


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 km²), 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; Moullot 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; Moullot 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 km² area) and crops (three species studied at commercial farms across a 5000 km² 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 km² 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 unconvincing. 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 m² 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 GAsPerM() 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 $13.7\% \pm 1.8\%$ (mean \pm 95% CI across plant species) of abundance and $14.7\% \pm 2.0\%$ 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: $10.5\% \pm 1.9\%$ of abundance, $14.3\% \pm 2.9\%$ of pollination; crops: $18.5\% \pm 3.1\%$ of abundance, $15.3\% \pm 2.7\%$ 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

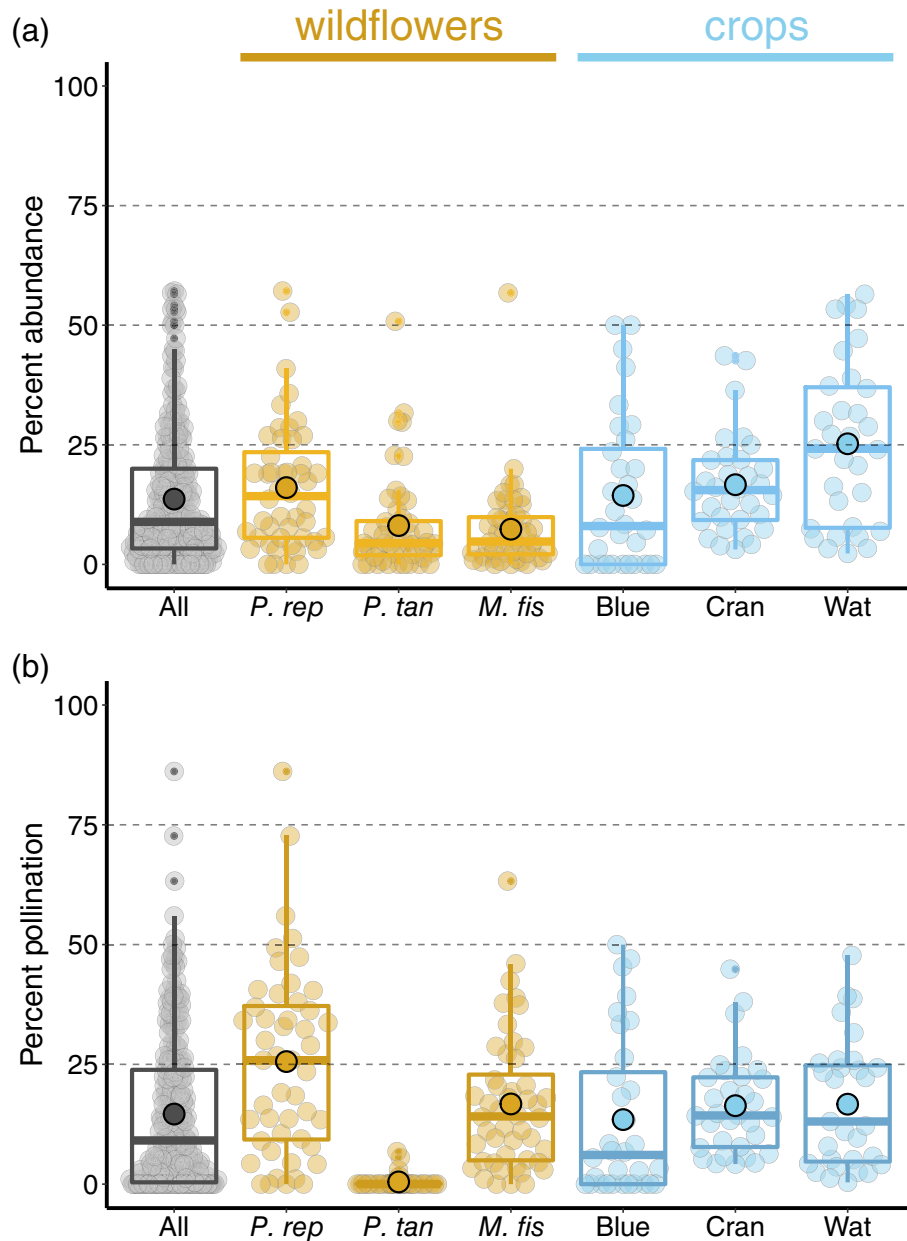


FIGURE 1 Boxplots showing (a) the percent of total abundance accounted for, and (b) the percent of total function provided, by rare and declining bee species. In both panels, each data point is one site-year. The gray boxplot combines all datapoints across plant species, within each panel. Abbreviations 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 ($7.4 \pm 1.3\%$ of abundance, $7.2 \pm 1.4\%$ pollination), while declining species accounted for 114% ($7.5 \pm 1.4\%$ of abundance, $8.6 \pm 1.6\%$ 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

