

How much do rare and crop-pollinating bees overlap in identity and flower preferences?

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Funding information

Rutgers University; US Environmental Protection Agency; Garden Club of America; Natural Resources Conservation Service

Handling Editor: Guadalupe Peralta

Abstract

1. The biodiversity-centred approach to conservation prioritizes rare species, whereas the ecosystem services approach prioritizes species that provide services to people. The two approaches align when rare species provide ecosystem services, or when both groups of species benefit from the same management action. We use data on bee pollinators and the plant species they forage on to determine if there are rare species among the most important crop pollinators, and the extent to which plant species selected to support crop pollinators would support rare species as well.
2. We used pre-existing, regional-scale datasets to determine which bee species are regionally rare, and which are regionally important crop pollinators. To assess the plant preferences of these two groups of bee species, we collected two datasets on plant–pollinator interactions, one experimental and one observational. The experiment consisted of monospecific plots of 17 plant species from which we collected bees over 3 years. The observational data consisted of bees collected from 66 species of plants growing in semi-natural meadows, also over 3 years.
3. Nineteen percent of the dominant crop-pollinating species were regionally rare. Both rare species and crop-pollinating species had strong preferences for certain plants, and the preferences of rare and crop-pollinating bees were significantly but not strongly ($r \leq .54$) correlated. Ten plant species were significantly preferred by both rare and crop-pollinating bees.
4. *Synthesis and applications.* We found several dominant crop pollinators that are rare at a regional scale, supporting the idea that rare species can be important providers of ecosystem services. The flower preferences of rare and crop-pollinating bees are significantly positively associated, suggesting that plants chosen to support crop pollinators will benefit rare species as well. We identify plant species that are preferred by regionally rare bees and by crop pollinators, including 10 plant species preferred by both types of bees, and recommend these for use in pollinator habitat plantings.

KEYWORDS

agri-environment, biodiversity, conservation, crop pollination, ecosystem services, pollinator, rare species, wild bees

1 | INTRODUCTION

Biodiversity conservation has traditionally focused on rare species, which are at higher risk of extirpation as compared with common species. In contrast, the ecosystem services approach focuses on species that provide goods and services to human societies (Pearson, 2016). The two approaches converge when biodiversity generally, or rare species in particular, are important for ecosystem services (Lyons, Brigham, Traut, & Schwartz, 2005; Tilman, Isbell, & Cowles, 2014; Winfree et al., 2018). The goals are at odds, however, when a small number of common species provide most of the ecosystem services. The importance of rare versus common species to ecosystem services in general is not yet clear. However, even if rare species are not important contributors to ecosystem services they could still benefit from management actions targeting ecosystem service providers if the resource needs of these two groups coincide.

Pollinators have become a model system for testing hypotheses about ecosystem services because they contribute to the reproduction of most of the world's wild plant species and to increased yields for most leading global food crops (Klein et al., 2007; Ollerton, Winfree, & Tarrant, 2011). There is also considerable interest in determining which pollinator species are rare and in need of protection, particularly for bees, which are the main pollinator taxon (Goulson, Nicholls, Botias, & Rotheray, 2015). Europe has the most complete information on its bee fauna, and a European Red List for bees was published in 2014 (Niето et al., 2014). Some Red List evaluations have revealed high rates of endangerment; for example, in the Netherlands, over half of all native bee species are categorized as 'Susceptible' or worse (Peeters & Reemer, 2003). North America lags behind Europe in systematically assessing its bee fauna. No federal or state-level assessments of the entire bee fauna have been completed, although particular taxa such as the bumblebees (the genus *Bombus*) have been assessed (Williams, Thorp, Richardson, & Colla, 2014). Thus, the USA, and indeed the rest of the world outside of Europe, is at an earlier stage where regional evaluations of rarity can only be done using data from large-scale surveys or museum records. In this situation, rarity is often assessed using the quantiles of the species-abundance or species-occupancy distributions (Harrison, Gibbs, & Winfree, 2018b; Hercos, Sobansky, Queiroz, & Magurran, 2013; Mouillot et al., 2013).

The main management action currently being undertaken for bees is improving habitat by planting bee-attractive plants. Floral resources (pollen and nectar) are likely a limiting resource for bees, and the loss of floral resources has been implicated in bee decline (Goulson et al., 2015; Roulston & Goodell, 2011; Scheper et al., 2014). Floral plantings are well known to increase the abundance of

common species (Scheper et al., 2013), and in some cases can increase rare and/or specialized species as well (Kremen & M'Gonigle, 2015; Pywell et al., 2012; Scheper et al., 2015). The largest source of funding for wild pollinator conservation comes from governmental agricultural agencies, which are particularly interested in maintaining crop pollinators (Williams et al., 2015; Winfree, 2010). Thus, the opportunity exists to support both crop-pollinating and rare bee species if plant species that are attractive to both groups can be included in floral plantings.

