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ARTICLE

Rare and declining bee species are key to consistent pollination of wildflowers and crops across large spatial scales

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Abstract

Biodiversity promotes ecosystem function (EF) in experiments, but it remains uncertain how biodiversity loss affects function in larger-scale natural ecosystems. In these natural ecosystems, rare and declining species are more likely to be lost, and function needs to be maintained across space and time. Here, we explore the importance of rare and declining bee species to the pollination of three wildflowers and three crops using large-scale (72 sites across 5000 km^2), multi-year datasets. Half of the sampled bee species (82/164) were rare or declining, but these species provided only ~15% of overall pollination. To determine the number of species important to EF, we used two methods of "scaling up," both of which have previously been used for biodiversity-function analysis. First, we summed bee species' contributions to pollination across space and time and then found the minimum set of species needed to provide a threshold level of function across all sites; according to this method, effectively no rare and declining bee species were important to pollination. Second, we account for the "insurance value" of biodiversity by finding the minimum set of bee species needed to simultaneously provide a threshold level of function at each site in each year. The second method leads to the conclusion that 25 rare and eight declining bee species (36% and 53% of all rare and declining bee species, respectively) are included in the minimum set. Our findings provide some of the strongest evidence yet that rare and declining species are key to meeting threshold levels of EF, thereby providing a more direct link between real-world biodiversity loss and EF.

KEYWORDS
biodiversity, declining, ecosystem function, pollination, rare, space, species, time

INTRODUCTION

Hundreds of ecological experiments have shown that species richness increases ecosystem function in relatively small-scale experiments (Cardinale et al., 2012). Observational studies in larger-scale natural ecosystems have suggested that drivers of function include species richness (Duffy et al., 2017; Liang et al., 2016), abundance

(Lohbeck et al., 2016; Winfree et al., 2015), evenness (Hillebrand et al., 2008; Maureaud et al., 2019; Stevens & Carson, 2001; Wilsey & Potvin, 2000), or a mixture of these (Genung et al., 2020). These observational studies differ from experiments in at least two ways. First, in nature, the effects of biodiversity loss on ecosystem function (hereafter, EF) will depend disproportionately on the functional importance of rare and declining species, which are more likely to be lost (Davies et al., 2004; Loiseau et al., 2020), but most experiments simulate random species loss (Isbell et al., 2017). Second, while there is broad interest in "scaling up" research on how biodiversity affects EF (Gonzalez et al., 2020; Qiu & Cardinale, 2020), different approaches to analyzing datasets at larger scales have been employed, and variation in the results of previous studies may be partly due to variation in methodology. These two issues are not independent, because the importance of rare and declining species may depend on the scale at which importance is measured, as we describe later in the introduction.

Despite recognition that rare species are more likely to be lost from ecological communities, we know relatively little about the contribution of these species to function in nature (Lyons et al., 2005; Säterberg et al., 2019; Violle et al., 2017). A simple and widely-applicable view of EF is that it can be expressed as the product of a species' abundance and per capita function (Balvanera et al., 2005). In this view, rare species would need high per-capita function to make major contributions to EF; but there is limited evidence that this occurs (Gaston et al., 2018; Lohbeck et al., 2016; Smith & Knapp, 2003; Vázquez et al., 2005). Notable exceptions can be found in microbial ecology, where numerically rare species act as keystone species, contributing a much higher percent of EF than their abundance would suggest (Jousset et al., 2017). Among plants and animals, rare species often have unique functional traits, such that they could plausibly sustain functions that other species cannot (Leitão et al., 2016; Mouillot et al., 2013); however, links between rare species' unique functional traits and quantifiable delivery of EF remains an assumption. The points discussed above are specific to the functional importance of one rare species at a specific point in time and space, but this is a limited way to think about the importance of rare species. As most species are rare (McGill et al., 2007; Mouillot et al., 2013), rare species as a group may provide substantial EF. Also, in general, many more species are needed to maintain function across many sites and years at once (Isbell et al., 2011; Winfree et al., 2018); however, no studies have examined whether this pattern holds specifically for rare species.

Even less is known about the EF provided by declining (as opposed to rare) species. Although this might seem a surprising knowledge gap given documented steep declines in some mammal, bird, and insect taxa (Daskalova et al., 2020; Gaston, 2011; van Klink et al., 2020), in fact, ecologists know little about which species are declining for many taxa and many regions (Saunders et al., 2020). We do know that, within clades, declining species often share traits. For example, declining mammals tend to have small geographic ranges, low population densities, and large body sizes (Davidson et al., 2009; Jones et al., 2003). Declining bee species similarly have small geographic ranges and large body sizes (Bartomeus et al., 2013; Hung et al., 2019), and additionally show limited dietary and phenological breadth (Biesmeijer et al., 2006). Traits common to declining species may be functionally relevant. In the case of bees, large body size (commonly considered an important functional trait for bees; e.g., Forrest et al., 2015; Kratschmer et al., 2019) is linked with high pollination efficiency (Kremen et al., 2002), and limited diet breadth suggests declining bee species may be critical for a subset of plant species, namely those that they visit and pollinate (Brosi, 2016).

A second unresolved challenge lies in understanding how the biodiversity-function (BEF) relationship changes with scale (Gonzalez et al., 2020; Qiu & Cardinale, 2020), and what this means for the functional role of rare species. There is a widely acknowledged mismatch between the spatial and temporal scale of experiments, for which typical scales are a 20-L bucket and less than one organismal generation, respectively (Cardinale et al., 2009), and the larger scales that are relevant for EF in nature (Cardinale et al., 2012; Isbell et al., 2017; Jiang et al., 2009). An additional issue is that real-world studies done at large spatial scales (e.g., regional, continental) have generally sampled at many sites to increase extent, rather than increasing grain (i.e., adding many relatively small sites rather than sampling a larger area; Fauset et al., 2015; Kleijn et al., 2015; Lohbeck et al., 2016; Thompson et al., 2018; Winfree et al., 2018). The resulting multi-site (and multi-year) data have been analyzed with different approaches, affecting the apparent importance of rare and declining species, as described below.

One analytical approach is to sum species' contributions to function across space and time, to ask which species are most important to function at broad spatial and temporal scales. Studies taking this approach have concluded that common species drive EF, with rare species playing a less important role (Fauset et al., 2015; Kleijn et al., 2015; Lohbeck et al., 2016). For example, Kleijn et al. (2015), using visitation frequency at crop flowers as a measure of pollination function and combining the data across all sites and dates within a given study, concluded that 80% of all crop pollination at the global scale was done by only 2% of wild bee species. While this is an important point, it is also predictable based on species-abundance distributions. All ecological communities have few common and many rare species, and theoretical (Šizling et al., 2009), empirical (Lima et al., 2020), and meta-analytic (Ulrich et al., 2010) studies suggest this pattern holds not only for local samples of single sites but also for such data summed across many sites. Because function is strongly associated with abundance for pollination (Vázquez et al., 2005; Winfree et al., 2015) and at least some other EFs (seed dispersal, Vázquez et al., 2005; seed dispersal, pest control, nitrogen translocation, Gaston et al., 2018) we should expect that a few species will account for most of the function when data are combined across space and time.

However, maintaining EF not just in aggregate, but at many different places and times separately, is a qualitatively different goal that requires considering compositional turnover (beta diversity) in addition to summed abundances (Bond & Chase, 2002; Thompson et al., 2018; Winfree et al., 2018). The idea that different species are important at different times, or in different places, is a key component of the insurance hypothesis, which holds that seemingly redundant species (i.e., those that perform the same function) provide insurance against the chance that some species fail (McNaughton, 1977; Yachi & Loreau, 1999). An analytical approach that captures the essence of the insurance hypothesis is to find the set of species that are needed to provide an EF at each of many sites and/or years (Winfree et al., 2018). Studies taking this approach have concluded that a high proportion of the species studied are needed to maintain function (Isbell et al., 2011; Winfree et al., 2018). For example, a synthetic analysis of grassland BEF experiments concluded that 84% of plant species were important to function in some place or time (Isbell et al., 2011). However, how many of these species were rare or declining is unknown. Finding that species are not only important to function, but also at high risk of extirpation in nature due to their rarity, would provide stronger inference for how real-world biodiversity loss affects the maintenance of EF.

Here, we study rare and declining wild bee species and their contributions to the pollination of both wildflowers (three species experimentally placed across a 400 km^2 area) and crops (three species studied at commercial farms across a 5000 km^2 area). We collected data on the wildflower species (*Monarda fistulosa*, *Phacelia tanacetifolia*, and *Polemonium reptans*) at 24 sites over 2 years. We collected data on the crops (watermelon, *Citrullus lanatus*; highbush blueberry, *Vaccinium corymbosum*; cranberry, *Vaccinium macrocarpon*) at 48 sites (16 sites per crop) over 2 years. Every bee species in our study was assessed to determine if it was rare and/or declining at the regional scale based on two independent datasets containing a total of 105,729 records of individual bees collected across 1511 locations (see Section *Methods*). Our principal interest is understanding the functional consequences of realistic species loss. For this reason, we mostly do not separate the two groups and instead consider the combined effect of losing rare and declining species, both of which are at risk (albeit in different ways). However, some discussion points are specific to either rare or declining species. We used a genetic algorithm optimizer to find the minimum number of bee species needed to meet pollination thresholds across an increasing number of sites and years at once, that is, to ask how the need for bee biodiversity increases with increasing spatial and temporal scale. Specifically, we asked three questions: Q1. What percentage of all pollination carried out by native bees is done by species that are rare and/or declining? Q2. How many rare and/or declining bee species are found to be important pollinators when the data are summed across sites and years? Q3. How many rare and/or declining bee species are found to be important pollinators when the data are analyzed for each site and year separately?

