

The bee fauna associated with Pacific Northwest (USA) native plants for gardens

Aaron G. Anderson  | Lucas Costner | Lincoln Best | Gail A. Langellotto 

Department of Horticulture, Oregon State University, Corvallis, Oregon, USA

Correspondence

Aaron G. Anderson, Department of Horticulture, Oregon State University, 4017 Agriculture and Life Sciences Building, Corvallis, OR 97331, USA.
Email: andeaaro@oregonstate.edu

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Abstract

Growing public awareness of pollinator declines has led to an increase in gardening for pollinators, particularly bees. In most regions of the United States a better understanding of the plants that support abundant and species rich bee communities will help urban pollinator conservation programs. To address this, we compared the relative attractiveness of 23 native Pacific Northwest plant species to bees. We performed timed bee counts and vacuum-sampled bee communities, weekly, when plots were in peak bloom. Across three field seasons, we found that Douglas' aster (*Symphyotrichum subspicatum*), California poppy (*Eschscholzia californica*), varileaf phacelia (*Phacelia heterophylla*), Canada goldenrod (*Solidago canadensis*), farewell-to-spring (*Clarkia amoena*), globe gilia (*Gilia capitata*), and Oregon sunshine (*Eriophyllum lanatum*) consistently harbored high bee abundance and species richness, and show great potential for garden pollinator plantings. These findings can be applied to residential and community gardens, municipal parks and other plantings, as well as by restoration professionals and policy makers interested in creating and supporting pollinator habitat.

KEYWORDS

gardens, native plants, pollinator, urban ecology

1 | INTRODUCTION

Documented and highly publicized declines in managed honey bees (Neumann & Carreck, 2010; Paudel et al., 2015; vanEngelsdorp et al., 2010) and wild bumble bees (Bartomeus et al., 2013; Goulson et al., 2015; Wood et al., 2019) have focused public attention on protecting pollinators (Wilson et al., 2017). Many groups have implemented bee conservation programs across the US, including efforts by government agencies and extensive programming by non-profits.

Several bee conservation programs include efforts in urban areas (e.g., Bee City USA, Million Pollinator Garden

Challenge) and these programs often promote floral plantings. Although extreme urbanization is typically associated with declines in native species richness (McKinney, 2008; Piano et al., 2020), several studies have found abundant and diverse bee assemblages in highly urbanized landscapes across the United Kingdom (Baldock et al., 2015; Sirohi et al., 2015), United States (Frankie et al., 2005; Matteson et al., 2008; Tonietto et al., 2011; Turo et al., 2021), and Canada (Normandin et al., 2017; Tommasi et al., 2004). In fact, some studies have found that urban areas harbor comparable bee richness to surrounding natural areas (Baldock et al., 2015; Fetridge et al., 2008), which has led to calls to recognize the

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unique conservation value that cities can offer bees (Hall et al., 2017).

Notably, Lowenstein et al. (2014) found that not only did bee abundance and richness increase with increasing human population density in Chicago, IL, but so did pollination services. This study may be the first to show an ecosystem service increasing (outside of cultural and recreational services) with human population density. This relationship was likely mediated by people's gardening choices. Densely populated neighborhoods had smaller gardens and prioritized flowering plants instead of turfgrass (Lowenstein et al., 2014). Abundance of flowers has repeatedly been identified as a strong driver of bee abundance and species richness (Egerer et al., 2020; Matteson & Langelotto, 2010; Pardee & Philpott, 2014; Quistberg et al., 2016).

Residential gardens are uniquely situated to provide necessary habitat for pollinators in urban landscapes. Yards and gardens comprise about 25%–30% of all urban land (Mathieu et al., 2007), and recent surveys suggest that one in four adults base at least some of their gardening purchase decisions on a plant's purported benefits to wildlife (National Gardening Survey, 2020). Gardens managed for bees could provide habitat amid an otherwise resource-poor urban landscape (Quistberg et al., 2016). Studies have found that local factors (e.g., higher floral abundance) drive bee abundance and richness more strongly than landscape-level factors (Matteson & Langelotto, 2010; Quistberg et al., 2016). Even small urban habitat patches have value (Griffiths-Lee et al., 2022; Soanes et al., 2019), and if many gardeners considered conservation an essential aspect of their gardening activities, urban gardens could scale-up from the lot to the landscape level (Belaire et al., 2014).

Garden plant communities are frequently dominated by non-native, ornamental plants (Burghardt et al., 2009; Martins et al., 2017; Smith et al., 2006). Many bee species are generalists that often show no preference for native over exotic plants (Martins et al., 2017; Matteson & Langelotto, 2011). However, observational studies suggest that gardens with more native plant species may experience higher bee visitation (Fukase & Simons, 2016) and increased native plant diversity can result in higher bee diversity (Hostetler & McIntyre, 2001) or abundance (Pardee & Philpott, 2014). Additionally, more native bee and wasp larvae may be found in urban areas seeded with native wildflowers (Turo & Gardiner, 2021). This may be due to coevolutionary relationships between native flora and fauna, or because native plants are adapted to local climates and frequently bloom later into the summer than exotic plants (Tuell et al., 2008), providing season-long resources to pollinators.

Better understanding which plants best support bee communities can help fine-tune conservation programs,

especially those focused on urban gardeners. Empirical research on the relative attractiveness of regionally relevant native plants to wild bees has been published in the peer-refereed literature for only one location, the upper-Midwestern United States (Rowe et al., 2018; Tuell et al., 2008), and trials have been performed at botanical gardens including the Lady Bird Johnson Wildflower Center in Austin, TX, and the Mt. Cuba Center in Hockessin, DE. However, to our knowledge no such studies have been performed in the Pacific Northwest region of the United States, either rigorously or through casual comparison.

Our overarching research goal was to identify which native Pacific Northwest flowering plants (out of the 23 screened) support robust bee communities. To answer this, we asked which plants attract the highest bee abundance and support the highest bee species richness? We also sought to identify significant associations between native plants and wild bees. We considered bee abundance, bee species richness, and bee community composition as separate measures of native plant attractiveness to bees. We had no *a priori* hypotheses on which plants would be most attractive to bees, as all these plants were listed on one or more pollinator planting lists. Four non-native garden plants were also included in this study, as benchmarks for comparing native plants to ornamental species commonly found in gardens, with purported benefits to pollinators. In a related study (Anderson et al., 2021) we ascertained the aesthetic appeal of the study plants to gardeners. Because our ultimate research goal was to identify native plants that are attractive to bees *and* gardeners, we clustered the bee attractiveness results from this study into four groups, based upon plants' appeal to gardeners: (1) most attractive, (2) moderately attractive, (3) and least attractive plants to gardeners, and (4) non-native garden species.