There are a priori reasons both to expect that crop pollinators and rare species do prefer the same plants, and to expect that they do not. On the one hand, some plant species (often those that produce high quality and/or quantity of pollen and nectar) are highly attractive to pollinators in general, whereas other species are not. On the other hand, bees show between-species differences in their preference for particular plants (MacLeod, Genung, Ascher, & Winfree, 2016; Waser & Ollerton, 2006). The single investigation thus far of overlap in plant preferences between rare and crop-pollinating bees found that in Switzerland, rare bee species visit a subset of the plants visited by crop pollinators, and that the sets of plants most highly preferred by the two groups were different (Sutter, Jeanneret, Bartual, Bocci, & Albrecht, 2017). There is less information on this topic in North America; in most parts of the continent, it is not even known which bee species are rare, nor which are the dominant crop pollinators.

Here we use five large datasets on 499 bee species found in the mid-Atlantic region of the eastern USA to answer the following questions: (i) Are there regionally rare species among the dominant crop pollinators? (ii) Are the floral preferences of rare and crop-pollinating bees correlated? (iii) Are there plant species that managers could use to support rare and crop-pollinating bees simultaneously? In order to answer these questions, we first had to determine which bee species are rare (based on a low frequency of occurrence at a regional scale), and which are the most important crop pollinators (based on frequency of visits to flowers of seven crops in our study region), because there are no published sources of this information for the eastern North American bee fauna.

2 | MATERIALS AND METHODS

2.1 | Data to identify the regionally rare and crop-pollinating species

2.1.1 | Regionally rare species

To generate the list of regionally rare species, we used two independent datasets. First, we used a previously published dataset (Bartomeus

et al., 2013) consisting of 29,976 specimens of 447 bee species that were collected from 2,581 localities covering roughly a 700,000 km² area throughout the Mid-Atlantic and Northeastern USA between 1870 and 2011. This dataset (hereafter, 'museum dataset') was generated from specimens housed in museums, primarily the American Museum of Natural History in New York, New York, USA. The second dataset consisted of 68,311 specimens of 355 species collected at 196 sites covering roughly a 100,000 km² area in the states of New Jersey, New York, and Pennsylvania from 2014 to 2018 by members of the Winfree research group (hereafter, 'contemporary dataset'). For both datasets, bees were collected from a wide variety of habitat types and throughout the growing season. Methods for these datasets are summarized in the Supplementary Text, and are reported in more detail elsewhere (Bartomeus et al., 2013; Harrison, Gibbs, & Winfree, 2018a; Roswell, Dushoff, & Winfree, 2019; Smith, Weinman, Gibbs, & Winfree, 2019; Winfree, Griswold, & Kremen, 2007; Winfree, Williams, Dushoff, & Kremen, 2014). Of the 493 species in these datasets, only 14 (3%) were non-native (*Apis mellifera*, the honey bee, is non-native but is not included in our datasets because it is a domesticated species in our study area). We include the non-native species in all analyses in this paper, but distinguish them from native species in the results. We filtered both datasets to use only one record per bee species per collection site, to reduce any effect of uneven sampling effort across bee species that may exist in the museum dataset (Bartomeus et al., 2013). Thus, the rarity analyses are based on regional occupancy data. Because our data do not include information about local abundance, we would count a species that is locally abundant in a small number of places (for example, a habitat specialist on an uncommon habitat, or a host plant specialist of an uncommon plant species) as regionally rare. Similarly, our methods could count a species that has a short flight season (i.e. is flying as an adult for fewer weeks than other species) as regionally rare if it was collected at only a small number of sites due to the shorter period of time it was present.

2.1.2 | Crop-pollinating species

The data used to identify dominant crop pollinators consists of bee specimens collected from the flowers of seven crops (highbush blueberry, *Vaccinium corymbosum*; cranberry, *Vaccinium macrocarpon*; apple, *Malus pumila*; tomato, *Solanum lycopersicum*; watermelon, *Citrullus lanatus*; muskmelon, *Cucumis melo*; and bell pepper, *Capsicum annuum*) on commercial farms in New Jersey and Pennsylvania, USA. Members of the Winfree research group collected these data between 2004 and 2012; methods for each study are summarized in the Supplementary Text, and more detailed methods are reported elsewhere (Cariveau, Williams, Benjamin, & Winfree, 2013; Kleijn et al., 2015; Winfree, Fox, Williams, Reilly, & Cariveau, 2015; Winfree et al., 2018). The crop datasets contained a total of 11,100 individual bees of 146 species; of these, there were seven non-native species accounting for 0.1% of the individuals (excluding the domesticated honey bee, which was not collected). While the frequency with which a given species visits flowers does not necessarily predict its

contribution to pollination, analysis of our crop data showed that flower visitation and pollen deposition were strongly correlated (mean Pearson's $r = .86$; Kleijn et al., 2015). Thus, we hereafter refer to the bee species collected from crops as crop pollinators.

2.2 | Data collection on wildflower visitation by bees

To determine which flowering plant species are preferred by rare and crop-pollinating bees, we collected two new datasets, one experimental and one observational.

To measure wild bee species' preferences for different plants, we established an experimental array of 17 native, perennial plant species in an old field near Cape May, New Jersey, USA (39.07N, -74.46W) in the fall of 2009. We established 1 m² monoculture plots each of which contained nine mature individual plants, using a randomized block design with six replicate plots per species, for a total of 102 plots; plots were separated by a 2 m strip of mowed grass. Given that the bee species in our study forage from 100 to over 1,000 m (Greenleaf, Williams, Winfree, & Kremen, 2007) and our entire study array was 18 × 57 m, our design creates a choice experiment for foraging bees. From May to September in each of 2011–2013, we netted all flower-visiting bees at each plot on three separate days during the peak bloom of that plant species. Further details of the experiment can be found in MacLeod et al. (2016).