METHODS

Study species and study design

Our wildflower study took place over 2 years (2017–2018) at 24 study sites in central New Jersey (i.e., 48 site-years per plant species). Sites were distributed across a 400 km^2 area in a grid design with 5 km between sites (Appendix S1: Figure S1). At each site, we placed a single fenced array of potted, experimental study plants, with three 7-gallon pots of each of three plant species. All arrays were in a sunny areas 10–20 m from natural forests, such that bee communities typical of both forests and more open habitats would be present. The first experimental plant species (*Polemonium reptans*) is a forest species while the other two (*Phacelia tanacetifolia* and *Monarda fistulosa*) are found in more open habitats. The wildflower species were chosen based on whether: (1) their floral morphology was amenable to single-visit deposition experiments; (2) their flowering phenologies had little overlap so we could more easily shift sampling effort from one species to another; (3) they were pollinated by, and attractive to, wild bees. *M. fistulosa* could be found in the local flora near our arrays. *P. reptans* is a native species but It is now very rare or locally extirpated across our wildflower study sites. The experimental plants and the wild individuals flowered at roughly the same time. *P. tanacetifolia* is not native to our study region. We also studied two native (blueberry, *Vaccinium corymbosum*; and cranberry, *Vaccinium macrocarpon*) crops and one non-native crop (watermelon, *Citrullus lanatus*) that rely on wild bees for pollination. Each crop was studied at 16 commercial farms (hereafter, sites) in a 100 km × 50 km region in central and southern New Jersey and eastern Pennsylvania over 2 years (i.e., 32 site-years per crop species). The wildflower data have not been previously published and were collected for the purpose of this study; the crop data are previously published and more details on these data sets can be found in Winfree et al. (2015, 2018).

For this analysis, we focused on bees and excluded other pollinators for three reasons. First, bees represented most flower visits (84% and 90% of sampled individuals in the wildflower and blueberry data, respectively; non-bees were not sampled off cranberry or watermelon), with flies representing almost all the remainder. Second, for the common fly taxa (bombyliids, syrphids), we assessed pollen deposition rates and found them to be very low. Finally, there are far fewer historical records and regional collections of non-bee pollinators available, which would make our designations of rare and/or declining species (hereafter simply "rare and declining" for brevity) for other taxa such as flies unreliable.

In principle, we are interested in the reliability of pollination over both space and time (i.e., sites and years). However, we have much better replication in space (16–24 sites per plant species) than in time (2 years per plant species). Therefore, an analysis for time (for example, "how many bee species are needed to meet pollination thresholds across all sites in 1 year versus 2 years?") would be uncompelling. Instead, we consider each site-year as the unit in which the pollination threshold must be met. Requiring thresholds to be met for each site-year has implications for finding the number of important pollinators, as described in the *Minimum set analysis* section, below.

Bee sampling

For the wildflowers, in each of 2017 and 2018, we vacuum-collected individual bees throughout the flowering of each plant species (April–May for *P. reptans*, June–July for *P. tanacetifolia*, July–August for *M. fistulosa*) so that we could identify bees to the species level. Sampling occurred when temperatures were at least 17°C and wind speed was less than 4.5 m/s. Due to variable weather conditions and flowering duration, there were differences in sampling time across site-years. For this reason, we express each bee species' contribution to pollination function on a per-minute basis (i.e., in units of pollen grains delivered per minute; details in the *Per-visit pollen deposition* section, below). Variation in sampling time could have in principle also affected bee richness, and thus our chance of finding rare and declining bee species, but we found no evidence of this (Appendix S2).

For crops, bees were net-collected along fixed 50–200 m^2 transects of crop row at the same time each day. Collection effort was 60 min site^{-1} day^{-1} for blueberry and watermelon, and 120 min site^{-1} day^{-1} for cranberry, with 2 years of sampling for each crop (blueberry, 2010–2011; cranberry, 2010–2011; watermelon, 2009–2010). Sampling corresponded with peak bloom of each crop: (April–May for blueberry; May–July for cranberry; July for watermelon). Weather conditions for sampling varied by crop because the crops bloom at different times of year but were standardized across sites and dates within a crop. For more details, see (Winfree et al., 2015). We did not collect European honey bees (*Apis mellifera*), which are a managed species in our study region. Distances between sites exceeded the flight range of most bee species in our study, such that sites were considered independent replicates.

Sampling bias between net and vacuum collection is expected to be small (Stephen & Rao, 2007), especially when (as was the case here) bees are not collected at heights that vacuums cannot reach and vacuums are strong enough to sample all bee species. Bees collected off wildflowers were identified by JG. Bees collected off crops were identified by professional taxonomists (see the *Acknowledgements* section). All specimens are housed in the Winfree laboratory at Rutgers University. Over 98% of specimens are identified to species, with 99.9% identified to at least species pairs that are hard to distinguish even for taxonomists.

Per-visit pollen deposition

We use per-flower-visit pollen deposition as a proxy for per-flower-visit pollination. This proxy necessarily focuses on the quantity-related aspect of pollination function while ignoring pollen quality aspects, which also can contribute to differences in plant reproduction success (Aizen & Harder, 2007; Chacoff et al., 2008; Herrera, 1987). Despite such streamlining of the complexity of pollination function, our approach goes significantly beyond other commonly-used approaches which consider flower visitation rates as proxies for pollinator importance (Kleijn et al., 2015; Vázquez et al., 2005).

For both crops and wildflowers, to estimate how much pollen different bee species deposit per visit, we performed "single-visit experiments" in which we allowed a single bee to visit an unpollinated flower. After a waiting period to allow pollen to adhere, we removed stigmas, preserved them in ethanol, and stained them (Appendix S1) so we could count the number of conspecific pollen grains deposited. In the single visit experiments, we assigned bees to morphogroups because it was not possible to identify most bee species on the wing and to get enough data to estimate pollen deposition rates (details in Appendix S3). Thus, estimates of per-visit pollen deposition are at the morphogroup, rather than species, level. Pollen deposition rates largely depend on body size (Földesi et al., 2021) and hairiness (Stavert et al., 2016), such that morphologically similar pollinators should have similar deposition rates. The morphogroup approach could overestimate (or underestimate) the functional importance of a species, if that species' true pollen deposition rate is lower (or higher) than the group mean. However, there is no reason to expect our approach consistently over- or underestimates the functional importance of rare and declining species. For each bee species, we multiplied flower visitation frequency (measured at the species level through sampling from flowers) by mean per-visit pollen deposition (measured at the morphogroup level during pollen deposition experiments) to get an estimate of that species' contribution to pollination to each plant species, for each site-year combination (Winfree et al., 2015, 2018).

Defining rare bee species

We defined species as regionally rare based on two independent datasets. The first, or "contemporary" dataset includes specimens collected from pan traps and plants in New Jersey and Pennsylvania between 2003 and 2016 by the Winfree lab group, which are stored on the campus of Rutgers University (New Brunswick, New Jersey, USA). This dataset contains 87,026 specimens collected from 228 sites. More details on the study designs and collection methods used to generate these data sets can be found in MacLeod et al. (2020). The second, or "museum", dataset includes specimens collected in the states of Pennsylvania, New Jersey, and New York between 2003 and 2011, which are stored at the American Museum of Natural History (New York, New York, USA). This dataset contains 18,703 specimens collected from 1283 sites by at least 1550 different collectors. More details on the generation of this data set can be found in Bartomeus et al. (2013).

We defined rare species as those occupying <5% as many sites as the commonest species, following the methods of Mouillot et al. (2013), in either the contemporary or museum dataset. To avoid including species on our rare list that are in fact abundant but were not collected within one of our two datasets (potentially because the species' habitat or host plant was under-sampled in that dataset), we removed from the rare species list any species that was rare in one dataset but within the top 10% of most frequently collected species in the other dataset. This resulted in removing 5 of 72 species from the rare species list. See Appendix S4 for the complete list of bee species we considered rare as well as more details on our methodology.

Defining declining bee species

The declining bee fauna in our region has already been assessed by Bartomeus et al. (2013), who defined declining bee species as those showing a significant decline in sampling detection between 1870 and 2011. For their analysis, Bartomeus et al. (2013) used bee collection data from across the northeastern United States (30,138 specimens from 11,295 sites). See Appendix S4 for declining species list, which is identical to that published in Bartomeus et al. (2013).