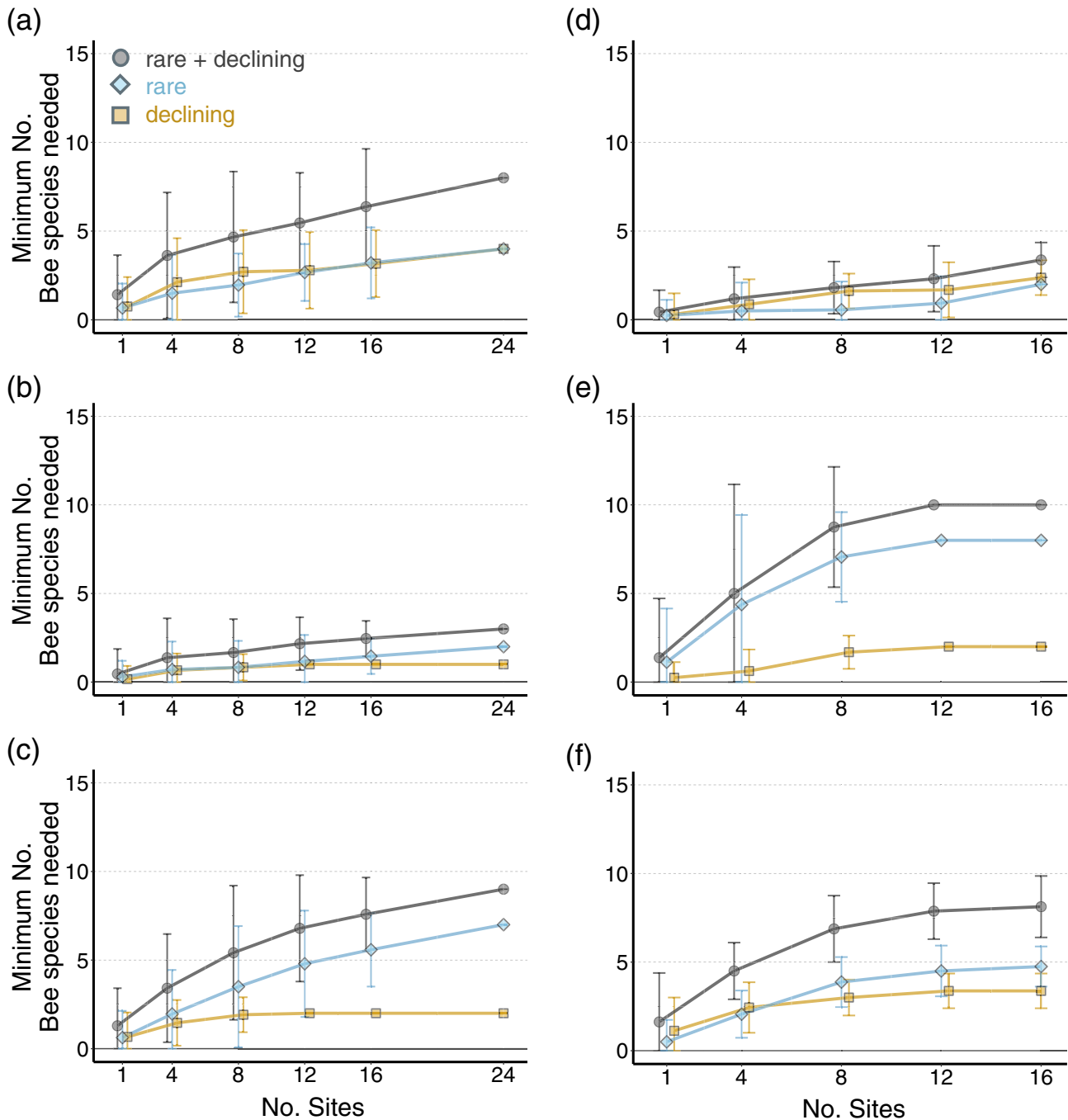


FIGURE 2 The minimum number of bee species that can meet pollination thresholds increases as the thresholds must be met at more sites. The initial site is chosen at random, and the minimum set is calculated to meet the threshold in both years of data. Beginning with the second site, sites added in order 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

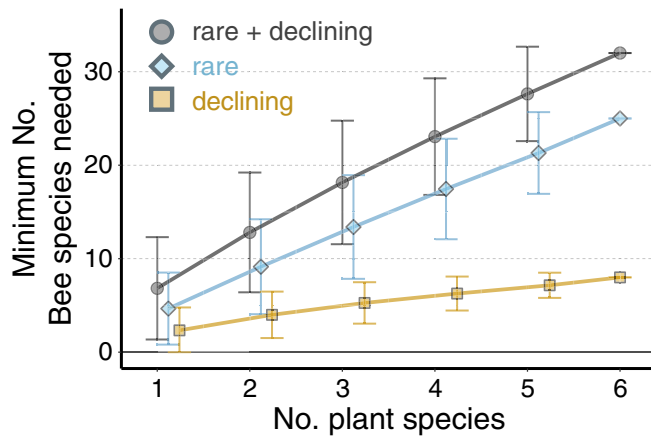


FIGURE 3 The minimum number of bee species that can meet pollination thresholds increases as the thresholds must be met for one to six plant species (*Polemonium reptans*, *Phacelia tanacetifolia*, *Monarda fistulosa*, blueberry (*Vaccinium corymbosum*), cranberry (*Vaccinium macrocarpon*), and watermelon (*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 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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