyzed.

	-	Observed
Network	Plant species	interactions
Baldpate	Monarda fistulosa	895
Baldpate	Rudbeckia hirta	866
Baldpate	Pycnanthemum muticum	452
Baldpate	Trifolium campestre	336
Baldpate	Erechtites hieraciifolius	328
Baldpate	Linaria vulgaris	271
Baldpate	Daucus carota	255
Baldpate	Phytolacca americana	181
Baldpate	Nepeta cataria	166
Baldpate	Asclepias tuberosa	129
Baldpate	Verbascum thapsus	108
Baldpate	Hypericum perforatum	104
Baldpate	Erigeron strigosus	91
Baldpate	Cirsium vulgare	69
Baldpate	Trifolium repens	61
Baldpate	Pycnanthemum tenuifolium	47
Baldpate	Verbena urticifolia	42
Baldpate	Penstemon hirsutus	35
Baldpate	Conyza canadensis	33
Baldpate	Potentilla recta	23
Baldpate	Plantago lanceolata	21
BW_2014	Lespedeza cuneata	76
BW_2014	Monarda fistulosa	54
BW_2014	Erigeron annuus	39
	Symphyotrichum novae-angliae	39
BW_2014	Echinacea purpurea	34
BW 2014	Gaillardia pulchella	29
 cm13	Pycnanthemum tenuifolium	797
cm13	Symphyotrichum novae-angliae	275
cm13	Eupatoriadelphus maculatus	233
cm13	Asclepias tuberosa	199
cm13	Rudbeckia laciniata	135
cm13	Veronicastrum virginicum	110
cm13	Oligoneuron rigidum	88
cm13	Penstemon hirsutus	83
cm13	Vernonia noveboracensis	66
cm13	Asclepias incarnata	62
cm13	Rudbeckia hirta	57
cm13	Lobelia siphilitica	50
cm13	Solidago rugosa	50

cm13	Verbena hastata	50
cm13	Zizia aurea	41
cm13	Euthamia graminifolia	37
cm13	Agastache scrophulariifolia	34
Cold Soil	Lythrum salicaria	303
Cold Soil	Monarda fistulosa	277
Cold Soil	Pycnanthemum tenuifolium	256
Cold Soil	Daucus carota	254
Cold Soil	Chamaecrista fasciculata	211
Cold Soil	Erigeron strigosus	177
Cold Soil	Rudbeckia hirta	123
Cold Soil	Solidago juncea	122
Cold Soil	Solidago gigantea	108
Cold Soil	Trifolium pratense	82
Cold Soil	Heliopsis helianthoides	81
Cold Soil	Plantago lanceolata	79
Cold Soil	Achillea millefolium	59
Cold Soil	Vernonia noveboracensis	54
Cold Soil	Echinacea purpurea	49
Cold Soil	Leucanthemum vulgare	48
Cold Soil	Penstemon digitalis	44
Cold Soil	Euthamia graminifolia	36
Cold Soil	Apocynum cannabinum	33
Cold Soil	Melilotus albus	29
Cold Soil	Erigeron annuus	28
Cold Soil	Trifolium repens	23
Cold Soil	Cirsium arvense	22
Fox Hill	Daucus carota	900
Fox Hill	Ratibida pinnata	660
Fox Hill	Erigeron strigosus	375
Fox Hill	Monarda fistulosa	322
Fox Hill	Leucanthemum vulgare	285
Fox Hill	Cirsium arvense	141
Fox Hill	Rudbeckia hirta	110
Fox Hill	Asclepias syriaca	107
Fox Hill	Cichorium intybus	106
Fox Hill	Verbena urticifolia	84
Fox Hill	Centaurea stoebe	78
Fox Hill	Echinacea purpurea	76
Fox Hill	Melilotus officinalis	62
Fox Hill	Cirsium vulgare	59
Fox Hill	Clinopodium vulgare	45
Fox Hill	Solidago juncea	44
Fox Hill	Penstemon digitalis	36
Fox Hill	Apocynum cannabinum	33