Minimum set analysis

There is no definitive method for identifying "important" species, but one option is a minimum set analysis, which finds the minimum number of species that can provide a target threshold of function. In BEF research, this is often determined by measuring function across many sites, and then finding 50% of either average or maximum function (Allan et al., 2011; Winfree et al., 2018). A minimum set analysis tells us the number *and* identities of the species that represent the most efficient path to meeting the EF thresholds at all sites where data were collected, which we argue is a first approximation of the most important species for maintaining function across a larger spatial extent. Knowing how many rare and declining species are included in the minimum set provides information about the robustness of function to species loss. If many are included, it is likely that EF will be lost rapidly as biodiversity declines.

To determine how many rare and declining species are important to function when the data are summed across sites and years (Q2), we first divided data by plant species. Second, we summed each bee species' contributions to pollination across sites and years and sorted these contributions from highest to lowest. Then, it is a simple matter of adding species in order of their pollination until 50% of total function was accounted for. This gives us the minimum set, and we can finally check how many of the included bee species were rare and declining.

To determine how many rare and declining species are important to function when the data are analyzed for each site and year separately (Q3), we again divided data by plant species. However, in this case we needed an optimizer; we chose to use a genetic optimizer algorithm (the GAPerm() function in R package *gaoptim*). This optimizer finds the minimum set of species that can provide 50% of mean observed pollination for an increasing number of site-years, where the mean was taken across all site-years for the chosen plant species. The first site is chosen at random ($n = 999$ replicates), with subsequent sites added in order of geographic proximity. For each chosen site, we require the threshold to be met in both years before moving on to the next site. In other words, for each site, we account for how variation in the bee community over time increases the size of the minimum set (to the limited extent possible, given 2 years of data).

Once we had the minimum set for each plant species, we found the number of unique bee species important to maintaining pollination for an increasing number of plant species. In this analysis, for all possible combinations of one to six plant species, we found the intersection of the minimum sets of each included plant species, which was the number of unique bee species that were important to maintaining pollination for that combination of plant species. We then determined how many of the bee species selected in this minimum set were rare and declining. This analysis builds on recent studies (Allan et al., 2011; Isbell et al., 2011; Winfree et al., 2018) by asking how many species (here, specifically rare and declining species) are important to maintaining function for at least one plant species, in at least one place and time.

Throughout the main text we use 50% of the mean observed function (mean across sites and years) as the threshold level of pollination that must be met at each site in each year. Defining thresholds based on a percent of observed function across samples is a common approach in biodiversity research (Allan et al., 2011; Gamfeldt et al., 2008; Winfree et al., 2018; Zavaleta et al., 2010). While some other studies have set the threshold as 50% of the maximum observed function in any sample (e.g., Allan et al., 2011; Gamfeldt et al., 2008), we chose to use 50% of the mean because the mean is far less sensitive to sample size (i.e., an increasing number of sites). Setting the pollination threshold based on mean function makes our results more conservative. If we had set a higher threshold (e.g., 50% of maximum function), more rare and declining species would have been needed. See Appendix S5: Figure S1 for sensitivity analysis on the choice of threshold.

RESULTS

We collected 8474 individual bees of 110 species visiting wildflowers, and 6520 bees of 111 species visiting crops. Of the combined total of 164 unique bee species, 70 (43%) were rare and 15 (9%) were declining. Three species (2%) were both rare and declining, such that 82 (50%) of the bee species we observed in our study were rare and/or declining (Appendix S4: Table S1). Rare and declining bee species accounted for 13.7% ± 1.8% (mean ± 95% CI across plant species) of abundance and 14.7% ± 2.0% of pollination (i.e., total number of pollen grains deposited) (Figure 1). A non-statistical comparison of average percent abundance and percent function across site years shows that rare and declining bees accounted for a lower percent of abundance on wildflowers compared with crops but provided a similar percent of function to both (wildflowers: 10.5% ± 1.9% of abundance, 14.3% ± 2.9% of pollination; crops: 18.5% ± 3.1% of abundance, 15.3% ± 2.7% of pollination).

When the entire dataset for each plant species was summed across sites and years prior to finding the minimum set of functionally important bee species, plant species needed zero or one (mean across plant species: 0.67) rare and declining bee species. The threshold level of pollination for all six plant species together could be met by three rare and declining bee species, which is only 4% of the 82 rare and declining species in the study. Thus, this analysis approach leads to the conclusion that few rare and declining species are functionally important.

When the analysis required a threshold level of pollination to be met at each site and in each year, the minimum set of bee species needed by a plant species included 6.9 rare and declining bee species, on average (Figure 2). For some plant species, these accumulation curves reached a clear asymptote, but for other plant species the number of rare and declining bee species needed would likely increase if more sites were added (Figure 2).

To meet the threshold for all six plant species at once, a total of 32 of 82 (40%) rare or declining bee species were needed. The increase in the size of the minimum set across plant species was nearly linear (Figure 3). This linear increase suggests that adding more plant species to our analysis would substantially increase the number of important rare and declining bee species. Of the 32 functionally important species, 24 were only rare, seven were only declining, and one was both rare and declining. Thus, 25 of 70 (36%) of rare species and 8 of 15 (53%) of declining species were needed. It is critical to note that a species can be “declining” only if it is sampled often

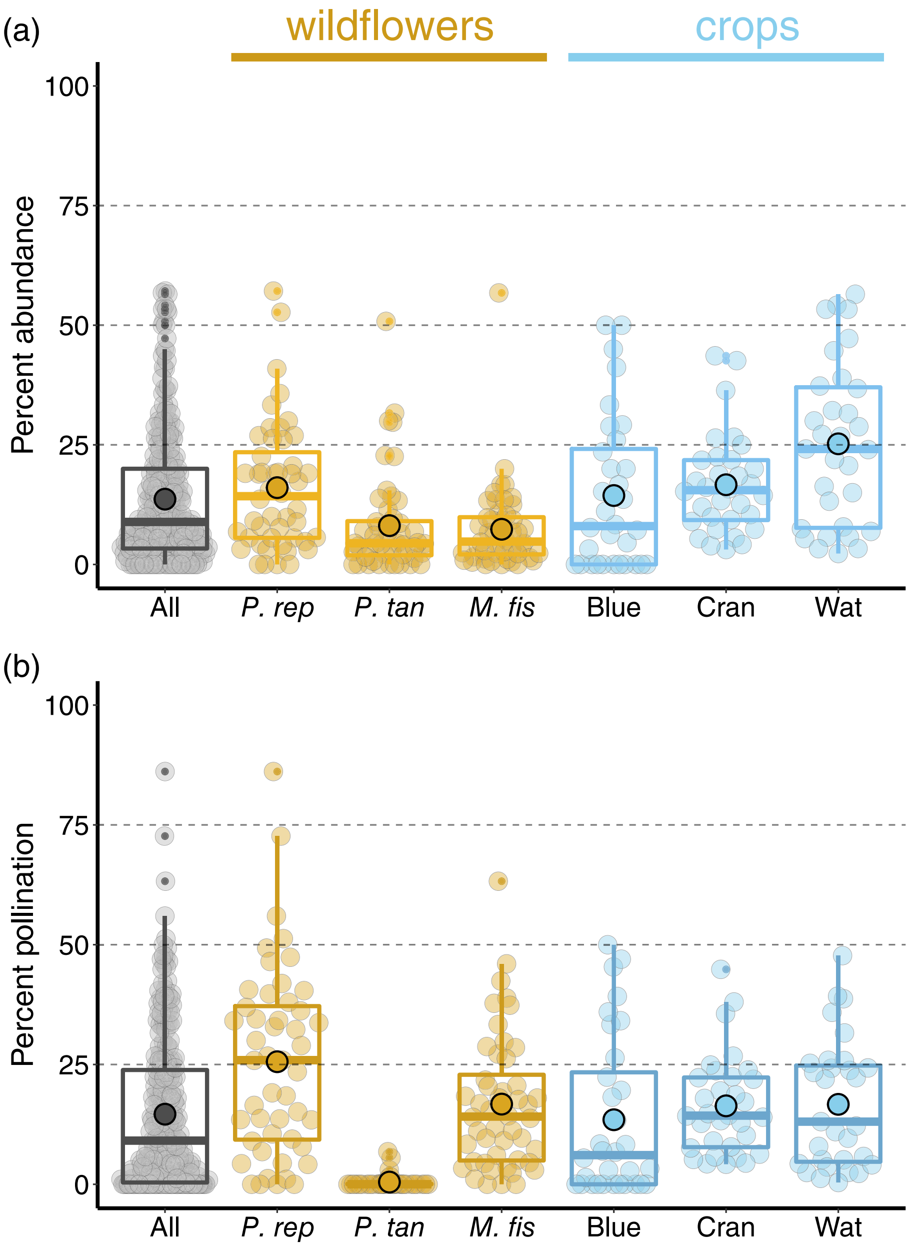

FIGURE 1 Boxplots showing (a) the percent of total abundance accounted for, and (b) the percent of total function provided, by rare and declining bee species. In both panels, each data point is one site-year. The gray boxplot combines all datapoints across plant species, within each panel. Abbreviations on the *x*-axis are, from left to right: *Polemonium reptans*, *Phacelia tanacetifolia*, *Monarda fistulosa*, blueberry (*Vaccinium corymbosum*), cranberry (*Vaccinium macrocarpon*), and watermelon (*Citrullus lanatus*). Boxplot lines show the median, 25th and 75th percentiles. Whiskers extend to the highest and lowest values no more than 1.5 times the interquartile range.

enough for analysis of temporal trends, and there may be rare species that are declining but were not detected as such. As a result, our results may have underestimated the number of important declining species, while overestimating the percent of important declining species. Regardless of the exact numbers, this analysis leads to the conclusion that many rare and declining species are functionally important.