To determine the plant species used by wild bees foraging in diverse semi-natural plant communities, we collected bees of all species from flowers at seven sites in New Jersey, USA. Each site consisted of two paired meadows, one of which had been specifically planted and maintained for pollinators, and a second that was a mid-successional old field. In each meadow, we constructed two 40 × 2 m transects where all data were collected. Researchers walked along each transect and hand-netted all wild bees (which excludes honey bees *A. mellifera*, which is a managed species in our study region) observed visiting flowers, while also recording the plant species each bee was collected from. The plant species in bloom were recorded using 10 vegetation quadrats per transect. Sites were sampled approximately once a month from June through September for a total of 4 days of data collection per year in each of 3 years (2013–2015). For both the experimental and the observational studies, all bees collected were pinned, labelled and identified to its species (or for a few species, to a species complex including 2–3 morphologically similar species) by JG or John Ascher of the National University of Singapore. Specimens are stored in the Winfree laboratory at Rutgers University in New Brunswick, NJ, USA.

2.3 | Data analysis

(i) *Are there regionally rare species among the dominant crop pollinators?*

When we determined which species were rare, we did so for each of the two datasets (museum and contemporary) separately. We then created our final list of rare species by using the union of species that

were rare in *either* dataset. We did the analysis this way, rather than combining the datasets prior to analysis, because the two data sets were collected using different methods, and over different geographical areas and time periods. Thus, our rare species list would include species that, for example, were more abundant in the past (did not qualify as rare in the museum dataset) but are rare now (did qualify as rare in the contemporary dataset). We defined a species as rare if it occupied less than 5% as many localities as the species occupying the greatest number of localities in that same dataset (the method of Mouillot et al., 2013). For the museum dataset, this meant a rare species was found at fewer than 64 of 2,581 localities, and for the contemporary dataset, it meant a rare species was found at fewer than 9 of 196 localities.

To determine which species were the most important crop pollinators, we used Kleijn et al.'s (2015) definition of a dominant crop pollinator as a species that accounts for at least 5% of the total number of individual bees collected from a given crop. Because the dataset used to define crop pollinators is independent of that used to define rare species, it is possible for a species to be abundant in the crop pollinator dataset (i.e. abundant on the flowers of a particular crop) while also being rare at the regional scale.

To determine whether there are more or fewer regionally rare dominant crop pollinators than would be expected by chance, we first estimated the overall probability of a given species being regionally rare, $P(\text{rare} \mid \text{present in regional occurrence datasets})$. This is the same as the proportion of species that we categorized as rare in this study (82%). Under the null hypothesis that dominant crop pollinators are no more or less likely to be regionally rare than are other species, we would expect $P(\text{rare} \mid \text{dominant crop pollinator})$ to equal $P(\text{rare} \mid \text{present in regional occurrence datasets})$. Thus, we calculated the observed number of dominant crop pollinator species that are regionally rare, $P(\text{rare} \mid \text{dominant crop pollinator})$, and compared it to the expected number, $P(\text{rare} \mid \text{present in regional occurrence datasets})$, using a binomial test.

(ii) *Are the floral preferences of rare and crop-pollinating bees correlated?*

For both datasets, we summed the bees collected on each plant species within each year. Thus, preference as we measured it includes any effects of phenological overlap between plant and bee species. For example, a bee species whose population peak is in the spring will likely show a preference for plant species that bloom in the spring, as compared with plants that bloom in summer when few individuals of that bee species are active.

2.3.1 | Experimental dataset

To determine what plant species were preferred by rare and crop-pollinating bees, we used two general linear mixed models, one for each category of bee. The outcome variable was the number of bees (whether rare or crop-pollinating) collected from each of the 17 plant species in our experimental array, plant species was a fixed effect, and plot and year were random effects. Prior to running the models, bee abundances were $\ln(x + 1)$ transformed.

2.3.2 | Observational dataset

We repeated the analyses described above for the observational dataset, running one model for rare bees and one for crop pollinators, but with two key modifications to model structure. First, because the observational data were collected at seven different sites, we added a random effect of site to the model (and removed the random effect of plot). Second, because plant abundances in the meadows varied greatly by plant species, we would expect that at any given site, many more bees would be netted from the numerically dominant plant species. Thus, we added plant abundance as a covariate, resulting in a mixed model with two fixed effects (plant abundance and plant species) and two random effects (site and year). The use of plant abundance data from each site allows our model to better estimate bee preference for different plant species as opposed to estimating merely use. To reduce error from under-sampling, only plant species that were recorded in at least five quadrats were included in the analysis. As for the experimental dataset, all abundances were $\ln(x + 1)$ transformed. Model assumptions (linearity, normality, constant variance, outliers, etc.) were checked for all fitted models. We found that log transformation of bee abundances greatly improved both normality of residuals and constant variance across the range of fitted values in all cases. Analyses were performed using the `LMER()` function from the `LME4` package (Bates, Machler, Bolker, & Walker, 2015) in R (R_Core_Team, 2017).