Fox Hill	Trifolium repens	32
Fox Hill	Potentilla recta	27
HP_2011	Clinopodium vulgare	111
HP_2011	Echinacea purpurea	103
HP_2011	Erigeron philadelphicus	34
HP_2011	Pastinaca sativa	31
HP_2011	Solidago gigantea	31
HP_2011	Daucus carota	22
HP_2011	Solidago canadensis	21
IAS	Pycnanthemum tenuifolium	689
IAS	Daucus carota	515
IAS	Solidago juncea	380
IAS	Penstemon digitalis	323
IAS	Liatris spicata	311
IAS	Achillea millefolium	264
IAS	Heliopsis helianthoides	139
IAS	Rudbeckia hirta	124
IAS	Trifolium pratense	119
IAS	Hypericum perforatum	100
IAS	Monarda fistulosa	96
IAS	Tradescantia ohiensis	34
IAS	Symphyotrichum novae-angliae	31
IAS	Cirsium arvense	30
IAS	Drymocallis arguta	30
IAS	Baptisia tinctoria	24
Lord Stirling	Eutrochium maculatum	554
Lord Stirling	Penstemon digitalis	382
Lord Stirling	Cirsium arvense	254
Lord Stirling	Apocynum cannabinum	196
Lord Stirling	Monarda fistulosa	154
Lord Stirling	Pycnanthemum tenuifolium	140
Lord Stirling	Achillea millefolium	137
Lord Stirling	Lythrum salicaria	51
Lord Stirling	Lotus corniculatus	43
Lord Stirling	Securigera varia	39
Lord Stirling	Daucus carota	36
Lord Stirling	Rudbeckia hirta	32
Lord Stirling	Solidago juncea	21
MU_2013	Solidago gigantea	140
MU_2013	Monarda fistulosa	65
MU_2013	Cirsium arvense	57
MU_2013	Galium palustre	42
MU_2013	Lythrum salicaria	31
MU_2013	Coreopsis lanceolata	23
RO_2014	Centaurea maculosa	54

RO_2014	Leucanthemum vulgare	51
RO_2014	Solidago canadensis	35
RO_2014	Euthamia graminifolia	34
RO_2014	Monarda fistulosa	31
RO_2014	Rudbeckia laciniata	22
URWA	Pycnanthemum tenuifolium	356
URWA	Centaurea stoebe	287
URWA	Solidago juncea	137
URWA	Erigeron strigosus	136
URWA	Penstemon digitalis	115
URWA	Daucus carota	103
URWA	Lotus corniculatus	92
URWA	Apocynum cannabinum	87
URWA	Leucanthemum vulgare	78
URWA	Rosa carolina	47
URWA	Rudbeckia hirta	45
URWA	Achillea millefolium	23
URWA	Clinopodium vulgare	20

Table S3. Bee species and the number of plant visits by that species observed in the dataset as analyzed. Colors are as in Figure S8: Species that were dominant in their community (> 5% of observations) are in blue, rare species (< 1% of observations) are in red, and subdominants (1-5% of observations) are in grey. Bee species that were important to at least one plant species in its network (i.e., providing >5% of visits to that plant species) are bolded.

Network	Bee species	Observations
Baldpate	Augochlora pura	1263
Baldpate	Bombus impatiens	935
Baldpate	Bombus griseocollis	387
Baldpate	Ceratina calcarata	380
Baldpate	Bombus bimaculatus	209
Baldpate	Halictus ligatus	209
Baldpate	Hylaeus affinis_modestus	180
Baldpate	Andrena wilkella	150
Baldpate	Augochloropsis metallica	120
Baldpate	Augochlorella aurata	105
Baldpate	Ceratina strenua	69
Baldpate	Lasioglossum imitatum	65
Baldpate	Lasioglossum versatum	65
Baldpate	Lasioglossum hitchensi_weemsi	33
Baldpate	Agapostemon virescens	31
Baldpate	Halictus confusus	30
Baldpate	Megachile mendica	22
Baldpate	Ceratina dupla	21
Baldpate	Halictus parallelus	18
Baldpate	Megachile exilis	18
Baldpate	Lasioglossum illinoense	17
Baldpate	Hylaeus mesillae	16
Baldpate	Xylocopa virginica	12
Baldpate	Lasioglossum cressonii	11
Baldpate	Lasioglossum cattellae	10
Baldpate	Osmia bucephala	10
Baldpate	Lasioglossum tegulare	9
Baldpate	Ceratina mikmaqi	8
Baldpate	Sphecodes heraclei	8
Baldpate	Bombus perplexus	7
Baldpate	Megachile campanulae	7
Baldpate	Halictus rubicundus	6
Baldpate	Lasioglossum coriaceum	6
Baldpate	Bombus citrinus	5
Baldpate	Bombus fervidus	5
Baldpate	Lasioglossum trigeminum	5
Baldpate	Heriades carinata	4
Baldpate	Lasioglossum abanci	4