Rare and declining species are both at increased risk of extirpation, making both groups especially relevant for any links between species loss and EF. However, if these groups are analyzed separately, there are minor differences. First, rare species accounted for 96% as much pollination as expected based on their abundance (7.4 ± 1.3% of abundance, 7.2 ± 1.4% pollination), while declining species accounted for 114% (7.5 ± 1.4% of abundance, 8.6 ± 1.6% of function) (Appendix S4: Figure S1). This aligns with previous research showing that larger-bodied bees, which are more effective pollinators (Földesi et al., 2021), are more likely to be in

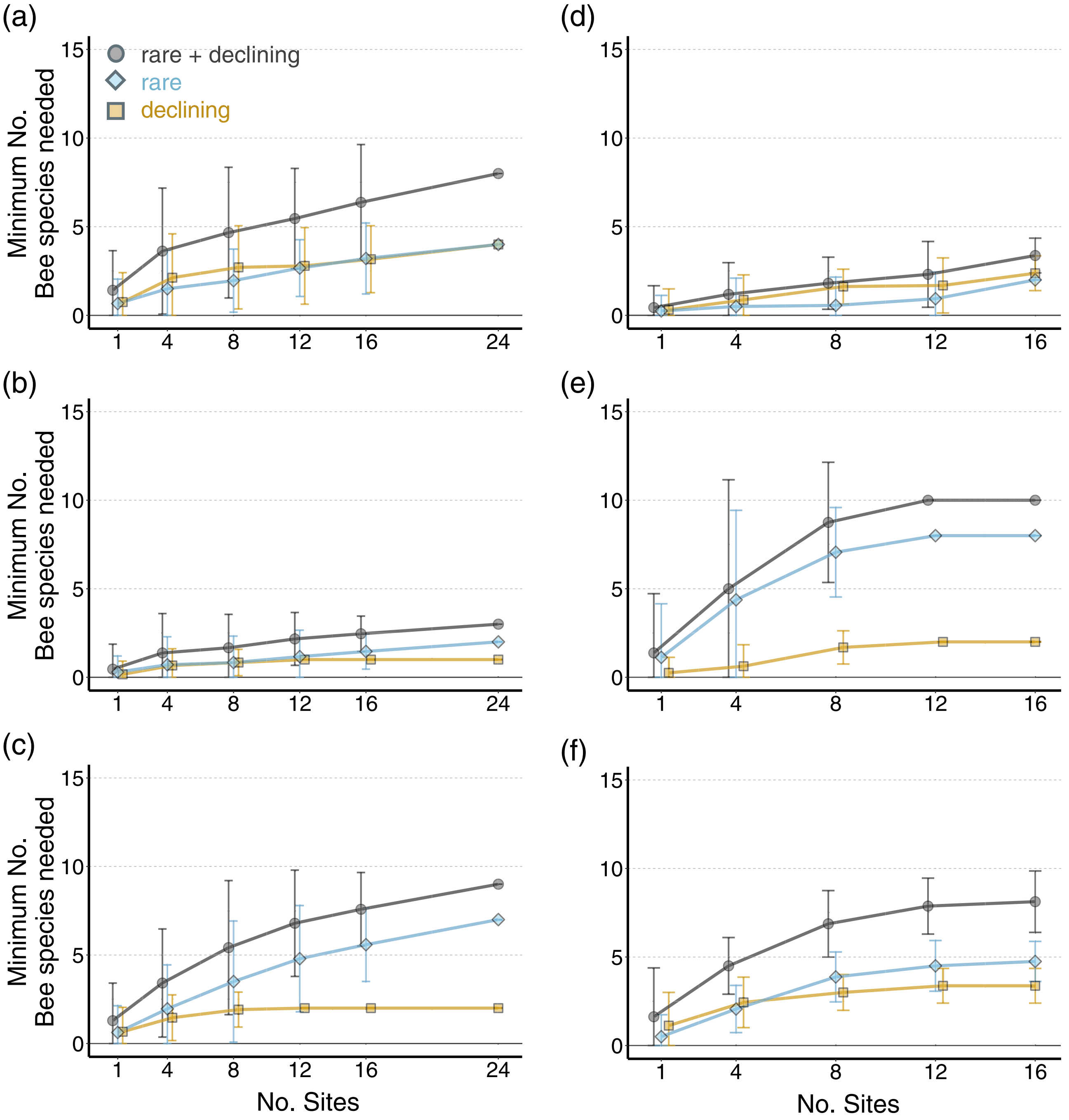

FIGURE 2 The minimum number of bee species that can meet pollination thresholds increases as the thresholds must be met at more sites. The initial site is chosen at random, and the minimum set is calculated to meet the threshold in both years of data. Beginning with the second site, sites added in order of geographic proximity to the first site. Error bars reflect different patterns of adding sites at random. Each panel is one plant species: (a) *Polemonium reptans*, (b) *Phacelia tanacetifolia*, (c) *Monarda fistulosa*, (d) blueberry (*Vaccinium corymbosum*), (e) cranberry (*Vaccinium macrocarpon*), and (f) watermelon (*Citrullus lanatus*).

decline (Bartomeus et al., 2013; Biesmeijer et al., 2006). Second, on a per-species basis, declining species were more important, as 53% of declining species were important to maintaining function compared with only 36% of rare species.

DISCUSSION

Biodiversity clearly enhances EF in experiments (Cardinale et al., 2012), but questions remain about whether more or fewer species are important to EF in

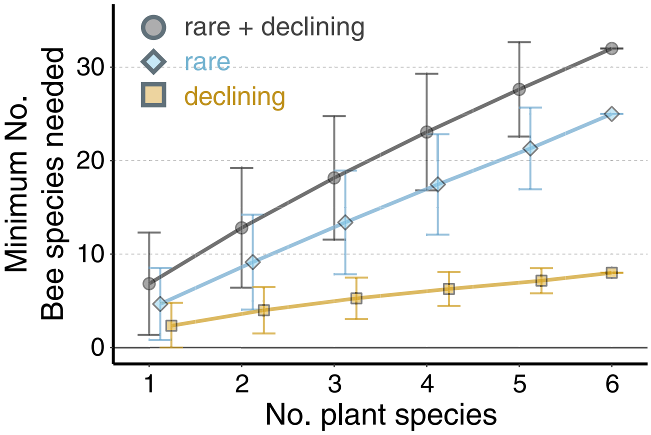

FIGURE 3 The minimum number of bee species that can meet pollination thresholds increases as the thresholds must be met for one to six plant species (*Polemonium reptans*, *Phacelia tanacetifolia*, *Monarda fistulosa*, blueberry (*Vaccinium corymbosum*), cranberry (*Vaccinium macrocarpon*), and watermelon (*Citrullus lanatus*). Error bars reflect different patterns of adding plant species at random.

nature, given the realistic loss of rare and declining species (Genung et al., 2020; Srivastava & Vellend, 2005; Wardle, 2016) at larger spatial and temporal scales (Cardinale et al., 2012; Isbell et al., 2011; Jiang et al., 2009). Our results show that these issues are fundamentally linked, as the number of rare and declining bee species that were important to pollination varied dramatically depending on the spatial scale at which pollination needed to be maintained. Averaging across site-years, the 50% (82/164) of bee species that are rare and/or declining accounted for only 15% of pollination (Figure 1). However, there was wide variability among site-years, with rare and declining bee species providing up to 86% of function in particular places and times. This variability is the key property governing the importance of spatial scale. When we summed species' pollination across site-years (ignoring variability among site-years), only three rare and declining bee species were needed to meet pollination thresholds for all plant species. However, when we required pollination to be maintained across all site-years simultaneously, an order of magnitude more rare and declining bee species ($n = 32$) were needed. Thus, rare and declining bee species were important not through exceptional per-capita function, but rather based on the requirement that function be maintained across space and time. These results lend strong support to the idea that species known to be rare or declining are essential for maintaining EF across space and time in nature.

Our first method, in which data were summed across site-years, has been commonly used to "scale up" BEF research. Previous studies using similar approaches have found that rare species contribute little to EF (Fauset et al., 2015; Kleijn et al., 2015; Lohbeck et al., 2016). We might expect this result given that ecological communities contain few numerically dominant and many rare species (McGill et al., 2007; Ulrich et al., 2010) regardless of the scale at which the community is sampled (Lima et al., 2020; Šizling et al., 2009; Ulrich et al., 2010). This argument assumes that species' abundances and contributions to function are reasonably well-matched, an assumption that seems to hold for pollination: pollinator species vary more in abundance than they do in per-capita function, such that the species delivering the most pollen at the species scale tend to be the most abundant species (Ballantyne et al., 2017; Vázquez et al., 2005; Winfree et al., 2015). When we combined data across plant species, rare and declining bee species accounted for nearly the same percent of abundance and pollination. However, at the level of individual plant species, we observed that rare and declining bee species sometimes provided much high, or much lower, percent pollination relative to their percent abundance (Figure 1). Thus, while there is no overall trend of rare and declining bee species overcoming their low abundances with high per-capita pollination rates, it is possible for some plant species.