2 | METHODS

2.1 | Study plants

Across three field seasons, we documented bee visitation to 23 plants with native ranges that include Oregon's Willamette Valley, where our field study occurred (Table 1). We selected plants for summer drought tolerance and ability to grow in full sun (to maximize success at our study site), as well as for their potential to produce resources for bees. To assess these criteria, we reviewed pollinator planting lists and native plant gardening lists for the Willamette Valley and western Oregon published by organizations like the USDA NRCS, Oregon State Extension, Oregon Metro, and the Xerces Society (McMahan, 2008;

TABLE 1 List of 27 plants included in a 3 year field study of bee visitation to plants that are native to the Willamette Valley region of Oregon (United States) that have promise as garden ornamentals, and popular non-native garden plants that can be found on pollinator planting lists

Plant species	Plant life cycle	Native range
Smallflower lotus (<i>Acmispon parviflorus</i>)	Annual	Western US
Farewell-to-spring (<i>Clarkia amoena</i>)	Annual	Pacific Northwest US
Giant blue-eyed Mary (<i>Collinsia grandiflora</i>) ^a	Annual	Western US
Globe gilia (<i>Gilia capitata</i>)	Annual	Western US
Common sunflower (<i>Helianthus annuus</i>) ^a	Annual	US
Miniature lupine (<i>Lupinus micranthus</i>)	Annual	Western US
Common madia (<i>Madia elegans</i>)	Annual	Western US
Baby blue eyes (<i>Nemophila menziesii</i>) ^a	Annual	Western US
Varileaf phacelia (<i>Phacelia heterophylla</i>)	Annual/biennial	Western US
California poppy (<i>Eschscholzia californica</i>)	Annual/perennial	Western US
Common yarrow (<i>Achillea millefolium</i>)	Perennial	US
Pearly everlasting (<i>Anaphalis margaritacea</i>)	Perennial	US
Showy milkweed (<i>Asclepias speciosa</i>)	Perennial	US
Western columbine (<i>Aquilegia formosa</i>)	Perennial	Western US
Great camas (<i>Camassia leichtlinii</i>)	Perennial	Pacific Northwest US
Oregon sunshine (<i>Eriophyllum lanatum</i>)	Perennial	Western US
Wild strawberry (<i>Fragaria vesca</i>)	Perennial	US
Oregon iris (<i>Iris tenax</i>)	Perennial	Pacific Northwest US
Cream stonecrop (<i>Sedum oregonense</i>) ^b	Perennial	Pacific Northwest US
Rose checkermallow (<i>Sidalcea asprella</i> ssp. <i>virgata</i>)	Perennial	Pacific Northwest US
Idaho-blue-eyed grass (<i>Sisyrinchium idahoense</i>)	Perennial	Pacific Northwest US
Canada goldenrod (<i>Solidago canadensis</i>)	Perennial	US
Douglas' aster (<i>Symphyotrichum subspicatum</i>)	Perennial	Western US
“Grosso” lavender (<i>Lavandula X intermedia</i> “Grosso”)	Perennial	Eurasia
Catnip (<i>Nepeta cataria</i>)	Perennial	Eurasia
Oregano (<i>Organum vulgare</i>)	Perennial	Eurasia
Pineapple sage (<i>Salvia elegans</i>)	Perennial	Guatemala/Mexico

^aDropped from data analyses, due to poor germination across the 3 years of this study.

^bDropped from data analyses, due to slow growth and poor flowering.

Metro, 2013; Pendergrass et al., 2008). This resulted in 63 candidate species. We chose the final plants in consultation with a landscape designer, who prioritized plants with high potential appeal to home gardeners (S. Danler, personal communication).

In addition to the native plants, we included four non-native species (Table 1) that are commonly found on pollinator planting lists (Garbuzov & Ratnieks, 2014), for a total of 27 plants used in this study. These were not for direct comparison; instead they served as benchmarks for pollinator activity that could be easily communicated to many gardeners. For example, we expected that we could tell gardeners that a particular native plant “had more (or less) bees” or “a greater (or less) diversity of bees”

than one of the non-native comparison plants, and that gardeners would intuitively understand the value of specific plants for bee conservation.

Because we are interested in plants that gardeners and other urban land managers will use, we organized the study plants into groups based on their aesthetic appeal (Anderson et al., 2021). These were: (1) Most attractive: western columbine (*Aquilegia formosa*), Oregon iris (*Iris tenax*), Idaho blue eyed grass (*Sisyrinchium idahoense*), great camas (*Camassia leichtlinii*), globe gilia (*Gilia capitata*). (2) Moderately attractive: showy milkweed (*Asclepias speciosa*), Douglas' aster (*Symphyotrichum subspicatum*), yarrow (*Achillea millefolium*), California poppy (*Eschscholzia californica*), Oregon sunshine (*Eriophyllum lanatum*),

woodland strawberry (*Fragaria vesca*), common madia (*Madia elegans*), miniature lupine (*Lupinus micranthus*). (3) Least attractive: pearly everlasting (*Anaphalis margaritacea*), rose checkermallow (*Sidalcea asprella* spp. *virgata*), goldenrod (*Solidago canadensis*), varileaf phacelia (*Phacelia heterophylla*), smallflower lotus (*Acmispon parviflorus*). (4) Non-native garden species: lavender (*Lavandula X intermedia* “Grosso”), oregano (*Origanum vulgare*), catnip (*Nepeta cataria*), pineapple sage (*Salvia elegans*).

2.2 | Study site and study design

We established five replicate plots of each plant species in a randomized complete block design at Oregon State University's North Willamette Research and Extension Center (NWREC) in Aurora, OR, a peri-urban suburb of Portland, OR. Pesticide applications are restricted or rarely used at NWREC. We divided the plots into five blocks to account for variation within the site, including edge effects. Each block contained twenty-seven 1 m² plots. Each plot was planted with one of the 27 study plant species, at densities needed to fill the entire the m² area when plants reached maturity. Like Tuell et al. (2008), each 1 m² plot was separated from neighboring plots by 6 m in all directions. This was also similar to distances by Rowe et al. (2018) (5 m) and Williams et al. (2015) (10 m). We seeded the space between study plots with perennial ryegrass (*Lolium perenne*). For plots located on the outer edge of the field site, we left at least 6 m separating these outside plots from the edge of the field. This area was also seeded with perennial ryegrass. Turf areas were mowed every 1–2 weeks by farm crews.