Baldpate	Lasioglossum fuscipenne	4
Baldpate	Hoplitis pilosifrons	3
Baldpate	Hoplitis producta	3
Baldpate	Lasioglossum subviridatum	3
Baldpate	Osmia pumila	3
Baldpate	Andrena rudbeckiae	2
Baldpate	Bombus vagans	2
Baldpate	Calliopsis andreniformis	2
Baldpate	Lasioglossum ellisiae	2
Baldpate	Lasioglossum pectorale	2
Baldpate	Lithurgus chrysurus	2
Baldpate	Megachile petulans	2
Baldpate	Megachile rotundata	2
Baldpate	Megachile xylocopoides	2
Baldpate	Melissodes desponsus	2
Baldpate	Melissodes subillatus	2
Baldpate	Osmia atriventris	2
Baldpate	Agapostemon sericeus	1
Baldpate	Anthophora abrupta	1
Baldpate	Bombus auricomus	1
Baldpate	Coelioxys octodentatus	1
Baldpate	Coelioxys sayi	1
Baldpate	Hoplitis spoliata	1
Baldpate	Lasioglossum callidum	1
Baldpate	Lasioglossum coeruleum	1
Baldpate	Lasioglossum foxii	1
Baldpate	Lasioglossum rozeni	1
Baldpate	Megachile frugalis	1
Baldpate	Megachile pugnata	1
Baldpate	Melissodes denticulatus	1
BW_2014	Bombus impatiens	65
BW_2014	Bombus griseocollis	38
BW_2014	Ceratina calcarata	36
BW_2014	Halictus ligatus	18
BW_2014	Megachile mendica	15
BW_2014	Bombus bimaculatus	14
BW_2014	Augochlora pura	11
BW_2014	Hylaeus mesillae	9
BW_2014	Lasioglossum pilosum	8
BW_2014	Xylocopa virginica	8
BW_2014	Lasioglossum hitchensi_weemsi	7
BW_2014	Ceratina strenua	6
BW_2014	Hylaeus affinis_modestus	5
BW_2014	Lasioglossum trigeminum	5
BW_2014	Lasioglossum imitatum	4

BW_2014	Megachile inimica	3
BW_2014	Agapostemon texanus	2
BW_2014	Agapostemon virescens	2
BW_2014	Megachile brevis	2
BW_2014	Megachile exilis	2
BW_2014	Megachile pugnata	2
BW_2014	Bombus fervidus	1
BW_2014	Bombus perplexus	1
BW_2014	Coelioxys sayi	1
BW_2014	Heriades variolosa	1
BW_2014	Lasioglossum leucocomum	1
BW_2014	Lasioglossum pectorale	1
BW_2014	Lasioglossum platyparium	1
BW_2014	Lasioglossum versatum	1
BW_2014	Stelis lateralis	1
cm13	Bombus griseocollis	429
cm13	Bombus impatiens	340
cm13	Lasioglossum vierecki	246
cm13	Agapostemon virescens	173
cm13	Lasioglossum leucocomum	168
cm13	Megachile mendica	136
cm13	Halictus ligatus_poeyi	128
cm13	Agapostemon texanus	66
cm13	Xylocopa virginica	57
cm13	Ceratina mikmaqi	53
cm13	Hoplitis pilosifrons	53
cm13	Lasioglossum pilosum	44
cm13	Hylaeus mesillae	39
cm13	Bombus bimaculatus	37
cm13	Halictus confusus	36
cm13	Augochloropsis metallica	31
cm13	Lasioglossum tegulare	31
cm13	Bombus pensylvanicus	30
cm13	Sphecodes cressonii	24
cm13	Augochlorella aurata	21
cm13	Hylaeus affinis_modestus	21
cm13	Lasioglossum pectorale	21
cm13	Ceratina calcarata	20
cm13	Apis mellifera	18
cm13	Coelioxys sayi	13
cm13	Coelioxys octodentatus	11
cm13	Epeolus lectoides	11
cm13	Melissodes subillatus	11
cm13	Megachile brevis	10
cm13	Megachile inimica	10