When we required pollination thresholds to be met for all sites and years separately, our conclusion was starkly different: 40% ($n = 32/82$) of the rare and declining bee species were needed. The fact that rare and declining bee species are more important when function must be maintained across space and time is not necessarily surprising, as biodiversity should provide insurance effects that maintain function when some species fail (McNaughton, 1977; Yachi & Loreau, 1999). Observational studies of the BEF relationship support this idea; for example, there is spatial (Fauset et al., 2015) and temporal (Allan et al., 2011) turnover in the identity of dominant species, such that different species are key for function in different times or places (Isbell et al., 2011; Winfree et al., 2018). However, showing that rare and declining species are important to maintaining function is a new advance, not least because it is suggests extensibility of experimental results, such as those showing that nearly all species contribute to EF under some conditions (Isbell et al., 2011), to natural communities where many species are rare and/or declining (McGill et al., 2007; Mouillot et al., 2013; Young et al., 2016).

Overall, rare and declining bee species accounted for similar percentages of flower visits and pollination (gray points, Figure 1). However, focusing on this pattern obscures differences among plant species. The two non-native plant species (*P. tanacetifolia* and watermelon) received roughly 8% less pollination than expected from rare and declining bee species (Figure 1). Because pollinators are the main selective agent for floral traits (Caruso et al., 2019), this may reflect a mismatch between non-native plant floral morphology and native pollinator traits and foraging behavior (Aslan et al., 2012). In contrast, the native wildflower species received roughly 9% more pollination than expected from rare and declining species, and percent abundance and pollination were almost exactly matched for the native crops (Figure 1).

Biologically, there are properties of rare and declining species that make them likely to contribute to function at specific times or in specific places, even if they are not widespread or abundant. Regionally rare pollinator species are more likely to be floral specialists (Willmer, 2011). As a result, they may be locally abundant and thus key pollinators at sites where their host plant occurs but still regionally rare because they occur at few other sites. This held for blueberry and cranberry, which are native crops with specialized bee communities. For example, *Colletes validus* and *Melitta americana*, two regionally rare bee species, accounted for 15% and 8% of visits to blueberry and cranberry, respectively. A different set of mechanisms applies to declining species. First, some declining bee species are still regionally abundant despite negative trends. In our study, the declining but still highly abundant *Lasioglossum imitatum* was an important pollinator of both *P. tanacetifolia* and *M. fistulosa* by virtue of its abundance, despite being a relatively inefficient pollinator. Second, declining bees may be important pollinators because they tend to be large-bodied (Bartomeus et al., 2013; Biesmeijer et al., 2006) and large-bodied bees generally deposit more pollen (Földesi et al., 2021). Our results were consistent with these expectations, as declining bee species deposited 14% more pollen than would be expected based on their abundance (Appendix S4: Figure S1). The clearest illustration of this pattern is *Bombus fervidus*, a large-bodied declining bumblebee which provided 364% and 496% more pollination than expected based on its abundance to *P. reptans* and *P. tanacetifolia*, respectively.

Despite concerns about how biodiversity loss affects EF, we know little about how often, and how much, rare species (Dee et al., 2019) and declining species contribute to EF. Because pollination is driven by abundance (Ballantyne et al., 2017; Vázquez et al., 2005; Winfree et al., 2015), our results may underestimate the number of important rare species relative to other types of EF that depend less on species' abundances. Rare species, and to a lesser extent declining species, may be more important for maintaining EFs in cases where species exhibit greater variation in per-capita contribution (Kirby & Potvin, 2007), because their low abundance could more easily be counteracted by exceptional per-capita function. Continuing to explore when and where rare and declining species are important for delivering measurable contributions to function is key for BEF research, which at its core aims to understand how ongoing biodiversity changes affects the ecosystems functions that support human well-being.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Genung et al., 2022a) are available in Dryad at https://doi.org/10.5061/dryad.qnk98sfkc. Code (Genung et al., 2022b) is available in Zenodo at https://doi.org/10.5281/zenodo.6711198.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Ecology

Rare and declining bee species are key to consistent pollination of wildflowers and crops across large spatial scales

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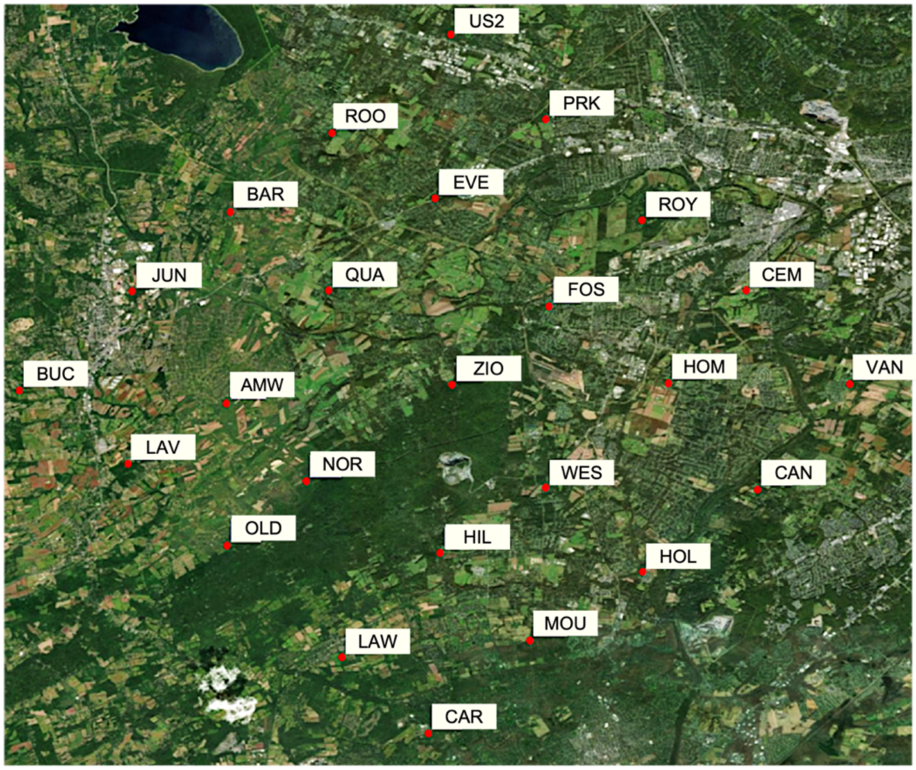
Appendix S1. Detailed methods

Figure S1. Site map. Sites were arranged in a 5x5 grid in central New Jersey as seen in the satellite image below. Sites are between latitudes 40.357 and 40.614 N and longitudes 74.557 and 74.892 W. Site "NOR" is not included in our analyses because we could not get permission from private landowners to use their property by the time the study began.



“Pollen deposition per visit” methods.

Detailed protocols on the single-visit experiments for crop plants are already published in (Cariveau et al. 2013). Here, we provide a detailed single-visit protocol for the wildflowers. First, we excluded pollinator visits to flowers of each focal species using mesh coverings. In the case of *P. reptans* and *P. tanacetifolia* we placed entire pots within tulle cages, whereas with *M. fistulosa* we secured fine mesh pouches over indehiscent flower heads and reinforced the bagged stems by securing them to bamboo posts. Mesh pouches were too large for *P. reptans* and *P. tanacetifolia* given the spacing of flower heads. On appropriate sampling days we selected inflorescences with receptive stigmas individually, cut them from the plant 1-5 cm below the inflorescence, and immediately placed the cut end within a floral water tube. If we suspected any other flowers within the cages were disturbed, we carefully discarded those flowers to minimize potential for contamination. With the selected inflorescence (hereafter “focal inflorescence”) in hand we monitored a small garden population of the same plant species for visitors. While monitoring for visitors we carefully monitored the focal inflorescence for possible contamination. If we suspected contamination by events such as a gust of wind or a brush with vegetation, or if we were unable to locate a visitor within 15 minutes of beginning our search then we discarded the focal inflorescence and restarted the process.

When an appropriate visitor was spotted on a conspecific flower, we presented the focal inflorescence as near to the visitor as possible without allowing the flowers to touch and allowed the visitor to either fly or walk onto the experimental flowers. We held the focal inflorescence steady to allow the visitor to work undisturbed. At initial contact with the focal inflorescence, we began a stopwatch to record the duration of the visit. We also made note of the morphogroup (Appendix 3), sex, resource collected (i.e., pollen, nectar, or both), and a description of the flower handling strategy used by the pollinator. If a visitor departed from the flower having only made brief contact with non-reproductive flower structures, we classified it as non-foraging contact and restarted the process with a new focal inflorescence.