In order to test whether there was a correlation between the preferences of rare and crop-pollinating bees across plants, for each dataset, we performed a simple linear regression of the coefficients of the plant species effect (which is our measure of bees' preference for that plant species, relative to the other plant species in the same dataset) from the rare bee model against the coefficients from the crop-pollinating bee model. All coefficient values are with respect to the mean across plant species, hence plants with coefficient values greater than zero can be interpreted as being more preferred than the mean. This analysis was performed separately for the experimental dataset and the observational dataset, yielding two correlations. Analysis was performed using the `LM()` function in R (R_Core_Team, 2017).

(iii) *Are there plant species that managers could use to support rare and crop-pollinating bees simultaneously?*

To determine what plant species were preferred by each group of bees, we performed contrasts of each plant species' coefficient against the mean of all plant species in that dataset. By this method, plants significantly above the mean were considered to be preferred, and all other plants were not. Plants significantly above the mean of both rare and crop-pollinating bees were considered to be preferred by both groups. Because only seven of the 76 plant species were present in both the experimental and the observational datasets, we were not able to test the hypothesis that bee preference was similar between the two datasets. Contrasts were performed using the `LMER()` function from the `LME4` package (Bates et al., 2015) in R (R_Core_Team, 2017). Lastly, because practitioners often seek to have continuous bloom throughout the season, we also calculated preference within each of three time periods to choose the best plant species for early, mid, and late summer.

3 | RESULTS

In the plant choice experiment and the field observations, we collected a total of 9,331 individual bees of 141 species foraging on 76 plant species. Six (4%) of the bee species were non-native, but these species accounted for only 0.9% of the individuals (the honeybee was not included in our datasets). In contrast, 36% of the plant species were non-native. See Table S1 for all bee and plant species names, and Table S2 for more detailed sample size information.

3.1 | Are there regionally rare species among the dominant crop pollinators?

Using the crop dataset, we found that 26 of the 146 species were categorized as dominant crop pollinators, or 18%. This 18% of species accounted for 82% of the individuals collected from crop flowers, consistent with the steep rank-abundance distributions (Figure 1). None of the dominant crop pollinators was non-native, and although seven of the 146 species collected from crops were non-native, only one of them (*Osmia cornifrons*) was represented by more than a single individual.