cm13	Augochlora pura	9
cm13	Lasioglossum hitchensi	9
cm13	Ceratina dupla	7
cm13	Colletes simulans	6
cm13	Megachile exilis	6
cm13	Megachile xylocopoides	5
cm13	Sphecodes atlantis	5
cm13	Nomada vegana	4
cm13	Andrena atlantica	3
cm13	Heriades leavitti	3
cm13	Megachile texana	3
cm13	Agapostemon splendens	2
cm13	Ceratina strenua	2
cm13	Lasioglossum coreopsis	2
cm13	Megachile campanulae	2
cm13	Stelis Iouisae	2
cm13	Andrena nasonii	1
cm13	Bombus fervidus	1
cm13	Eucera hamata	1
cm13	Megachile gemula	1
cm13	Megachile rotundata	1
cm13	Melissodes trinodis	1
cm13	Nomada affabilis	1
cm13	Nomada australis	1
cm13	Sphecodes mandibularis	1
Cold Soil	Bombus impatiens	607
Cold Soil	Halictus ligatus	402
Cold Soil	Bombus griseocollis	191
Cold Soil	Lasioglossum imitatum	150
Cold Soil	Hylaeus affinis_modestus	116
Cold Soil	Lasioglossum versatum	107
Cold Soil	Hylaeus mesillae	80
Cold Soil	Halictus confusus	74
Cold Soil	Ceratina calcarata	67
Cold Soil	Xylocopa virginica	56
Cold Soil	Ceratina strenua	55
Cold Soil	Lasioglossum oceanicum	50
Cold Soil	Andrena wilkella	41
Cold Soil	Bombus bimaculatus	41
Cold Soil	Ceratina mikmaqi	40
Cold Soil	Ceratina dupla	36
Cold Soil	Melissodes denticulatus	28
Cold Soil	Lasioglossum illinoense	25
Cold Soil	Augochlora pura	22
Cold Soil	Lasioglossum hitchensi_weemsi	22

Cold Soil	Melissodes subillatus	19
Cold Soil	Augochlorella aurata	17
Cold Soil	Megachile sculpturalis	17
Cold Soil	Andrena rudbeckiae	16
Cold Soil	Megachile mendica	16
Cold Soil	Halictus rubicundus	12
Cold Soil	Megachile montivaga	12
Cold Soil	Augochloropsis metallica	11
Cold Soil	Agapostemon virescens	10
Cold Soil	Hoplitis pilosifrons	10
Cold Soil	Megachile brevis	10
Cold Soil	Lasioglossum trigeminum	9
Cold Soil	Lasioglossum viridatum	9
Cold Soil	Megachile frugalis	9
Cold Soil	Bombus fervidus	6
Cold Soil	Heriades carinata	6
Cold Soil	Melissodes agilis	6
Cold Soil	Anthidium manicatum	5
Cold Soil	Lasioglossum zephyrum	5
Cold Soil	Megachile exilis	5
Cold Soil	Megachile rotundata	5
Cold Soil	Melissodes bimaculatus	5
Cold Soil	Sphecodes dichrous	5
Cold Soil	Anthidium oblongatum	4
Cold Soil	Lasioglossum admirandum	4
Cold Soil	Lasioglossum bruneri	4
Cold Soil	Lasioglossum callidum	4
Cold Soil	Anthidiellum notatum	3
Cold Soil	Bombus perplexus	3
Cold Soil	Lasioglossum coriaceum	3
Cold Soil	Megachile pugnata	3
Cold Soil	Hylaeus leptocephalus	2
Cold Soil	Lasioglossum leucozonium	2
Cold Soil	Megachile campanulae	2
Cold Soil	Bombus vagans	1
Cold Soil	Calliopsis andreniformis	1
Cold Soil	Coelioxys alternatus	1
Cold Soil	Coelioxys germanus	1
Cold Soil	Coelioxys hunteri	1
Cold Soil	Coelioxys obtusiventris	1
Cold Soil	Coelioxys octodentatus	1
Cold Soil	Heriades variolosa	1
Cold Soil	Hoplitis producta	1
Cold Soil	Lasioglossum atwoodi	1
Cold Soil	Lasioglossum cressonii	1