When the visitor departed, we protected the focal inflorescence from further visits. We removed all anthers from open flowers and removed any unopened flower buds or post-anthesis flowers. This was after flower visitors had completed their visit and thus the removal of anthers could not affect visitation patterns or behavior. We assigned each flower within an inflorescence a unique ID number and recorded notes on the order of pollinator visitation. Each species received a distinct post visit processing treatment. For *P. reptans* we marked or removed any flowers on the inflorescence that we were certain did not receive a direct visit. We counted these flowers separately as a control group. We also marked flowers individually and noted the order that the pollinator visited them. For *P. tanacetifolia* we removed any flowers with fully desiccated petals that were not adjacent to an active flower. The flowers of *P. tanacetifolia* are held in tightly packed cymes and the stigmas remain receptive for a short period after the petals have wilted, leaving the possibility of incidental pollination of unattractive flowers. We counted pollen grains on all stigmas in the inflorescence. For *M. fistulosa* we removed any flowers from the head on which the stigma lobes had not yet split (indicating the stigma was too young to receive pollen) or the style had fully reflexed or desiccated (indicating the stigma was no longer receptive). We counted pollen grains on all stigmas in the inflorescence. We did not remove the anthers from *M. fistulosa* flowers, as tests with anthers on flowers yielded miniscule contamination and removing anthers proved logistically challenging. *P. tanacetolia* and *M. fistulosa* flowers were time-consuming to process. To limit processing time, if the visitor was from a morphogroup for which we already had three data points we subsampled the flowers within the inflorescence by removing each alternate flower along the inflorescence. Comparing subsampled and non-subsampled flowers revealed no differences.

On each sample day we also collected focal inflorescences to act as a control group. Control inflorescences were removed from the plant and handled the same as single-visit flowers, including mimicking the motions of searching for a visitor, for five minutes, but were then processed without allowing a visitor to interact with the flower. For *P. reptans*, we found no differences between these controls and the "unvisited flowers" controls described above.

We stored the focal inflorescences still in the flower vials for 24 hours inside of a closed container at room temperature to allow pollen grains to adhere to the stigma surface. After this waiting period, we plucked the stigmas from the focal inflorescence, including as much of the style as possible to aid with handling. We placed the stigma from each flower into a separate microcentrifuge vial containing 70% EtOH and allowed them to rest for another 24 hours.

We mounted the stigmas on microscope slides with fuchsin stain suspended in glycerin. The slides were heated on a hotplate and a 1mm cube of fuchsin gel was placed in the center and allowed to melt. We gently dried the tissues by brushing the style with a Kimwipe, then placed the stigma within the drop of fuchsin and gently pressed a cover slip on top. We allowed the slides to cool upside down on a rack to encourage pollen grains to migrate upward on the slide. We stored completed slides in a refrigerator until we were able to count pollen grains. We counted pollen grains under a compound light microscope within 5 days of mounting the stigmas to avoid deterioration of the fuchsin stain. We defined the stigmatic surface on *P. reptans* as the adaxial surface of the stigma starting from the point of separation between the three carpels and extending upward. For *P. tanacetifolia* we considered the stigmatic surface as the papillate surface at the very tip of the style. We defined the stigma of *M. fistulosa* as the surface of both lobes of the stigma above the fork in the style. We counted any grain in direct contact the stigmatic surface or within 1 pollen grain diameter of the stigmatic surface as long as no other pollen grains were in between it and the surface. This buffer area was applied because grains often move slightly away from receptive surfaces when the cover slip is placed. This means that in multilayered clumps of pollen only those of the first layer were counted because grains beyond that layer were unlikely to lead to successful pollen tube development. We identified each grain on the stigmatic surface as either conspecific or heterospecific and counted each group separately.

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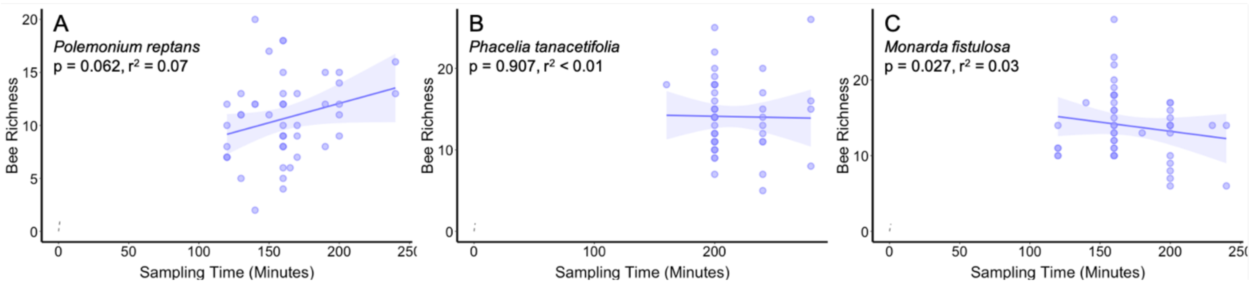
Rare and declining bee species are key to consistent pollination of wildflowers and crops across large spatial scales

Mark A. Genung[1,*], James Reilly[1], Neal M. Williams[2], Andrew Buderi[3], Joel Gardner[4], Rachael Winfree[1]

Appendix S2. Wildflower sampling time

In the wildflower data, sampling time varied among sites due to weather, short and unpredictable flowering time, and intermittent site access issues (all sites were on private land that we did not own). For each bee species, we express pollination function (and therefore the pollination threshold) as pollen grains per minute; thus, we prevent the undesirable case in which sites do not reach the threshold because of less sampling. However, it is still possible that sampling effort varies enough to affect sampled bee richness, which could affect the minimum set analysis. If sampling varies enough to affect bee richness, then under-sampled sites may be missing rare (and to a lesser extent, declining) species that could be part of the minimum set.

Figure S1. Sampling time and bee richness. Panels shows the relationship between sampling time and bee richness for the three wildflower species. None of the relationships are statistically significant, and even the borderline-significant relationship in panel A has low explanatory power.


A
Polemonium reptans
p = 0.062, r² = 0.07
B
Phacelia tanacetifolia
p = 0.907, r² < 0.01
C
Monarda fistulosa
p = 0.027, r² = 0.03
Bee Richness
0
5
10
15
20
Sampling Time (Minutes)
0
50
100
150
200
25

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Appendix S3. Assignment of bee species to morphogroups

During the “pollen deposition per flower visit” protocol, we identified bees on the wing to the most precise taxonomic group possible (either species or genus). It was practically impossible to estimate “pollen deposition per flower visit” for every bee species, because not all species could be identified on the wing, many bee species are rare, the protocols and time-consuming, and a small sample size would not produce a reliable estimate. Therefore, we grouped morphologically similar species together (Cariveau et al. 2013) and calculated group means for “pollen deposition per flower visit”. The same bee species is sometimes in different morphogroups across plant species, because the clearest approach for alleviating sample size concerns varied across plant species. Some species are split into female (♀) and male (♂) designations because of sexual dimorphism. For some species we sampled females but not males (or *vice versa*), so not all species-sex combinations are included. Morphogroups for the crop species are given in (Table S1 in Winfree et al. 2015).

Species and group notes

The "core" morphogroups, present for all wildflowers, are tribe Augochlorini, genus *Bombus*, genus *Ceratina*, "Medium", "Small Dark", and "Tiny Dark", and genus *Xylocopa*. Obviously, some of these groups are taxonomically broader than others. Because of their size, small and tiny dark bee species are difficult to separate on the wing, leading to them being lumped together. "Medium" is a catch-all for medium-sized bee species that are not classified in other groups (e.g., Augochlorini, Megachilidae, genus *Melissodes*). Family Megachildae was a morphogroups for two of three wildflower species (we did not have enough sample size for a Megachilidae group for *P.reptans*). Finally, there are a few groups that are unique to one wildflower species, listed at the bottom of the following table.

Table S1. List of bee species in each morphogroup, by plant species

Polemonium reptans	***Phacelia tanacetifolia***	***Monarda fistulosa***
Augochlorini *Augochlora pura* *Augochlorella aurata* *Augochloropsis metallica*	Augochlorini *Augochlora pura* *Augochlorella aurata* *Augochloropsis metallica*	Augochlorini *Augochlora pura* *Augochlorella aurata* *Augochloropsis metallica*
Bombus *Bombus bimaculatus* *Bombus fervidus* *Bombus griseocollis* *Bombus impatiens* *Bombus perplexus*	*Bombus* *Bombus bimaculatus* *Bombus fervidus* *Bombus griseocollis* *Bombus impatiens* *Bombus perplexus*	*Bombus* *Bombus bimaculatus* *Bombus fervidus* *Bombus griseocollis* *Bombus impatiens* *Bombus perplexus* *Bombus vagans* *Ptilothrix bombiformis*
Ceratina *Ceratina calcarata* *Ceratina dupla* *Ceratina miqmaki* *Ceratina strenua*	*Ceratina* *Ceratina calcarata* *Ceratina dupla* *Ceratina miqmaki* *Ceratina strenua*	*Ceratina* *Ceratina calcarata* *Ceratina dupla* *Ceratina miqmaki* *Ceratina strenua*
Medium	Medium	Medium