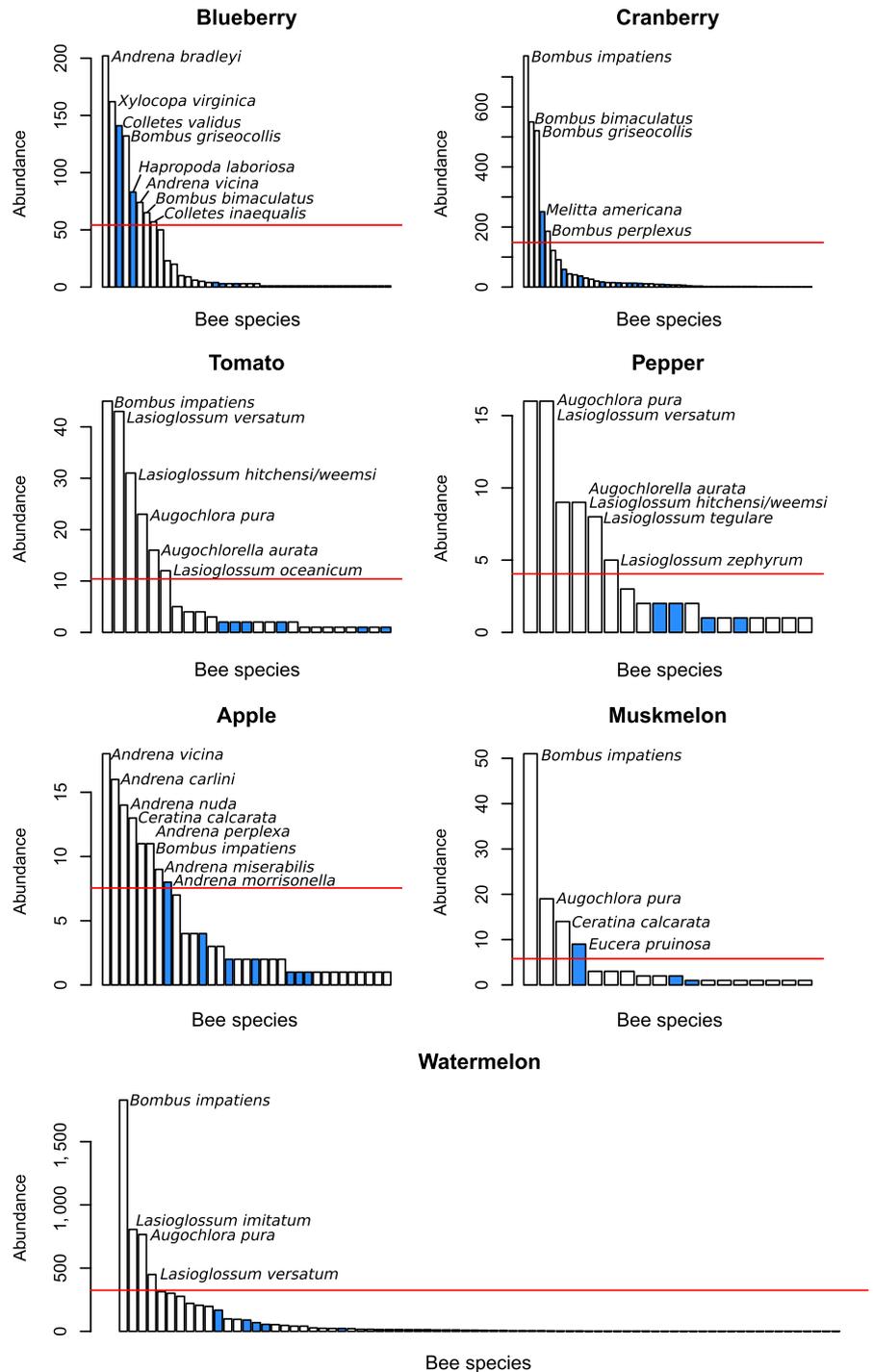


FIGURE 1 The identity of dominant pollinators in each of the seven study crops. The Y axis is the number of individuals of each bee species that was collected from the flowers of that crop. Bee species with abundances above the red line each accounted for at least 5% of the total number of individual bees collected from that given crop, and were thus dominant (important) crop pollinators by our definition. Species that are regionally rare are shown in blue. Thus, the contribution of regionally rare bee species to the pollination of a given crop is visualized as the blue bars that exceed the red line (regionally rare species that are dominant pollinators of that crop), plus all the blue bars that are below the red line, but which may still in combination make a meaningful contribution. The number of regionally rare species out of all species collected on the crop is as follows: 8/42 for blueberry, 5/53 for cranberry, 4/76 for watermelon, 4/18 for muskmelon, 6/25 for tomato, 6/18 for pepper and 8/33 for apple

Using the regional occurrence datasets, we found that 405 of 493 species were regionally rare, or 82% (Figure S1; see Figures S2 and S3 for sensitivity analysis on the choice of 5% as the threshold for rarity). These 82% of species accounted for only 23% of the occurrence records, consistent with the steep rank-abundance distributions (Figure S1). Three percent of the rare species (11 of 405) were non native.

If dominant crop pollinators were as likely to be regionally rare as are the entire set of species in the regional occurrence datasets, we would expect 21 of the 26 dominant crop pollinator species to also be regionally rare species ($26 \times 0.82 \approx 21$). However, we found that only five dominant crop pollinator species were regionally rare. This corresponds to a binomial $p \ll .01$, and indicates that dominant crop pollinators are, in general, unlikely to be regionally rare. The five crop pollinators that are rare at the regional scale were *Habropoda laboriosa* (blueberry), *Colletes validus* (blueberry), *Melitta americana* (cranberry), *Eucera pruinosus* (muskmelon), and *Andrena morrisonella* (primarily important for apple). See Figure 1 for a visual portrayal of the prevalence of regionally rare species on crops, and Table S1 for the complete lists of the regionally rare and crop-pollinating bee species.

3.2 | Are the floral preferences of rare and crop-pollinating bees correlated?

In both the experimental and the observational datasets, the plant preferences of regionally rare and crop-pollinating bees were significantly positively correlated, although not strongly so ($r = .541$, $p = .025$, Figure 2a, and $r = .448$, $p = .0002$, Figure 2b, respectively). Sensitivity analysis showed that the statistical significance of these results did not change with the rarity threshold used for either dataset, but for the observational dataset only, the correlation coefficient increased with the number of species defined as

rare, suggesting that the results reported here are conservative (Figure S3).

3.3 | Are there plant species that managers could use for rare and crop-pollinating bees simultaneously?

Of the 17 plant species in the choice experiment, only one was preferred by both crop-pollinating and regionally rare bees (Figure 2a, blue square with red circle inside), although two others were marginally preferred by both. When preference was computed within each of three time periods (early, mid, and late summer), four additional species were added (Table 1; Table S3, Figure S4). Of the 66 plant species recorded in the field observations, four species were preferred by both rare and crop-pollinating bees (Figure 2b, blue squares with red circles inside). When preference was computed within each of three time periods (early, mid, and late summer), one additional species was preferred and one additional species was marginally preferred (Table 1; Table S3). One species was preferred in the season-long analysis but not in any individual time period.

4 | DISCUSSION

4.1 | Some dominant crop pollinators are regionally rare

We found that 19% of the most important crop-pollinating bee species in our region are rare at the regional scale. Our findings contribute to the small but a growing number of studies documenting rare species making important contributions to ecosystem function (Jousset et al., 2017; Lyons et al., 2005; McIntyre,