2.3 | Plant installation and maintenance, bloom phenology, and water availability

We planted the plots at densities intended to achieve complete coverage when plants matured, thinning annual plots when necessary. We direct-seeded annual species into plots at the end of April 2017, early March 2018, or early December 2018, followed by a subsequent seeding in early March 2019. Four plant species: giant blue-eyed Mary (*Collinsia grandiflora*), common sunflower (*Helianthus annuus*), baby blue-eyes (*Nemophila menziesii*), and cream stonecrop (*Sedum oregonense*) had poor germination or flowering across all 3 years. We removed these species from our analyses, to avoid underrepresenting their potential attractiveness to bees. This left us with a total of 23 study plants: 19 native plants and 4 non-native benchmark plants. However, some of these remaining study plants did not bloom every year, which we factored into analyses (see Section 2.5).

We weeded study plots and turfgrass areas throughout the course of this study. To facilitate plant establishment in the field, we irrigated plots after planting and weekly throughout the 2017 growing season. In 2018 and 2019 we used no supplemental irrigation. However, we hand watered annual plots that appeared drought stressed, as needed.

Each field season, we noted the onset of bloom (when the first buds opened into flowers) and end of floral bloom (the last open flowers with viable pollen on anthers) at each plot. We estimated when between 26% and 50% of buds on plants within a plot were in bloom by counting flowers and buds (which we referred to as pre-peak bloom), and when 51% or more of the buds were in bloom (which we referred to as peak bloom).

2.4 | Bee counts and collections

At each plot, we estimated bee abundance by counting the number of bees that contacted open flowers during 5-min observations period. We performed these 5-min timed counts when a plot was in pre-peak bloom, the week of peak bloom, and the week immediately following peak bloom. Some plots bloomed continuously at a peak-bloom level for more than 1 week, such as lavender. In these cases, we continued sampling plots until the number of flowers in a plot declined from the previous week. For each field season we gathered 3 weeks of pollinator observations for most plant species. However, in a few cases, the field conditions and/or plant phenology resulted in us sampling some plots for less than 3 weeks, resulting in an unequal sampling effort across all plant species (see Section 2.5).

We identified bees to morpho-category (sensu Winfree et al., 2007); honey bees (e.g., *Apis mellifera*), bumble bees (e.g., *Bombus* spp.), green bees (e.g., *Agapostemon* spp.), and other wild bees. Visits by other potential pollinators (e.g., butterflies, syrphid flies, beetles, moths) were also recorded, and will be reported in a separate manuscript.

On days we counted bee abundance, we also sampled the bee communities present on each plot. Using a “Vortis” insect suction sampler (Burkard Manufacturing Co. Ltd., Hertfordshire, UK), we took four overhead samples on each plot on each occasion. When vacuum-sampling study plots, we prioritized the collection of bee visitors. Thus, sampling was not random, but was intended to maximize the abundance and richness of bee species collected. Samples were put in individual Whirlpak or plastic sandwich bags filled with 90% ethanol upon return to the laboratory. Bee specimens were sorted and identified to genus, and then identified to species by a taxonomic expert (Lincoln Best).

2.5 | Statistical analyses

We used the statistical software R (version 3.5.1; R Core Team, Vienna, Austria), and RStudio (RStudio, Boston, MA) to perform all statistical analyses.

2.5.1 | Bee abundance

To investigate differences in bee abundance between plant species, we used analysis of variances (ANOVAs) on the variables “plant species” and “block”. We included the 3 weeks of “peak” bloom in these analyses, as described earlier. For plots that had more than 3 weeks in peak bloom, we sampled the extra weeks and then referred to field notes and photographs of the plots to select the 3-week period with the most open flowers. Conversely, some of our plots did not bloom for a 3-week period due to drought stress. In some cases we missed a week of observations due to poor weather conditions or wildfire smoke limiting our ability to be in the field. In these instances, we counted the subsequent week’s observations, unless the plot was no longer in bloom. Thus, we chose type II ANOVAs to account for this unequal number of sampling events per plot. All bee abundance data was natural log (+1) transformed to satisfy the assumption of normality.

We analyzed our three field seasons separately for several reasons. First, plant phenology varied all 3 years, particularly for perennial plants. Second, we only irrigated plots in 2017 to keep plot fees low, and 2017 also had higher precipitation totals compared with 2018 and 2019. Third, not every plant species bloomed every year. Finally, bee populations are known to be highly variable across years (Herrera, 1988), within years (Herrera, 1988), and even over short distances (Minckley et al., 1999).

For each year we performed two analyses: one including all bees, and one including wild bees only (excluding honey bees from the dataset), for a total of six ANOVAs (details in Appendix S1). We performed all ANOVAs with the “Anova” function in the “car” package (Fox & Weisberg, 2019).

When there was a significant effect of plant on bee abundance, we used Tukey’s honest significant difference test (HSD) to determine which study plant species attracted significantly more bees. Tukey’s method allows for all pairwise comparisons, which provided a holistic view of how plant species ranked against each other, in terms of bee abundance. To compare plant species, we used estimated marginal means, or least square means. We used the function “emmeans” from the R package “emmeans” (Length, 2021) to calculate these values.

2.5.2 | Bee species richness

For analyses of bee species richness, we pooled all the specimens we sampled across 2017–2019. Unlike our analyses of bee abundance, we did not parse our data down to three sampling dates for the plots that bloomed at a peak level for more than 3 weeks, in order to include all the collected specimens in the analysis. However, due to the uneven sampling effort, using raw richness numbers could artificially inflate the counts for more heavily sampled plots, increasing the chance of detecting otherwise rare species. To justify our choice to include all bees collected in our analyses of species richness, we created species accumulation curves to visually assess whether curves leveled off, suggesting that we had largely sampled the bee communities visiting each plant. We used the Chao2 estimator, from the “ChaoRichness” function in the R package “SpadeR” (Chao et al., 2016), to estimate total bee species richness for each plant species. This allowed us to determine how close our observed richness was to the estimated true richness.

Both the species accumulation curves (data not shown) and Chao2 estimated species richness suggested that we sufficiently sampled the bee species richness of most plant species in this study. Thus, we felt that our non-adjusted data was not artificially hiding the true richness of under-sampled plant species. Furthermore, plants with more than twice the estimated versus observed bee richness were already the most speciose. Thus, if they were under-sampled it would not change our practical estimation of these plant species performing well as bee plants.

2.5.3 | Bee community composition

We used an indicator species analysis to determine bee species that were significantly associated with particular plant species. We used the R function “multipatt” in the package “indicspecies” (De Cáceres & Legendre, 2009). This function defines an index between the bee species and grouping variable, and then looks for the groups corresponding to the highest association value, at an alpha level of 0.05. This test allows us to see which (if any) individual bee species significantly associated with each plant species, as well as redundancies between plant species (e.g., plants that attract similar bee species).