Agapostemon virescens *Andrena carlini* ♂ *Andrena cressonii* *Andrena erigeniae* *Andrena hippotes* *Andrena imitatrix* *Andrena mandibularis* *Andrena miserabilis* *Andrena nasonii* *Andrena pruni* ♂ *Andrena robertsonii* *Andrena violae* *Andrena wilkella* ♂ *Osmia albiventris* *Osmia atriventris* *Osmia conjuncta* *Osmia cornifrons* *Osmia distincta* *Osmia pumila*	*Agapostemon virescens* *Andrena cressonii* *Andrena imitatrix* *Andrena wilkella*	*Agapostemon virescens* *Andrena wilkella* *Colletes nudus* *Eucera pruinosa*
Small Dark *Halictus confusus* *Halictus ligatus* *Halictus rubicundus* *Hoplitis pilosifrons* *Hoplitis simplex* *Lagioglossum abanci* *Lasioglossum pilosum* *Lasioglossum versatum*	Small Dark *Halictus confusus* *Halictus ligatus* *Halictus rubicundus* *Lasioglossum abanci* *Lasioglossum coeruleum* *Lasioglossum coriaceum* *Lasioglossum foxii* *Lasioglossum gotham* *Lasioglossum nigroviride* *Lasioglossum nymphaearum* *Lasioglossum pilosum* *Lasioglossum smilacinae* *Lasioglossum versatum* *Lasioglossum zonulum*	Small Dark *Halictus confusus* *Halictus ligatus* *Halictus rubicundus* *Lasioglossum abanci* *Lasioglossum coeruleum* *Lasioglossum coriaceum* *Lasioglossum foxii* *Lasioglossum gotham* *Lasioglossum nympharaeum* *Lasioglossum pilosum* *Lasioglossum versatum* *Specodes heraclei*
Tiny Dark *Hylaeus affinis* *Hylaeus mesillae* *Hylaeus modestus*	Tiny Dark *Lasioglossum admirandum* *Lasioglossum atwoodi* *Lasioglossum callidum*	Tiny Dark *Hylaeus affinis* *Hylaeus mesillae* *Hylaeus modestus*

Lasioglossum atwoodi *Lasioglossum birkmanni* *Lasioglossum callidum* *Lasioglossum cattellae* *Lasioglossum coriaceum* *Lasioglossum cressonii* *Lasioglossum foxii* *Lasioglossum hitchensi* *Lasioglossum illinoense* *Lasioglossum imitatum* *Lasioglossum leucocomum* *Lasioglossum nigroviride* *Lasioglossum oblongum* *Lasioglossum obscurum* *Lasioglossum paradmirandum* *Lasioglossum quebecense* *Lasioglossum subviridatum* *Lasioglossum taylorae* *Lasioglossum tegulare* *Lasioglossum zephyrum* *Lasioglossum zonulum*	*Lasioglossum cressonii* *Lasioglossum ephialtum* *Lasioglossum gotham* *Lasioglossum hitchensi* *Lasioglossum illinoense* *Lasioglossum imitatum* *Lasioglossum laevissimum* *Lasioglossum obscurum* *Lasioglossum paradmirandum* *Lasioglossum subviridatum* *Lasioglossum taylorae* *Lasioglossum tegulare* *Lasioglossum trigeminum* *Lasioglossum viridatum* *Lasioglossum weemsi*	*Lasioglossum atwoodi* *Lasioglossum cattellae* *Lasioglossum cressonii* *Lasioglossum ephialtum* *Lasioglossum hitchensi* *Lasioglossum illinoense* *Lasioglossum imitatum* *Lasioglossum obscurum* *Lasioglossum paradmirandum* *Lasioglossum platyparium* *Lasioglossum subviridatum* *Lasioglossum tegulare* *Lasioglossum trigeminum* *Lasioglossum truncatum* *Lasioglossum viridatum* *Lasioglossum weemsi*
Xylocopa *Xylocopa virginica*	*Xylocopa* *Xylocopa virginica*	*Xylocopa* *Xylocopa virginica*
	Megachilidae (non-Heriades) *Coelioxys porterae* *Hoplitis pilosifrons* *Hoplitis producta* *Hoplitis spoliata* *Megachile mendica* *Megachile montivaga* *Megachile texana* *Osmia atriventris* *Osmia bucephala* *Osmia pumila*	Megachilidae *Coelioxys sayi* *Heriades carinata* *Heriades leavitti* *Heriades variolosa* *Hoplitis pilosifrons* *Hoplitis producta* *Lithurgus chrysurus* *Megachile brevis* *Megachile campanulae* *Megachile exilis* *Megachile georgica* *Megachile mendica* *Megachile montivaga* *Megachile rotundata*

		Megachile sculpturalis *Osmia atriventris* *Osmia pumila* *Stelis louisae*
	<u>*Heriades*</u> *Heriades carinata* *Heriades leavitti* *Heriades variolosa*	
	<u>*Hylaeus*</u> *Hylaeus affinis* *Hylaeus mesillae* *Hylaeus modestus* *Hylaeus sparsus*	
<u>Large Dark</u> *Andrena carlini* ♀ *Andrena pruni* ♀ *Andrena vicina* ♀ *Colletes inaequalis* *Osmia bucephala* *Osmia collinsae* *Osmia lignaria*		
		<u>*Melissodes*</u> *Melissodes bimaculata* *Melissodes denticulata* *Melissodes desponsa*

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Ecology

Rare and declining bee species are key to consistent pollination of wildflowers and crops across large spatial scales

Mark A. Genung[1,*], James Reilly[1], Neal M. Williams[2], Andrew Buderi[3], Joel Gardner[4], Rachael Winfree[1]

Appendix S4. List of rare and declining bee species, and results with rare and declining species separated.

Table S1. List of rare and declining bee species

Rare	**Declining**	**Rare and Declining**
Agapostemon texanus	*Andrena carlini*	*Colletes validus*
Andrena banksi	*Andrena erigeniae*	*Lasioglossum cinctipes*
Andrena barbara	*Bombus fervidus*	*Lasioglossum truncatum*
Andrena fenningeri	*Bombus vagans*	
Andrena ilicis	*Eucera pruinosa*	
Andrena morrisonella	*Halictus rubicundus*	
Andrena robertsonii	*Lasioglossum imitatum*	
Andrena violae	*Lasioglossum leucocomum*	
Augochloropsis sumptuosa	*Lasioglossum pilosum*	
Bombus sandersoni	*Megachile brevis*	
Coelioxys porterae	*Osmia atriventris*	
Colletes consors	*Osmia lignaria*	
Colletes nudus		
Habropoda laboriosa		
Heriades leavitti		
Hoplitis producta		
Hoplitis simplex		
Hoplitis spoliata		
Hoplitis truncata		
Hylaeus sparsus		

Lasioglossum abanci
Lasioglossum acuminatum
Lasioglossum admirandum
Lasioglossum albipenne
Lasioglossum atwoodi
Lasioglossum birkmanni
Lasioglossum cattellae
Lasioglossum coreopsis
Lasioglossum creberrimum
Lasioglossum ellisiae
Lasioglossum georgeickworti
Lasioglossum gotham
Lasioglossum illinoense
Lasioglossum laevissimum
Lasioglossum lineatulum
Lasioglossum nigroviride
Lasioglossum paradmirandum
Lasioglossum planatum
Lasioglossum platyparium
Lasioglossum rozeni
Lasioglossum smilacinae
Lasioglossum taylorae
Lasioglossum trigeminum
Lasioglossum viridatum
Megachile addenda
Megachile exilis
Megachile gemula
Megachile georgica
Megachile montivaga
Melissodes denticulatus
Melitta americana
Nomada luteola
Osmia albiventris
Osmia bucephala
Osmia collinsiae
Osmia conjuncta
Osmia distincta
Osmia inspergens
Osmia virga
Panurginus atramontensis

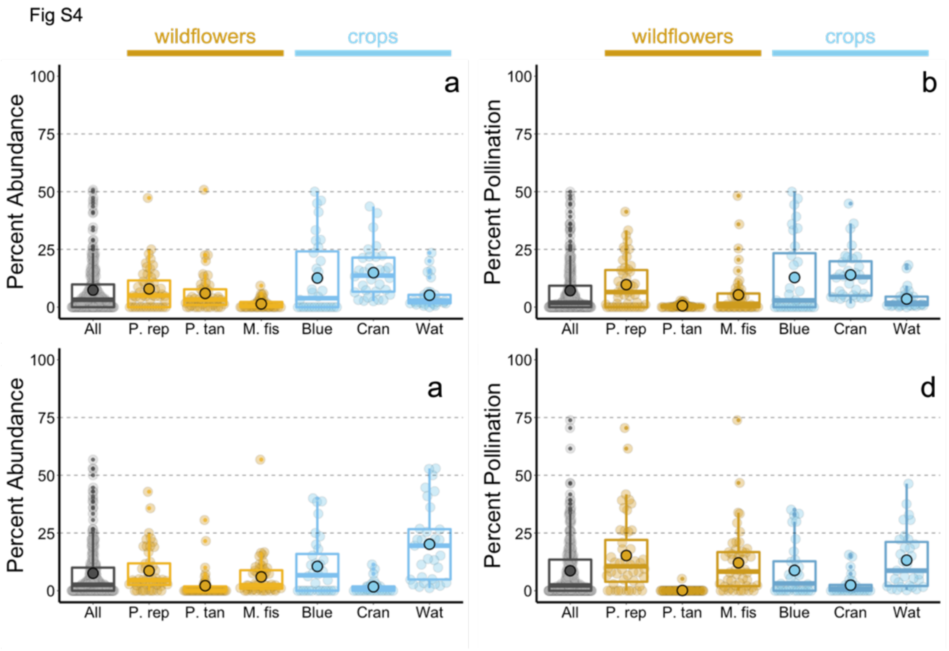
Ptilothrix bombiformis
Sphecodes aroniae
Sphecodes fattigi
Sphecodes heraclei
Sphecodes mandibularis
Stelis louisae
Triepeolus remigatus

Excluding species from being called rare.