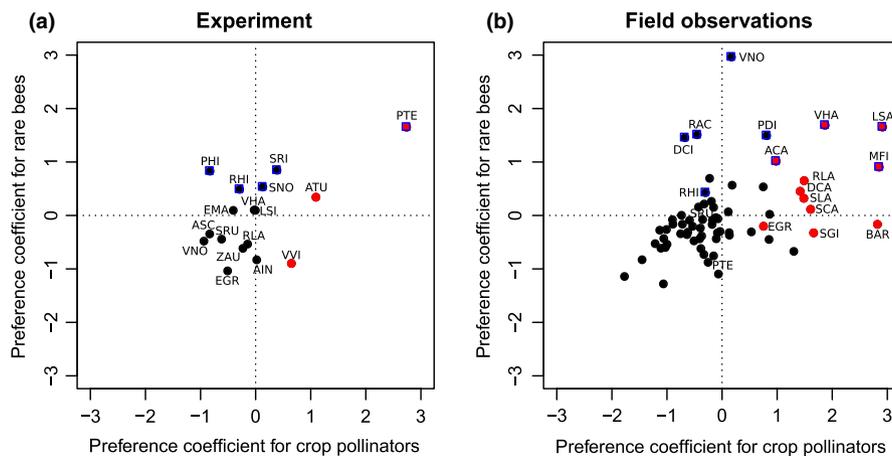


FIGURE 2 Plant species preferences of rare versus crop-pollinating bees in (a) the experiment, and (b) observations in semi-natural meadows. For both plots, each point represents a single plant species, and the coefficient of that plant species from a linear model using the number of bees collected as the outcome variable is plotted (x = model for crop-pollinating bees, y = model for rare bees). Dotted lines at zero show the mean plant species preference model coefficient. Plants that were preferred by rare bees are shown as points surrounded by a blue square, plants preferred by crop bees are shown as red points. Plants preferred by both are shown as red points surrounded by a blue square. For complete plant species names along with their abbreviations see Table 1 (preferred plant species only) and Table S1 (all species)

TABLE 1 The plant species recommended for rare and crop-pollinating bees, organized by season of bloom

Plant species	Abbreviations	Season	Rare	Crop	Experiment	Observations
<i>Asclepias tuberosa</i>	ATU	Mid	x	x	R, C	
<i>Lobelia siphilitica</i>	LSI	Mid	x	x	R, C	
<i>Pycnanthemum tenuifolium</i>	PTE	Mid, full	x	x	R, C	ns
<i>Symphotrichum novae-angliae</i>	SNO	Late	x	x	R, C	
<i>Solidago (Oligoneuron) rigida</i>	SRI	Late	x	x	R, C	
<i>Monarda fistulosa</i>	MFI	Mid, full	x	x		R, C
<i>Apocynum cannabinum</i>	ACA	Mid, full	x	x		R, C
<i>Daucus carota</i>	DCA	Mid	x	x		R, C
<i>Lythrum salicaria</i>	LSA	Mid, full	x	x		R, C
<i>Verbena hastata</i>	VHA	Full	x	x	ns	R, C
<i>Rudbeckia laciniata</i>	RLA	Mid	•	x	C	R*, C
<i>Rudbeckia hirta</i>	RHI	Mid	x		R	R
<i>Penstemon hirsutus</i>	PHI	Early	x		R	
<i>Eupatoriadelphus maculatus</i>	EMA	Mid	x		R	
<i>Agastache scrophulariifolia</i>	ASC	Late	x		R	
<i>Penstemon digitalis</i>	PDI	Mid	x			R
<i>Rumex acetosella</i>	RAC	Mid	x			R
<i>Desmodium ciliare</i>	DCI	Late	x			R
<i>Coreopsis lanceolata</i>	CLA	Mid	•			R*

Note: 'Experiment' and 'Observations' indicate which dataset(s) found the significant preference for the plant species. For a more detailed table of the preferred species in both studies, see Table S3, and for the complete list of all plant species in the experiment and their preference coefficients, see Table S1.

Bold = preferred by both rare and crop bees, underline = non-native, "full" = preferred in season-long analysis (i.e. not broken down by time period), R = preferred by rare bees, C = preferred by crop-pollinating bees, * = marginally significant, ns = non-significant trend.

Jones, Flecker, & Vanni, 2007; Soliveres et al., 2016). An important feature of our study is that the datasets we used to define the rare and ecosystem-service-providing species were regional in scale and independent of each other. More often, both rarity and function are measured at the local scale and within the same dataset (e.g. at the same site). In this situation, it is more likely that the locally common species will also drive function, simply on numerical grounds. But these same species may not be rare, or functionally important, at larger scales. Thus, they may not be relevant targets for conservation management.

There are at least two ways that a species that is rare at the regional scale (i.e. occurs at few sites across a larger region) could nonetheless be an important crop pollinator (i.e. account for a large proportion of visits to a crop grown within the region). First, the bee species could be strongly attracted to that flowering crop, and thus be more abundant in samples taken from flowers of that crop than it is in samples taken haphazardly across hundreds of plant species and habitat types (as is the case for our regional occurrence datasets). Because bee species can have strong floral preferences, focused sampling on a single plant species, as done to create the crop dataset, creates a strong filter on species composition. This appears to be an important mechanism in our study insofar as several of the five regionally rare dominant crop pollinators are known to be oligolectic (specialists at the species scale)

on the crop plant they were collected from. Specifically, *H. labriosa* is oligolectic on blueberries, *M. americana* is oligolectic on cranberries, and *C. validus* is oligolectic on the family Ericaceae. A fourth species, *E. pruinosa*, is oligolectic on the genus *Cucurbita* but was an important pollinator of muskmelon (*C. melo*) in our study, which is a related genus in the same family. Second, a bee species could be locally abundant at certain sites despite being present at relatively few sites within the region for reasons unrelated to floral preferences. While local abundance and the frequency of occurrence at sites throughout a larger region are in general positively correlated across species (Gaston et al., 2000), there are of course species that occur in few places, but are common where they do occur (Rabinowitz, 1981). Measuring rarity at larger, conservation-relevant scales, as we did here, provides scope for rare species to be functionally important in these ways.