3 | RESULTS

3.1 | Abundance

We observed 4472 individual bees visiting our study plots during our five-minute observations across all

TABLE 2 Results of type II ANOVAs of bee abundance during 5-min observation periods in 2017, 2018, and 2019, as a function of study plant species and block

Model	F	df	p
2017 all bees			
Plant species	35.70	16, 203	<.001***
Block	2.28	4, 203	.062
2017 wild bees			
Plant species	27.29	16, 223	<.001***
Block	1.48	4, 223	.209
2018 all bees			
Plant species	26.56	21, 257	<.001***
Block	3.68	4, 257	.006**
2018 wild bees			
Plant species	16.69	21, 257	<.001***
Block	3.14	4, 257	.015*
2019 all bees			
Plant species	29.86	20, 228	<.001***
Block	5.86	4, 228	<.001***
2019 wild bees			
Plant species	15.00	20, 228	<.001***
Block	4.71	4, 228	.001***

Note: All bee models include honey bee observations, and wild bee models exclude honey bee observations. Significant effects at probability levels of .05 (*), .01 (**), and .001 (***) levels are indicated by asterisks.

3 years (883 in 2017, 1618 in 2018, and 1971 in 2019). Of these, 43.0% were honey bees, 14.7% were bumble bees, 2.5% were green bees, and 39.8% were other wild bees.

The ANOVA of our abundance data of all bee visitors revealed significant effects of plant species and block on bee abundance at the 0.05 alpha level in 2017, 2018, and 2019 (Table 2). There were no significant interactions between species and block in 2017 and 2019. Thus, we removed the interaction term from these ANOVAs. A weakly significant interaction ($p = .042$) was observed in 2018. We removed this interaction term, because we had no a priori hypotheses regarding this interaction, and removing it made it possible to perform post-hoc means comparisons comparable to 2017 and 2019.

The ANOVAs of wild bee visitation (honey bees excluded) revealed similar results. We observed significant effects of plant species and block on wild bee abundance in 2017, 2018, and 2019 (Table 2). There was no significant interaction between plant species and block for any of the three study years.

3.1.1 | Gardeners' aesthetic groupings

Of the five plants most attractive to home gardeners, only globe gilia was heavily visited by bees (Figure 1). The other plants enjoyed by gardeners attracted between zero and two bee visitors per 5-min observation period.

On average, visitation was higher in the plants moderately attractive to gardeners, in particular California poppy, Douglas' aster, Oregon sunshine, and yarrow. However, several of these species—in particular showy milkweed, woodland strawberry, and miniature lupine attracted very few bees.

Of the plants least attractive to gardeners, varileaf phacelia and goldenrod attracted the highest bee abundances. Pearly everlasting and rose checkermallow attracted a moderate number of bees, while smallflower lotus attracted almost no bees.

Across all years, bee visits to the non-native plants oregano, lavender, and catnip were dominated by non-native honey bees (Figure 1). Although overall bee visitation was high to oregano and lavender, and moderate for catnip, these plants all ranked relatively low in bee abundance when only wild bees were considered. The native annual globe gilia was mostly visited by wild bees in 2017, but honey bees in 2018 (Figure 1). Similarly, showy milkweed was visited exclusively by honey bees, and globe gilia in 2018 and 2019 was visited by mostly honey bees. Several plants, including California poppy, varileaf phacelia, goldenrod, and Douglas' aster consistently attracted a high abundance of wild bees across all 3 years (Figures 1 and 2).

3.2 | Richness

Across all study plants and years, we collected 57 bee species. The bee species richness sampled from study plants varied from 0 to 19 bee species per plant, and the Chao2 estimated species richness varied from 0 to 74 bee species (Table 3). Study plants with low observed bee species richness include smallflower lotus and miniature lupine (no bees), showy milkweed (only honey bees), Idaho blue-eyed grass (two bee species), and great camas (four bee species). Study plants with the highest observed and estimated bee species richness were the native plants Douglas aster (19 observed, 74 estimated), farewell-to-spring (14, 45), California poppy (19, 45) globe gilia (16, 28), and Oregon sunshine (15, 21).

The non-native benchmark species ranked moderate to low, with oregano (9 observed, 19 estimated) and pineapple sage (6, 17) with the moderate bee species richness, and lavender (7, 8) and catnip (6, 8) with low bee species richness.