Cold Soil	Lasioglossum gotham	1
Cold Soil	Lasioglossum obscurum	1
Cold Soil	Lasioglossum paradmirandum	1
Cold Soil	Lasioglossum pilosum	1
Cold Soil	Lasioglossum rozeni	1
Cold Soil	Lasioglossum smilacinae	1
Cold Soil	Lasioglossum tegulare	1
Cold Soil	Megachile integra	1
Cold Soil	Melissodes desponsus	1
Cold Soil	Melissodes trinodis	1
Cold Soil	Nomada erigeronis	1
Cold Soil	Pseudoanthidium nanum	1
Cold Soil	Sphecodes heraclei	1
Cold Soil	Stelis lateralis	1
Cold Soil	Stelis Iouisae	1
Cold Soil	Triepeolus cressonii	1
Cold Soil	Triepeolus eliseae	1
Cold Soil	Triepeolus remigatus	1
Fox Hill	Halictus ligatus	760
Fox Hill	Augochlorella persimilis	515
Fox Hill	Hylaeus affinis_modestus	498
Fox Hill	Bombus griseocollis	265
Fox Hill	Ceratina calcarata	264
Fox Hill	Hylaeus mesillae	206
Fox Hill	Lasioglossum versatum	203
Fox Hill	Augochlorella aurata	132
Fox Hill	Bombus impatiens	128
Fox Hill	Lasioglossum imitatum	89
Fox Hill	Bombus bimaculatus	51
Fox Hill	Agapostemon virescens	49
Fox Hill	Lasioglossum hitchensi_weemsi	38
Fox Hill	Bombus perplexus	29
Fox Hill	Augochlora pura	26
Fox Hill	Ceratina dupla	26
Fox Hill	Lasioglossum oceanicum	25
Fox Hill	Ceratina strenua	24
Fox Hill	Lasioglossum gotham	23
Fox Hill	Halictus confusus	17
Fox Hill	Lasioglossum rozeni	17
Fox Hill	Andrena wilkella	15
Fox Hill	Ceratina mikmaqi	15
Fox Hill	Hoplitis pilosifrons	15
Fox Hill	Lasioglossum trigeminum	15
Fox Hill	Halictus rubicundus	9
Fox Hill	Lasioglossum tegulare	9

Fox Hill	Megachile mendica	9
Fox Hill	Heriades carinata	8
Fox Hill	Augochloropsis metallica	7
Fox Hill	Lasioglossum admirandum	7
Fox Hill	Lasioglossum cressonii	6
Fox Hill	Bombus vagans	5
Fox Hill	Megachile brevis	5
Fox Hill	Nomada pygmaea	5
Fox Hill	Andrena nasonii	4
Fox Hill	Lasioglossum cattellae	4
Fox Hill	Lasioglossum platyparium	4
Fox Hill	Osmia bucephala	4
Fox Hill	Hoplitis producta	3
Fox Hill	Lasioglossum illinoense	3
Fox Hill	Melissodes subillatus	3
Fox Hill	Osmia atriventris	3
Fox Hill	Osmia georgica	3
Fox Hill	Osmia pumila	3
Fox Hill	Xylocopa virginica	3
Fox Hill	Andrena pruni	2
Fox Hill	Lasioglossum callidum	2
Fox Hill	Lasioglossum coriaceum	2
Fox Hill	Megachile montivaga	2
Fox Hill	Melissodes bimaculatus	2
Fox Hill	Nomada maculata	2
Fox Hill	Andrena brevipalpis	1
Fox Hill	Andrena commoda	1
Fox Hill	Andrena imitatrix	1
Fox Hill	Anthidium manicatum	1
Fox Hill	Heriades variolosa	1
Fox Hill	Hoplitis spoliata	1
Fox Hill	Lasioglossum abanci	1
Fox Hill	Lasioglossum ellisiae	1
Fox Hill	Lasioglossum foxii	1
Fox Hill	Lasioglossum nigroviride	1
Fox Hill	Lasioglossum paradmirandum	1
Fox Hill	Lasioglossum smilacinae	1
Fox Hill	Lasioglossum zephyrum	1
Fox Hill	Megachile campanulae	1
Fox Hill	Megachile exilis	1
Fox Hill	Megachile sculpturalis	1
Fox Hill	Melissodes denticulatus	1
Fox Hill	Melissodes desponsus	1
HP_2011	Bombus impatiens	145
HP_2011	Bombus griseocollis	24