Our finding that rare species can be important crop pollinators contrasts with the results of previous studies finding that regionally rare species do not contribute to crop pollination because they are absent from the agricultural landscapes where most crop pollination takes place (Kleijn et al., 2015; Sutter et al., 2017). There are at least two reasons why we might have found rare bee species pollinating crops in our study. First, our study region is less agriculturally intensive, and correspondingly has greater diversity and abundance of wild bees, than many of those studied by Kleijn et al.

(2015). Second, two of the seven crop plants we studied (cranberry and highbush blueberry) are native to our study area in their wild form. Thus, the bee fauna of our region has a long evolutionary history with these plants. Indeed, both native crops had specialist pollinators that were dominant: *H. laboriosa* and *C. validus* on blueberry and *M. americana* on cranberry. Overall, though, we still found fewer regionally rare species among the dominant crop pollinators than would be expected by chance if the frequency of regionally rare species within the dominant crop pollinators was similar to that within the entire group of species in our regional occurrence datasets.

A limitation of our study is that our regional occurrence datasets was collected haphazardly and with unknown sampling effort (the museum dataset) or with a particular study design that dictated where collection sites were located, often with respect to habitat type or surrounding land cover, and what time of the year the bees were collected. Thus, there are likely biases in our rarity assessments stemming from our over- or under-sampling some species relative to others. The fact that our regional datasets are heterogeneous in terms of the habitats and times of year sampled, and in the sampling methods (Supplementary Text), is actually an advantage in terms of avoiding consistent biases. For example, 1,488 different individual collectors contributed specimens to the museum dataset, and it is unlikely that they all shared the same preferences about where, when, and how to collect bees.

Rarity is not a well-defined concept, and its meaning and measurement can vary across contexts. Studies of rare bees in Europe have used pre-existing Red List categorizations (Kleijn et al., 2015; Sutter et al., 2017). Red Lists for bees do not exist for North America, so we had to conduct our own rarity analysis based on region-wide species-occupancy distributions. An advantage of this approach is that it can be used in information-poor situations such as ours where we do not know (for example) geographic ranges or population trends over time. A limitation is that it may include more species in the rare category than do approaches using more information, which can eliminate species that are rare merely because they are at the edge of their range, or species that would rarely be detected in a region-wide survey but which are very abundant in certain habitats. These issues with sampling in space have analogs for sampling in time. For example, bee species with short flight seasons, such as many species of *Andrena* and *Colletes*, could show up as rare in datasets aggregated across the entire season, even if they were abundant at certain times of the year. A related point is that abundance measures, whether in space or time, are scale dependent (White et al., 2006); thus rarity will be assessed differently when measured at different scales (Gaston, 1994). In our study, we assessed rarity at the regional scale (>700,000 km²) spatially, and at the season-long scale (approximately 6 months) temporally. An important goal for future work is to develop more accurate measures of rarity for North American bee species that can take into account aspects of species' biology such as geographic range size, phenology, and habitat specialization.

4.2 | Correlated preferences of rare and crop-pollinating bees

We found modest potential for regionally rare bee species to be supported by habitat plantings targeting crop pollinators, in general, because there are positive associations between the plant species preferred by the two groups ($r = .54$ and $r = .45$ in the experimental and the observational datasets, respectively). These results agree with a similar study in Switzerland, which found that rare bees visited a nested subset of plants visited by crop-pollinating bees (Sutter et al., 2017).

4.3 | Plant species preferred by regionally rare and crop-pollinating bees

We identified 10 plant species that are significantly preferred by both regionally rare and crop-pollinating bees (Table 1). Identifying the best plant species to use in pollinator habitat creation is important for several reasons. First, it could have a large impact given the ongoing creation of thousands of hectares of pollinator habitat in the USA and elsewhere (Rowe, Gibson, Landis, Gibbs, & Isaacs, 2018; Williams et al., 2015; Wood, Holland, & Goulson, 2017). Second, the existing lists of plants recommended for pollinator habitat enhancements can probably be improved because these lists are not based on peer-reviewed, empirical studies (Garbuzov & Ratnieks, 2014). Third, the response of the pollinators themselves to floral plantings shows that many of the species most visited by pollinators are not even part of the original planting, but rather weedy 'volunteers'; this certainly suggests that there is room for improvement in the plant species chosen (Ouvrard, Transon, & Jacquemart, 2018; Warzecha, Diekotter, Wolters, & Jauker, 2018). There is also wide variation in pollinator preference among the planted species themselves, with a few key plant species out-performing the others. For example, in one study the top four plant species accounted for 80% of the pollinator visits (Rowe et al., 2018; Warzecha et al., 2018). We found a similar pattern in our study. The top plant in our experiment, *Pycnanthemum tenuifolium*, attracted four times as many crop-pollinating bees and twice as many rare bees as did the second most preferred plant species (Figure S4). With respect to these issues, our results should contribute to developing a better understanding of which plants will truly perform best when used in management actions. In fact, plants that were above the mean in our study but not the most preferred (i.e. have a positive coefficient in Table S1 but do not appear in Table 1) may turn out to be useful for management insofar as our floral preference datasets included many species that had been pre-selected for pollinator attractiveness. Finally, our study is only applicable to the summer and fall bee fauna, because our floral preference data were collected from late May through October. In eastern North America, there is also a spring bee fauna, including most of the species in the genera *Andrena*, *Nomada*, *Colletes*, and *Osmia*, which fly primarily during April and May. There is a largely unmet need for identifying the best plants to use for these spring-flying bee species (Smith et al., 2019; Wood et al., 2017, 2018).