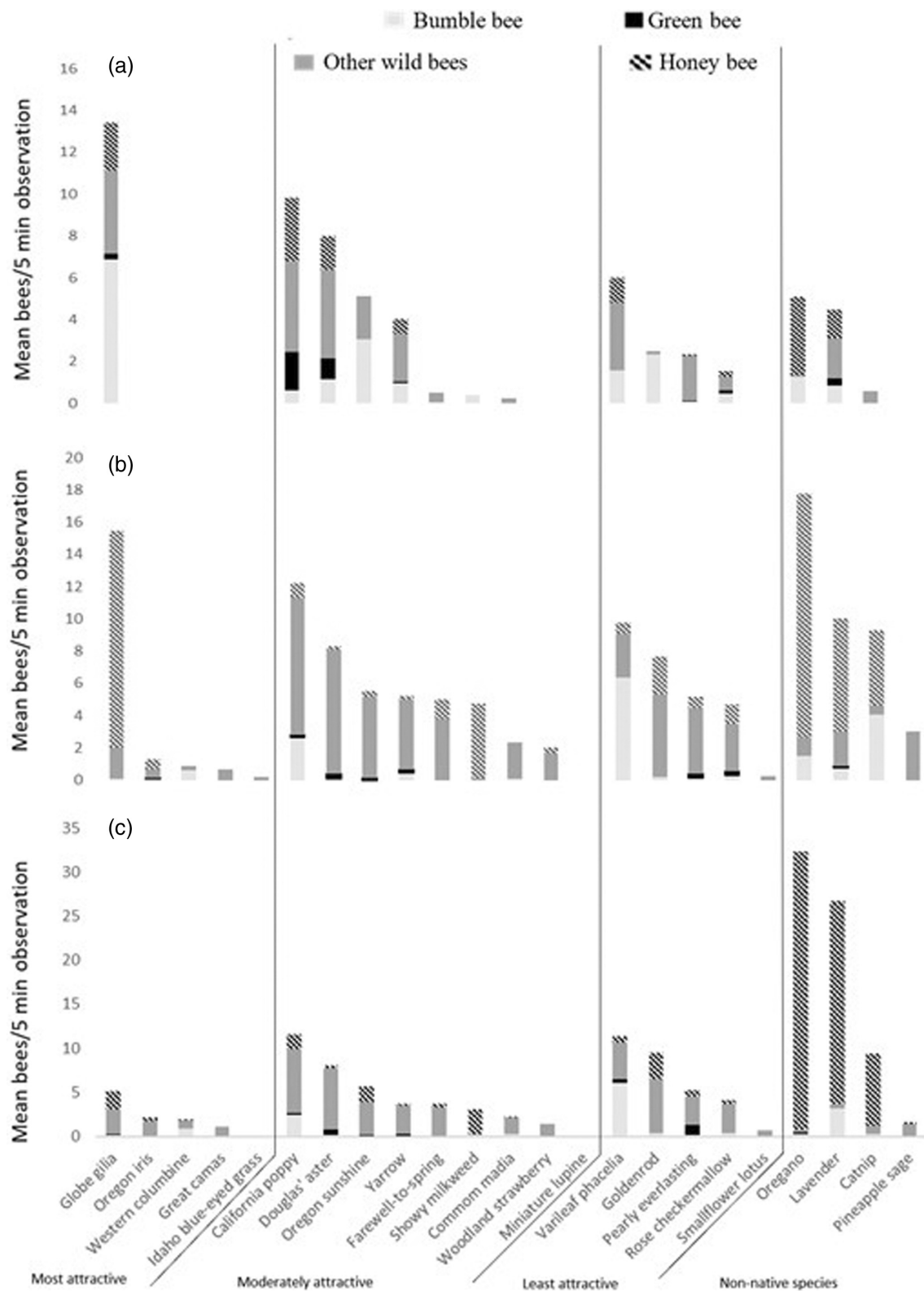


FIGURE 1 Mean bee visitation abundance, per five-minute observation period across three-week peak bloom periods, in: (a) 2017, (b) 2018, and (c) 2019 for both all bees observed (honey bees included). Plants are separated into four categories: most attractive, moderately attractive, least attractive to home gardeners, and non-native species. These were determined from survey results of gardeners (from Anderson et al., 2021)

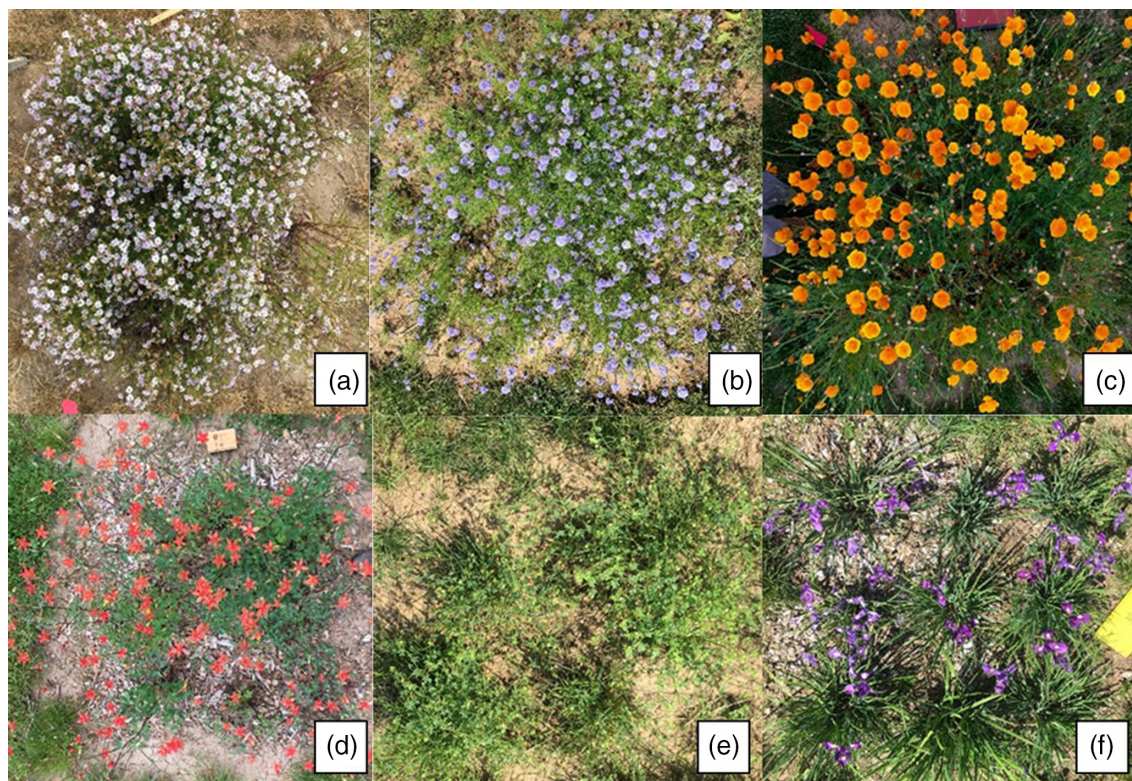


FIGURE 2 Examples of the bloom display of bee attractive (top row) and bee unattractive (lower row) plants. On top are (a) Douglas aster, (b) globe gilia, and (c) California poppy. On the bottom are (d) western columbine, (e) small flower lotus, and (f) Oregon iris

3.3 | Bee communities

The indicator species analysis found 12 bee species significantly associated with one plant species (Table 4). Four different bee species were only associated with Douglas aster. These were *Halictus ligatus* ($p = .01$), *Agapostemon texanus* ($p = .01$), *Melissodes lupinus* ($p = .02$), and *Melissodes robustior* ($p = .02$). Ten bee species were significantly associated with two plant species (Table 4). Of particular note, honey bees were significantly associated with non-native lavender and oregano ($p = .01$). The early season mining bees *Andrena cerasifolia* ($p = .01$) and *Andrena candida* ($p = .01$) were significantly associated with common yarrow and pearly everlasting (*Anaphalis margaritacea*). One bee (*Lasioglossum olympiae*) was significantly associated with three plant species: western columbine, Oregon iris, and California poppy ($p = .01$). Finally, one bee species (*Bombus vosnesenskii*) was significantly associated with four plant species: California poppy, globe gilia, lavender, and varileaf phacelia. ($p = .01$) (Table 4).

4 | DISCUSSION

Native plants unattractive to bees were generally more attractive to gardeners, and vice versa. Four of the top

five plants most preferred by gardeners (based upon aesthetic appeal) were the least attractive to pollinators. (Anderson et al., 2021). Western columbine, great camas, blue-eyed grass, and Oregon iris all had low counts for bee abundance, and all except Oregon iris had very low bee species richness. In contrast, varileaf phacelia, Canada goldenrod, and pearly everlasting were some of our best plants for bee abundance and/or species richness. However, these plants scored lowest for aesthetic appeal in the same survey (Anderson et al., 2021). Of the native plants that we found to be highly attractive to bees in the current field study, only globe gilia was favored by gardeners (Anderson et al., 2021).