HP_2011	Halictus ligatus	24
HP_2011	Lasioglossum imitatum	23
HP_2011	Hylaeus affinis_modestus	19
HP_2011	Hylaeus mesillae	18
HP_2011	Ceratina dupla	16
HP_2011	Ceratina mikmaqi	13
HP_2011	Ceratina strenua	11
HP_2011	Lasioglossum hitchensi_weemsi	9
HP_2011	Agapostemon virescens	7
HP_2011	Ceratina calcarata	7
HP_2011	Andrena brevipalpis	6
HP_2011	Lasioglossum versatum	5
HP_2011	Xylocopa virginica	5
HP_2011	Augochlorella aurata	4
HP_2011	Lasioglossum pectorale	4
HP_2011	Melissodes bimaculatus	2
HP_2011	Andrena hirticincta	1
HP_2011	Andrena nasonii	1
HP_2011	Andrena simplex	1
HP_2011	Anthidium manicatum	1
HP_2011	Augochlora pura	1
HP_2011	Colletes compactus	1
HP_2011	Colletes simulans	1
HP_2011	Hoplitis pilosifrons	1
HP_2011	Lasioglossum obscurum	1
HP_2011	Lasioglossum trigeminum	1
HP_2011	Pseudopanurgus andrenoides	1
IAS	Halictus ligatus	689
IAS	Hylaeus affinis_modestus	520
IAS	Bombus griseocollis	284
IAS	Bombus impatiens	277
IAS	Ceratina calcarata	216
IAS	Bombus bimaculatus	211
IAS	Hylaeus mesillae	191
IAS	Agapostemon virescens	135
IAS	Lasioglossum versatum	88
IAS	Lasioglossum oceanicum	46
IAS	Lasioglossum imitatum	44
IAS	Augochlorella aurata	43
IAS	Lasioglossum callidum	42
IAS	Andrena wilkella	38
IAS	Halictus confusus	32
IAS	Ceratina strenua	28
IAS	Xylocopa virginica	23
IAS	Megachile mendica	15

IAS	Hoplitis pilosifrons	14
IAS	Lasioglossum illinoense	14
IAS	Megachile exilis	13
IAS	Halictus rubicundus	11
IAS	Lasioglossum hitchensi_weemsi	11
IAS	Megachile sculpturalis	11
IAS	Heriades carinata	10
IAS	Lasioglossum gotham	10
IAS	Augochloropsis metallica	9
IAS	Ceratina dupla	9
IAS	Ceratina mikmaqi	9
IAS	Heriades variolosa	8
IAS	Megachile frugalis	8
IAS	Augochlora pura	7
IAS	Megachile campanulae	7
IAS	Megachile rotundata	7
IAS	Nomada pygmaea	7
IAS	Agapostemon sericeus	6
IAS	Bombus fervidus	6
IAS	Lasioglossum rozeni	6
IAS	Nomada bidentate_group	6
IAS	Anthidium oblongatum	5
IAS	Heriades leavitti	5
IAS	Lasioglossum trigeminum	5
IAS	Melissodes subillatus	5
IAS	Melissodes trinodis	5
IAS	Andrena nasonii	4
IAS	Halictus parallelus	4
IAS	Megachile inimica	4
IAS	Osmia bucephala	4
IAS	Sphecodes heraclei	4
IAS	Andrena carlini	3
IAS	Anthophora terminalis	3
IAS	Lasioglossum cattellae	3
IAS	Osmia distincta	3
IAS	Sphecodes dichrous	3
IAS	Lasioglossum admirandum	2
IAS	Lasioglossum tegulare	2
IAS	Lasioglossum zephyrum	2
IAS	Megachile montivaga	2
IAS	Nomada articulata	2
IAS	Osmia pumila	2
IAS	Andrena cressonii	1
IAS	Andrena spiraeana	1
IAS	Andrena vicina	1