As described in the main text, we used two datasets to define rare species, a "contemporary" dataset, and a "museum" dataset. A species was "rare" if it occupied <5% as many sites as the most common species (Mouillot et al. 2013, MacLeod et al. 2020) in *either* dataset. We made this choice because requiring a species to be rare in both datasets produced an unreasonably short list of rare species.

However, our list of rare species included several species that we do not consider rare based on our experience with the bee fauna of our study system. For this reason, we made two post-hoc adjustments to the rare species list. First, we excluded the 10% most abundant bee species in the contemporary dataset from being called rare. This removed the following species from the rare species list: *Andrena erigeniae*, *Augochlorella persimilis*, *Ceratina mikmaqi*, *Eucera pruinosa*, *Lasioglossum vierecki*. An analogous correction was not needed for the museum dataset, because none of the species that were highly abundant in the museum dataset were called rare. Second, we subset the geographically broad collections in the museum dataset to include records only from Pennsylvania, New Jersey, and New York. This removed the following species from the rare species list: *Lasioglossum oblongum*, *Lasioglossum obscurum* and *Megachile campanulae*. These exclusions make our results more conservative, because even more rare species would be important to function without these exclusions.

Figure S1. Separating rare and declining species. Figure 1 results from the main text divided into just rare species (top row) and just declining species (bottom row). Declining species were more important to the pollination of *P. reptans*, *M. fistulosa*, and watermelon, while the opposite was true for blueberry and cranberry (which, anecdotally, are native crops known to rely on specialist bee species).



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Ecology

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Appendix S5. Minimum set analysis and sensitivity analysis.

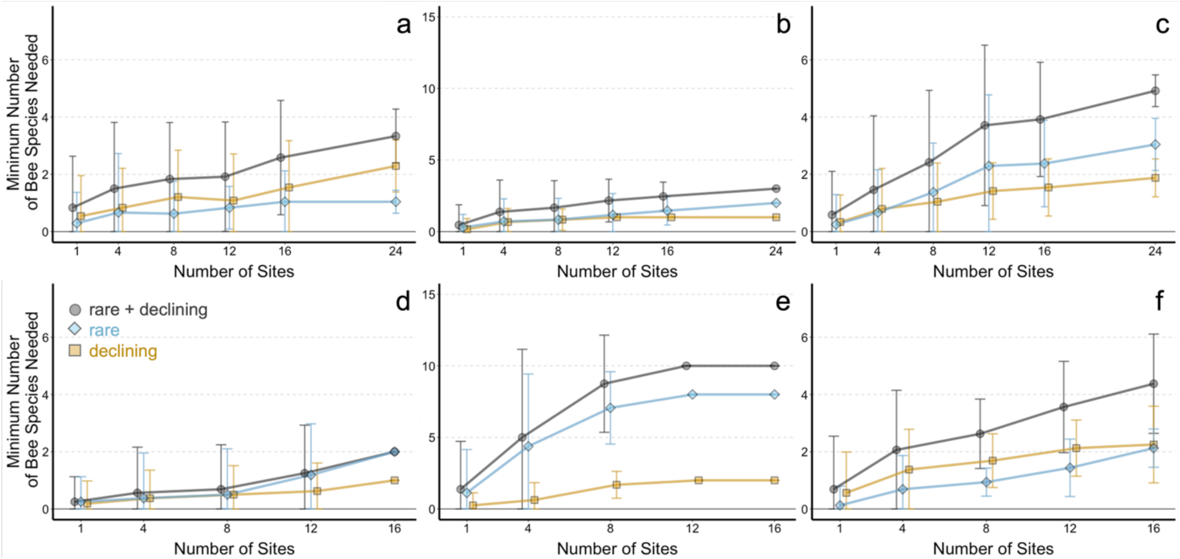
Minimum set analysis. We found the minimum set of bee species that can meet pollination thresholds using a genetic algorithm optimizer, namely the GAPerm() function in the "gaoptim" package in R (R Core Team 2021). We randomly chose a site and began with its first year (2017) of data. Species at this site were added from highest- to lowest-function until either the site met the pollination threshold, or all species had been added. Then we moved on to the second year (2018) for the chosen site and checked whether the species list from the previous year was sufficient to meet the threshold in 2018. If it did, we moved on to another randomly chosen site (again starting in 2017 and moving to 2018); if not, we added species as described above. We repeated this process until the threshold was met at all sites. However, the minimum set resulting from this method is not yet optimized. This optimization is accomplished by GAPerm(), which attempts to progressively remove species from the minimum set until it reaches 30 stable generations. We added sites at random; uncertainty in our results (see error bars in main text Figure 2) is due to this randomness. We stress that minimum set analyses do not separate the roles of richness and abundance, because when species are added to the minimum set, both richness and abundance increase (Winfree et al. 2018).

Sensitivity analyses. First, there are other ways to accumulate sites. For example, site can be added in order of geographic proximity instead of at random (while still maintaining the requirement that sites meet thresholds in both years), or we can ignore the fact that each site has two years of data and just add site-years at random. Both methods yielded nearly the same results (data not shown).

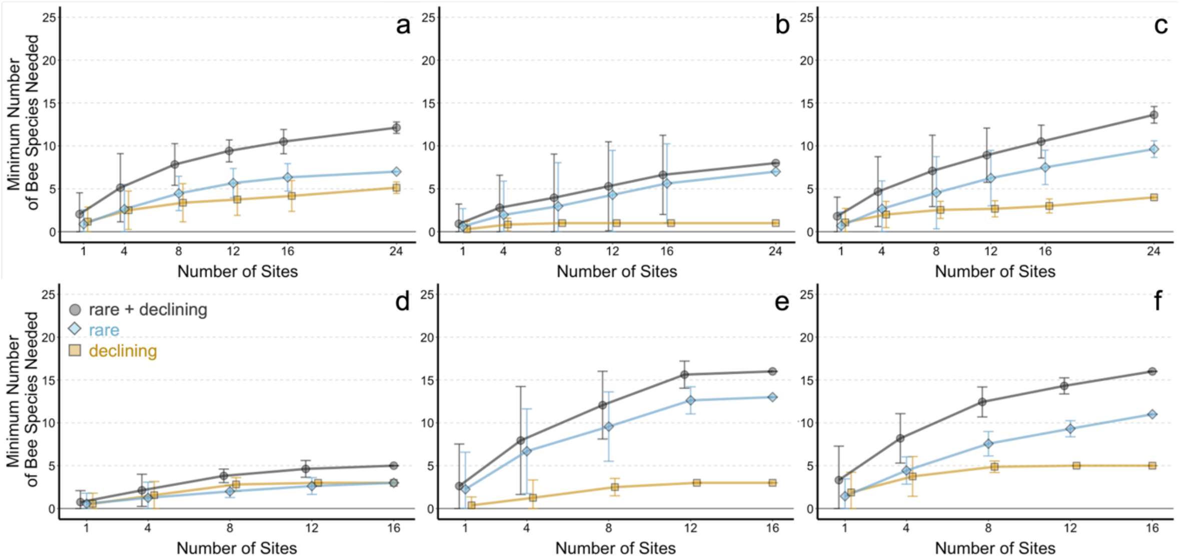
Second, we find the minimum set of species that can provide 50% of mean pollination (mean taken across sites), but the choice of any threshold is arbitrary. Thus, we explored the effects of changing the threshold to 25% or 75% of mean pollination (Figure S1). Our results were qualitatively unchanged, but the percent of species in the minimum set that were declining or rare necessarily increased as the threshold increased.

Figure S1. Sensitivity analysis. Lowering the threshold necessarily increases the percent of species meeting the threshold, and raising the threshold does the opposite. Our core results were consistent across all thresholds: (1) few or zero rare and/or declining species were in the minimum set for regional pollination (i.e., after aggregating species' pollination across sites) and (2) many rare and/or declining species were in the minimum set for local pollination (i.e., requiring every site to meet its pollination threshold). Further, the shapes of the curves remain similar across the different thresholds, with the 25% threshold perhaps showing less tendency to asymptote. Note a different y-axis scale for the 75% threshold.

25% threshold



75% threshold



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Appendix S6.

Figure S1. Plant species support different bee communities. Non-metric multidimensional scaling (NMDS) plot showing differences in bee community composition between plants species. All pairwise comparisons had p-values < 0.01. Differences in bee community composition suggest that the consistent results across plant species was not simply a result of the same rare and/or declining species being in the minimum set across all plant species.