We observed significant differences in bee abundances between study plant species. Similarly, we documented a wide range of estimated bee species richness visiting the plants (Chao1 estimate of 1–74). We had no a priori hypotheses on which plants would be most attractive to bees, and the broad difference in bee abundance and richness was somewhat surprising, as each of our study plants can be found on pollinator planting lists (e.g., McMahan, 2008; Metro, 2013; Pendergrass et al., 2008). However, previous studies have noted that few of these lists are based on empirical data (Garbuzov & Ratnieks, 2014).

However, we were able to address our overarching research goal. Based on these results, we recommend that

TABLE 3 Observed and estimated bee species richness associated with each study plant species

Plant species	Observed bee species richness	Estimated bee species richness	95% lower confidence interval	95% upper confidence interval
Common yarrow	17	21	17.79	37.37
Smallflower lotus	0	0	0	0
Pearly everlasting	12	14	12.17	24.70
Western columbine	5	8	5.33	26.86
Showy milkweed	1	1	1	1
Great camas	4	9	4.73	31.84
Farewell-to-spring	14	45	18.71	220.21
Oregon sunshine	15	21	16.04	47.77
California poppy	19	44	24.01	140.81
Woodland strawberry	5	7	5.17	25.58
Globe gilia	16	28	18.19	83.72
Oregon iris	8	11	8.35	25.84
“Grosso” Lavender	7	8	7.07	20.72
Miniature lupine	0	0	0	0
Common madia	10	22	11.62	101.66
Catnip	6	8	6.18	27.86
Oregano	9	19	10.91	60.85
Varileaf phacelia	13	16	13.37	31.68
Pineapple sage	6	17	7.42	86.78
Idaho blue-eyed grass	2	2	2.02	8.09
Rose checkermallow	14	26	16.16	90.98
Canada goldenrod	15	21	16.20	45.75
Douglas' aster	19	74	36.45	189.73

Note: Estimated species richness (and 95% confidence intervals) were calculated using the Chao2 estimator.

gardeners in western Oregon plant California poppy, Douglas' aster, and globe gilia to support wild bee communities and conservation. These plants supported high abundance and richness of wild bee species, and were important floral resources for sweat bees, long-horned bees, and bumble bees. In addition, they hold moderate appeal to home gardeners (Anderson et al., 2021). Native plants such as varileaf phacelia and Canada goldenrod are good choices to support wild bee abundance. Farewell-to-spring and Oregon sunshine are good choices to support wild bee species richness. Yarrow, pearly everlasting, and varileaf phacelia can collectively support specific associations with wild bees. In our study, western columbine, great camas, blue-eyed-grass, and smallflower lotus were not good pollinator plants in any of the measures that we considered: bee abundance, richness, and community structure.

Documenting floral attributes was beyond the scope of our study. However, the floral attributes that have

been found to be positively associated with bee abundance and/or richness include floral area (Rowe et al., 2021; Tuell et al., 2008), floral display size (Bauer et al., 2017), flower height (Rowe et al., 2020), and flower color (Campbell et al., 2010). Some of the most bee-attractive plants in our study had larger floral displays when compared to plants unattractive to bees (Figure 2), but not exclusively (see western columbine, Figure 2f). Pollinator and gardener preferences may align for some traits, such as large floral display. When preferences do not align, simply showing gardeners information on bee species that visit a plant significantly increases gardeners' impression of that plant (Anderson et al., 2021). This highlights the importance of outreach in public bee conservation efforts.

Certain plants attracted proportionately more honey bees. Honey bees are not native to the US, are domesticated, and are managed for agricultural purposes (Goulson, 2003). Goals of pollinator conservation efforts

TABLE 4 List of bee species associated with study plants or plant combinations, as determined by indicator species analysis

Bee species—study plant combination	Indicator value statistic	p
Bee species significantly associated with one plant		
Farewell-to-spring		
<i>Megachile brevis</i>	0.635	.01**
California poppy		
<i>Halictus farinosus</i>	0.786	.01**
<i>Halictus tripartitus</i>	0.628	.01**
Grosso lavender		
<i>Bombus fervidus</i>	0.545	.04*
Common madia		
<i>Lasioglossum titusi</i>	0.929	.01**
Varileaf phacelia		
<i>Bombus caliginosus</i>	0.740	.01**
Rose checkermallow		
<i>Nomada</i> sp. 1	0.657	.01**
Douglas' aster		
<i>Halictus ligatus</i>	0.74	.01**
<i>Melissodes robustior</i>	0.72	.01**
<i>Agapostemon texanus</i>	0.71	.01**
<i>Melissodes lupinus</i>	0.67	.01**
Bee species significantly associated with two plants		
Common yarrow + pearly everlasting		
<i>Andrena cerasifolii</i>	0.71	.01**
<i>Andrena candida</i>	0.68	.01**
Oregon sunshine + varileaf phacelia		
<i>Panurginus atriceps</i>	0.58	.02*
California poppy + Oregon iris		
<i>Lasioglossum (dialictus)</i> sp. 5	0.62	.01**
"Grosso" lavender + oregano		
<i>Apis mellifera</i>	0.83	.01**
"Grosso" lavender + varileaf phacelia		
<i>Bombus mixtus</i>	0.66	.01**
Common madia + Douglas' aster		
<i>Agapostemon virescens</i>	0.58	.04*
Varileaf phacelia + rose checkermallow		
<i>Eucera edwardsii</i>	0.78	.01**
Canada goldenrod + Douglas' aster		
<i>Melissodes microstictus</i>	0.85	.01**
Bee species significantly associated with three or more plants		
Western columbine + California poppy + Oregon iris		
<i>Lasioglossum olympiae</i>	0.70	.01**
California poppy + globe gilia + "Grosso" lavender + varileaf phacelia		
<i>Bombus vosnesenskii</i>	0.79	.01**

Note: The indicator value statistic represents the probability of association. Significant associations at probability levels of .05 (*) and .01 (**) levels are indicated by asterisks.

can vary, and attention on efforts that focus on honey bees may undercut native bee conservation (Colla & MacIvor, 2017). In this study we identified garden plants to support wild bee communities in urban landscapes. However, there are situations, like agricultural hedgerows, where the goal is to provide resources for all pollinators. This distinction is important when choosing pollinator plants based on the relative abundance of different bees they attract.

In our study, the non-native garden plants lavender, oregano, and catnip were highly attractive to honey bees, but were not particularly attractive to wild bees. Many people are familiar with honey bees, but not other species (Wilson et al., 2017). It is thus not surprising that plants which are highly attractive to honey bees are singled out as being good bee plants. In fact, oregano was found on 93% and lavender was found on 87% of the 15 pollinator plant lists analyzed by Garbuzov and Ratnieks (2014).