IAS	Anthidiellum notatum	1
IAS	Anthidium manicatum	1
IAS	Coelioxys porterae	1
IAS	Coelioxys sayi	1
IAS	Hylaeus fedorica	1
IAS	Hylaeus leptocephalus	1
IAS	Lasioglossum coreopsis	1
IAS	Lasioglossum cressonii	1
IAS	Lasioglossum ephialtum	1
IAS	Lasioglossum oblongum	1
IAS	Lasioglossum oenotherae	1
IAS	Lasioglossum paradmirandum	1
IAS	Lasioglossum pectorale	1
IAS	Lasioglossum smilacinae	1
IAS	Lasioglossum subviridatum	1
IAS	Megachile brevis	1
IAS	Megachile georgica	1
IAS	Megachile pugnata	1
IAS	Melissodes agilis	1
IAS	Melissodes denticulatus	1
IAS	Nomada lehighensis	1
IAS	Ptilothrix bombiformis	1
IAS	Sphecodes atlantis	1
Lord Stirling	Bombus impatiens	340
Lord Stirling	Ceratina calcarata	253
Lord Stirling	Halictus ligatus	215
Lord Stirling	Bombus griseocollis	201
Lord Stirling	Bombus bimaculatus	152
Lord Stirling	Lasioglossum versatum	125
Lord Stirling	Hylaeus affinis_modestus	81
Lord Stirling	Hylaeus mesillae	74
Lord Stirling	Lasioglossum imitatum	74
Lord Stirling	Augochlorella aurata	65
Lord Stirling	Ceratina strenua	54
Lord Stirling	Lasioglossum paradmirandum	44
Lord Stirling	Lasioglossum hitchensi_weemsi	41
Lord Stirling	Melissodes denticulatus	36
Lord Stirling	Augochlora pura	34
Lord Stirling	Xylocopa virginica	34
Lord Stirling	Agapostemon virescens	21
Lord Stirling	Ceratina dupla	21
Lord Stirling	Ceratina mikmaqi	18
Lord Stirling	Halictus confusus	17
Lord Stirling	Osmia pumila	12
Lord Stirling	Bombus perplexus	8

Lord Stirling Lasioglossum gotham 8 Lord Stirling Megachile sculpturalis 8 Lord Stirling Lasioglossum anomalum 7 Megachile frugalis 7 Lord Stirling 6 Lord Stirling Augochloropsis metallica Lord Stirling Bombus vagans 6 5 **Lord Stirling** Andrena wilkella Lord Stirling Halictus rubicundus 5 5 Lord Stirling Lasioglossum obscurum 5 Lord Stirling Megachile mendica 4 **Lord Stirling** Anthidium oblongatum 4 Lord Stirling Lasioglossum trigeminum Lord Stirling Osmia atriventris 4 Lord Stirling Coelioxys sayi 3 3 Lord Stirling Heriades carinata 3 Lord Stirling Lasioglossum tegulare 3 Lord Stirling Megachile montivaga Lord Stirling 2 Agapostemon sericeus 2 Lord Stirling Lasioglossum atwoodi 2 Lord Stirling Lasioglossum cressonii 2 Lord Stirling Lasioglossum oblongum 2 Lord Stirling Megachile campanulae 2 Lord Stirling Megachile exilis *Melissodes subillatus* 2 Lord Stirling 2 Lord Stirling Nomada pygmaea Lord Stirling Anthidium manicatum 1 1 Lord Stirling Anthophora terminalis 1 Lord Stirling Coelioxys modestus Lord Stirling 1 Hoplitis pilosifrons 1 Lord Stirling Lasioglossum coeruleum Lord Stirling Lasioglossum coriaceum 1 Lord Stirling Lasioglossum illinoense 1 Lord Stirling Lasioglossum nigroviride 1 1 Lord Stirling Lasioglossum oceanicum 1 Lord Stirling Lasioglossum platyparium Lord Stirling Lithurgus chrysurus 1 Lord Stirling 1 Megachile rotundata Lord Stirling Melissodes desponsus 1 1 Lord Stirling Osmia albiventris Lord Stirling Osmia distincta 1 1 Lord Stirling sand wasp_sp Lord Stirling Stelis louisae 1 MU_2013 **Bombus impatiens** 151 MU_2013 Ceratina calcarata 34 MU_2013 Halictus ligatus 26
MU_2013	Ceratina strenua	22
MU_2013	Andrena fragilis	20
MU_2013	Hylaeus affinis_modestus	14
MU_2013	Augochlora pura	13
MU_2013	Bombus bimaculatus	10
MU_2013	Lasioglossum oceanicum	10
MU_2013	Xylocopa virginica	10
MU_2013	Lasioglossum gotham	6
MU_2013	Bombus griseocollis	5
MU_2013	Andrena cressonii	4
MU_2013	Megachile mendica	4
MU_2013	Augochlorella aurata	3
MU_2013	Andrena vicina	2
MU_2013	Bombus fervidus	2
MU_2013	Halictus rubicundus	2
MU_2013	Hylaeus mesillae	2
MU_2013	Agapostemon virescens	1
MU_2013	Andrena alleghaniensis	1
MU_2013	Andrena nasonii	1
MU_2013	Andrena nivalis	1
MU_2013	Andrena nuda	1
MU_2013	Andrena platyparia	1
MU_2013	Andrena robertsonii	1
MU_2013	Anthidium manicatum	1
MU_2013	Augochloropsis metallica	1
MU_2013	Ceratina dupla	1
MU_2013	Ceratina mikmaqi	1
MU_2013	Hylaeus modestus	1
MU_2013	Lasioglossum hitchensi_weemsi	1
MU_2013	Lasioglossum imitatum	1
MU_2013	Lasioglossum obscurum	1
MU_2013	Lasioglossum trigeminum	1
MU_2013	Lasioglossum versatum	1
MU_2013	Lasioglossum viridatum	1
RO_2014	Halictus ligatus	74
RO_2014	Bombus impatiens	65
RO_2014	Augochlorella aurata	17
RO_2014	Lithurgus chrysurus	17
RO_2014	Augochlora pura	10
RO_2014	Lasioglossum versatum	10
RO_2014	Augochlorella persimilis	8
RO_2014	Bombus vagans	5
RO_2014	Ceratina calcarata	5
RO_2014	Bombus griseocollis	4
RO_2014	Agapostemon virescens	1