More generally, does it make sense to talk about the floral preferences of rare species as a group, or are rare species too diverse for such a concept? While we cannot answer that question based on this study, we can acknowledge some statistical issues that often accompany analyses of data on rare species. In our data, despite very large sample sizes overall (e.g. over 90,000 bee specimens analysed in this paper), our rare species data are characterized by small numbers, high uncertainty and unequal representation by species within the 'rare' category. For example, in our field observations, the five most abundant of the 56 rare species accounted for 67% of the total individuals collected, and in the experimental dataset the top three of 34 rare species accounted for 71% of the individuals. In this situation, we might expect high variation in the attributes of the category 'rare species', depending on which particular species dominate the category. To explore this issue and reduce the effect of the few abundant species, we reran the analyses using the incidence (i.e. presence/absence) of each bee species, rather than the aggregate abundance of individuals, in each replicate sample. This had little effect on the list of preferred plant species, although it did weaken the correlation between the preferences of rare and crop-pollinating bees in the experimental dataset (data not shown).

There are several limitations to this study in terms of identifying the plants that will most benefit bees. One is that our data record only the presence of a given plant–pollinator interaction, but in reality not all interactions are equal. For example, bees often forage differently for pollen versus nectar on different plant species, and this likely affects bee population growth, as does the seasonal timing of when a plant blooms (Hicks et al., 2016; Malfi, Crone, & Williams, 2019). Likewise, the extent to which plants are used by male versus female bees, or by individual bees that are post-reproductive, may make a plant species more or less beneficial to the bee population than the number of visits indicates. Another limitation to all studies of pollinator foraging preferences is that bees are choosing among all the plants within their foraging range, which can extend over many hectares (Greenleaf et al., 2007). Thus, variation in the 'background' availability of plants outside our study transects can affect the apparent preference we observe. This may be one reason why the seven plant species that were present in both the experimental and the observational study were not ranked in the same order in the two datasets. In general, we believe the experimental results are more rigorous because plant abundance was controlled and the plant species were replicated.

4.4 | Conclusions and management recommendations

Our finding that the set of most important crop pollinators in our study region includes several regionally rare species underscores the role of biodiversity in ecosystem services at large spatial scales. Our findings suggest that an important mechanism through which regionally rare species are important pollinators of particular crops is host plant specialization, which may lead to a bee species being rarely collected on a regional scale, but locally abundant in large monoculture plantations of a crop plant. With respect to floral plantings, the finding that rare and

crop-pollinating bees share at least some floral preferences is important for conservation practice. In many areas, rare bees are not specifically targeted in conservation efforts but receive restoration benefits only indirectly through efforts targeting crop pollinators. This may be because much of the funding available for pollinator habitat improvement is designated for agricultural areas, and involves stakeholders who value crop pollination. In addition, in most parts of the world, it is not known which bee species are rare, much less what their floral preferences are. Our work to identify the rare and crop-pollinating species of our region, and their floral preferences, is an initial effort in this direction for North America.

ACKNOWLEDGEMENTS

M.M. thanks the US Environmental Protection Agency (EPA) STAR Graduate Fellowship, Rutgers University (Ted Stiles Award, Buell Award, and Charlie Kontos Memorial Grant), and the Garden Club of America for funding. We are grateful to the staff of the Natural Resources Conservation Service (NRCS) Cape May Plant Materials Center for providing the site for and assistance with the field experiment, and to John S. Ascher for identification of bee specimens. The observational field study was funded by a Conservation Innovation Grant from the NRCS to the Xerces Society with RW as Co-PI and by Rutgers University through Aresty grants for undergraduate research to multiple undergraduates. We are grateful to the many landowners, field technicians, and staff of NRCS for their important contributions to this study. We also thank our editor and two reviewers for excellent comments on earlier versions of the manuscript.

AUTHORS' CONTRIBUTIONS

M.M. collected the experimental data; D.C. and M.R. collected observational data; J.G. identified bee specimens; J.R. did the analysis with help from M.G.; R.W. designed the study, oversaw data collection and analysis, and wrote the manuscript. All authors contributed to conceptual development and manuscript revisions.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.gf1vhhmjv> (MacLeod et al., 2019).

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SUPPORTING INFORMATION

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How to cite this article: MacLeod M, Reilly J, Cariveau D, et al. How much do rare and crop-pollinating bees overlap in identity and flower preferences? *J Appl Ecol*. 2020;57:413–423. <https://doi.org/10.1111/1365-2664.13543>