Although we analyzed our abundance data with and without honey bees (Figure 1, Table 2), subtracting them from our data set prior to analysis did not eliminate any effect they might have had on wild bees during our study. Honey bees identify high quality floral patches and do not switch between plants during foraging trips (Leonhardt & Blüthgen, 2012). Their high level of foraging can lead to competitive exclusion and resource competition with wild bees (Valido et al., 2019). This may explain the difference in bumble bee visitation on globe gilia between years. It is possible that honey bees identified globe gilia as a favored resource in 2018 and 2019, and that their presence depressed bumble bee visits relative to 2017.

The abundance of honey bees on lavender does not necessarily mean it is a poor resource for wild bees. *Bombus fervidus*, a bumble bee listed as "vulnerable" on the International Union for Conservation of Nature (IUCN) Red List, was significantly associated with "Grosso" lavender in our study. Additionally, we only found *Bombus caliginosus*, another IUCN Red List "vulnerable" bumble bee, on lavender. This suggests that appropriate non-native plants can play role in bee conservation efforts, especially when these plants are highly appealing to gardeners.

We should note that the plants that ranked low in our study are not necessarily poor pollinator plants; they were simply the least comparatively attractive in this isolated setting. In ecological contexts, these plants may provide resources for specialist or rare bees that were not present at our site. Additionally, few Lepidoptera and other non-Apoidea pollinators were observed at our research site, and these plants may be visited by other pollinator taxa in a more natural context. Choosing overall abundance and species richness as metrics for ecological impact may miss important relationships

with relatively rare or specialist insects. For example, western columbine ranked poorly by all our metrics, yet we observed *Bombus* spp. queens foraging on its flowers early in the season when little else was blooming. However, urban and suburban gardens (the landscapes this study is intended to address) lack many of these specialist species (Langellotto, 2017), and overall abundance and richness are likely the most useful benchmarks for assessing “good” pollinator plants for urban settings.

Our study had several imitations. Sampling during the middle of the day ignored the presence of nocturnal pollinators and species that forage at dawn and dusk. Additionally, though we modeled the 6-m of separation between plots after Tuell et al. (2008), we acknowledge this is not enough separation to ensure true independence between plots, and pollinators may have visited certain plots after initially being attracted by neighboring plots. However, we did attempt to account for this by using the randomized complete block experimental design.

We identified several flowering plants native to the Pacific Northwest that consistently attracted high bee abundance and species richness. It is impossible to assign a “one-sized-fits-all” recommendation, as plant choice will depend on season, the existing plant community, and the pollinators that a gardener is interested in supporting. However, Douglas’ aster, California poppy, varileaf phacelia, Canada goldenrod, farewell-to-spring, globe gilia and Oregon sunshine harbored a high overall bee abundance and high bee species richness, and show great potential for urban pollinator plantings.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Aaron G. Anderson  <https://orcid.org/0000-0002-0332-9827>

Gail A. Langellotto  <https://orcid.org/0000-0001-6705-2559>

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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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APPENDIX A

A.1 | STATISTICAL DESCRIPTIONS

A.1.1. | Gardener preference groupings

To create these groupings, we performed a generalized linear model on the results of a survey querying how

likely respondents would be to utilize each plant in their home garden (1–5 Likert scale). Though Likert data is ordinal non-parametric, some statisticians suggest that parametric tests can be used on these data if the sample size is sufficiently large. Furthermore, we only used these results to help us sort these flowers into broad groups for casual comparison.

We then used a Tukey HSD post-hoc test to determine pairwise differences in attractiveness between flowering plant species.

A.1.2. | ANOVA of bee abundance

The initial residual plots produced from these ANOVAs suggested that the homogeneity of variance assumption was not satisfied, as the residuals displayed heteroscedasticity. This appeared to be driven by two to three outlier residuals on each plot. We removed these from the dataset and reran the ANOVAs. This created more satisfactory residual plots without apparent heteroscedasticity, and the probability values for our two variables (“plant species” and “block”) did not change significance at the 0.05 alpha level. Because of this, we felt confident using the complete dataset (without outliers removed) for these analyses. This approach was recommended by an OSU statistical consultant (Skypeck, C., personal communication).

Tukey means separation test performed on all three field seasons, with and without honey bees. This test controls the family-wise error rate, and is similar to the Bonferroni correction. The confidence intervals represent 95% CIs, or an alpha of 0.05%. Plant species with overlapping group values do not significantly differ, at the .05 level.

2017 all bees.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Oregon sunshine	6	−0.024	0.198	220	−0.415	0.367	ab
Western columbine	15	0	0.141	220	−0.278	0.278	a
Pineapple sage	14	0.293	0.146	220	0.004	0.581	abc
Common yarrow	15	0.297	0.137	220	0.027	0.566	abc
Rose checkermallow	15	0.739	0.141	220	0.46	1.017	bcd
Pearly everlasting	15	1.032	0.141	220	0.754	1.311	de
Varileaf phacelia	6	1.051	0.228	220	0.602	1.5	cdef
Catnip	15	1.36	0.102	220	1.16	1.561	ef
Farewell-to-spring	15	1.449	0.129	220	1.195	1.704	efg
California poppy	15	1.696	0.141	220	1.418	1.974	efgh
Oregano	15	1.748	0.141	220	1.47	2.026	fgh
Canada goldenrod	12	1.786	0.159	220	1.473	2.1	fgh
Douglas' aster	15	2.04	0.141	220	1.762	2.318	ghi
Common madia	15	2.322	0.141	220	2.044	2.6	hi
Globe gilia	15	2.586	0.141	220	2.308	2.865	i

2017 wild bees, only.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Western columbine	15	0	0.149	220	−0.293	0.293	a
Oregon sunshine	6	0.003	0.209	220	−0.408	0.414	ab
Pineapple sage	14	0.296	0.154	220	−0.007	0.6	abc
Common yarrow	15	0.298	0.144	220	0.014	0.581	abc
Rose checkermallow	15	0.592	0.149	220	0.3	0.885	abcd
Oregano	15	0.624	0.149	220	0.331	0.916	abcd
Pearly everlasting	15	0.986	0.149	220	0.693	1.279	cdef
Catnip	15	1	0.107	220	0.789	1.21	de
Varileaf phacelia	6	1.077	0.239	220	0.601	1.549	bcdefgh
Farewell-to-spring	15	1.28	0.136	220	1.012	1.548	defg
Canada goldenrod	12	1.609	0.167	220	1.279	1.939	efgh
California poppy	15	1.696	0.149	220	1.403	1.989	fghi
Douglas' aster	15	1.879	0.149	220	1.586	2.172	ghi
Common madia	15	2.007	0.149	220	1.715	2.3	hi
Globe gilia	15	2.428	0.149	220	2.135	2.721	i