RO_2014	Bombus bimaculatus	1
RO_2014	Bombus fervidus	1
RO_2014	Bombus perplexus	1
RO_2014	Ceratina strenua	1
RO_2014	Halictus confusus	1
RO_2014	Megachile brevis	1
RO_2014	Megachile mendica	1
RO_2014	Megachile rotundata	1
RO_2014	Melissodes agilis	1
RO_2014	Osmia georgica	1
RO_2014	Xylocopa virginica	1
URWA	Ceratina calcarata	256
URWA	Hylaeus affinis_modestus	240
URWA	Hylaeus mesillae	149
URWA	Lasioglossum versatum	127
URWA	Halictus ligatus	125
URWA	Bombus griseocollis	102
URWA	Bombus impatiens	98
URWA	Bombus bimaculatus	62
URWA	Augochlorella aurata	36
URWA	Andrena wilkella	32
URWA	Lasioglossum gotham	32
URWA	Ceratina strenua	29
URWA	Ceratina dupla	26
URWA	Ceratina mikmaqi	25
URWA	Anthidium oblongatum	16
URWA	Augochlora pura	16
URWA	Halictus confusus	14
URWA	Lasioglossum hitchensi_weemsi	14
URWA	Andrena cressonii	13
URWA	Megachile sculpturalis	9
URWA	Bombus perplexus	8
URWA	Osmia pumila	6
URWA	Andrena imitatrix	4
URWA	Andrena robertsonii	4
URWA	Halictus rubicundus	4
URWA	Lasioglossum atwoodi	4
URWA	Megachile gemula	4
URWA	Megachile mendica	4
URWA	Andrena nasonii	3
URWA	Andrena vicina	3
URWA	Anthophora abrupta	3
URWA	Lasioglossum viridatum	3
URWA	Megachile brevis	3
URWA	Megachile frugalis	3

URWA	Osmia distincta	3
URWA	Xylocopa virginica	3
URWA	Andrena pruni	2
URWA	Augochloropsis metallica	2
URWA	Bombus vagans	2
URWA	Hoplitis pilosifrons	2
URWA	Lasioglossum admirandum	2
URWA	Lasioglossum foxii	2
URWA	Lasioglossum tegulare	2
URWA	Osmia bucephala	2
URWA	Agapostemon sericeus	1
URWA	Agapostemon virescens	1
URWA	Andrena hippotes	1
URWA	Andrena nuda	1
URWA	Andrena wilmattae	1
URWA	Anthidiellum notatum	1
URWA	Anthophora terminalis	1
URWA	Heriades carinata	1
URWA	Hoplitis producta	1
URWA	Hoplitis spoliata	1
URWA	Hylaeus leptocephalus	1
URWA	Lasioglossum birkmanni	1
URWA	Lasioglossum callidum	1
URWA	Lasioglossum oblongum	1
URWA	Lasioglossum obscurum	1
URWA	Lasioglossum oceanicum	1
URWA	Lasioglossum smilacinae	1
URWA	Lasioglossum trigeminum	1
URWA	Lithurgus chrysurus	1
URWA	Megachile melanophaea	1
URWA	Megachile montivaga	1
URWA	Megachile rotundata	1
URWA	Melissodes subillatus	1
URWA	Nomada articulata	1
URWA	Nomada bidentate_group	1
URWA	Osmia albiventris	1
URWA	Osmia georgica	1