2018 all bees.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Smallflower lotus	9	0.073	0.198	257	−0.317	0.464	a
Great camas	12	0.081	0.170	257	−0.254	0.416	a
Idaho blue-eyed grass	15	0.365	0.152	257	0.066	0.664	ab
Oregon iris	14	0.515	0.157	257	0.205	0.824	abc
Western columbine	15	0.516	0.152	257	0.217	0.815	abc
Woodland strawberry	15	0.777	0.152	25	0.478	1.076	abc
Common madia	15	1.017	0.152	257	0.718	1.316	bcd
Pineapple sage	4	1.100	0.297	257	0.515	1.686	abcde
Showy milkweed	7	1.486	0.224	257	1.044	1.928	cdef
Pearly everlasting	15	1.608	0.152	257	1.309	1.907	def
Oregon sunshine	15	1.624	0.152	257	1.325	1.923	def
Rose checkermallow	15	1.635	0.152	257	1.336	1.934	def
Farewell-to-spring	11	1.652	0.177	257	1.303	2.002	defg
Common yarrow	15	1.681	0.152	257	1.382	1.980	def
Canada goldenrod	12	1.895	0.170	257	1.560	2.229	efgh
Douglas' aster	13	2.083	0.163	257	1.761	2.404	efghi
Varileaf phacelia	15	2.274	0.152	257	1.975	2.573	efghi
Catnip	9	2.278	0.196	257	1.891	2.664	efghi
“Grosso” lavender	14	2.350	0.157	257	2.040	2.660	fghi
California poppy	15	2.481	0.152	257	2.182	2.780	ghi
Globe gilia	13	2.729	0.163	257	2.408	3.051	hi
Oregano	15	2.873	0.152	257	2.574	3.172	i

2018 wild bees, only.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Showy milkweed	7	0.081	0.225	257	−0.362	0.523	ab
Smallflower lotus	9	0.081	0.198	257	−0.309	0.472	a
Great camas	12	0.088	0.17	257	−0.248	0.423	a
Idaho blue-eyed grass	15	0.365	0.152	257	0.066	0.665	abc
Oregon iris	14	0.39	0.157	257	0.08	0.7	abcd
Western columbine	15	0.516	0.152	257	0.217	0.815	abcd
Woodland strawberry	15	0.704	0.152	257	0.405	1.003	abcde
Globe gilia	13	0.936	0.163	257	0.614	1.257	abcdef
Common madia	15	1.017	0.152	257	0.718	1.316	bcdef
Pineapple sage	4	1.109	0.297	257	0.523	1.695	abcdefgh
Oregano	15	1.154	0.152	257	0.855	1.453	def
Catnip	9	1.217	0.196	257	0.83	1.603	cdefg
Oregon sunshine	15	1.363	0.152	257	1.063	1.662	efg
Rose checkermallow	15	1.368	0.152	257	1.069	1.667	efg
“Grosso” lavender	14	1.52	0.157	257	1.21	1.83	fgh
Pearly everlasting	15	1.534	0.152	257	1.235	1.834	fgh
Common yarrow	15	1.602	0.152	257	1.303	1.902	fgh
Canada goldenrod	12	1.626	0.17	257	1.291	1.96	fghi
Farewell-to-spring	11	1.631	0.178	257	1.281	1.981	fghi
Douglas' aster	13	2.054	0.163	257	1.732	2.376	ghi
Varileaf phacelia	15	2.207	0.152	257	1.908	2.506	hi
California poppy	15	2.401	0.152	257	2.101	2.7	i

2019 all bees.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Smallflower lotus	6	0.301	0.225	228	−0.142	0.744	a
Great camas	12	0.552	0.156	228	0.245	0.86	ab
Woodland strawberry	15	0.724	0.14	228	0.449	0.999	abc
Pineapple sage	5	0.838	0.246	228	0.354	1.322	abcdef
Western columbine	15	0.862	0.14	228	0.587	1.137	abcd
Oregon iris	12	0.942	0.156	228	0.634	1.25	abcde
Common madia	10	0.991	0.171	228	0.654	1.328	abcdef
Common yarrow	15	1.336	0.14	228	1.061	1.611	cdef
Rose checkermallow	12	1.352	0.163	228	1.03	1.673	bcdefg
Showy milkweed	9	1.372	0.182	228	1.014	1.73	bcdefg
Farewell-to-spring	13	1.457	0.15	228	1.162	1.753	cdefg
Oregon sunshine	15	1.547	0.14	228	1.272	1.822	defgh
Globe gilia	9	1.701	0.181	228	1.344	2.058	efghi
Pearly everlasting	14	1.774	0.145	228	1.489	2.059	fghi
Douglas' aster	15	2.119	0.14	228	1.844	2.394	ghi
Catnip	13	2.128	0.15	228	1.832	2.424	ghi
Canada goldenrod	11	2.278	0.163	228	1.956	2.599	hi
Varileaf phacelia	8	2.45	0.193	228	2.069	2.831	ij
California poppy	15	2.487	0.14	228	2.212	2.762	i
“Grosso” lavender	15	3.238	0.14	228	2.962	3.513	jk
Oregano	15	3.435	0.14	228	3.16	3.71	k

2019 wild bees, only.

Plant species	N	emmean	SE	df	Lower CI	Upper CI	Group
Showy milkweed	9	0.189	0.184	228	−0.173	0.551	a
Smallflower lotus	6	0.332	0.228	228	−0.116	0.78	abc
Oregano	15	0.535	0.141	228	0.257	0.814	ab
Great camas	12	0.56	0.158	228	0.249	0.872	abc
Catnip	13	0.67	0.152	228	0.37	0.97	abcd
Pineapple sage	5	0.681	0.249	228	0.191	1.171	abcdef
Woodland strawberry	15	0.724	0.141	228	0.445	1.002	abcd
Oregon iris	12	0.834	0.158	228	0.522	1.146	abcde
Western columbine	15	0.835	0.141	228	0.557	1.114	abcde
Commo mada	10	0.951	0.173	228	0.61	1.292	abcdef
Common yarrow	15	1.287	0.141	228	1.009	1.566	cdefg
Rose checkermallow	12	1.292	0.165	228	0.966	1.617	bcdefgh
Globe gilia	9	1.336	0.183	228	0.975	1.698	bcdefgh
“Grosso” lavender	15	1.347	0.141	228	1.068	1.625	defgh
Farewell-to-spring	13	1.359	0.152	228	1.059	1.658	defgh
Oregon sunshine	15	1.468	0.141	228	1.19	1.746	efgh
Pearly everlasting	14	1.633	0.146	228	1.345	1.922	fghi
Canada goldenrod	11	1.881	0.165	228	1.556	2.206	ghi
Douglas' aster	15	2.067	0.141	228	1.789	2.346	hi
California poppy	15	2.356	0.141	228	2.078	2.635	i
Varileaf phacelia	8	2.41	0.196	228	2.024	2.795	i