Associations Between Blooming Plants and their Bee Visitors in a Riparian Ecosystem in Eastern Oregon

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Abstract

Native bees are declining worldwide, but conserving or restoring their habitat requires a better understanding of bee-flower associations. High quality bee habitat includes flowers that provide pollen and nectar preferred by bees. However, little data exist about which plants are commonly used by bees in the Pacific Northwest, or whether bees prefer certain plant characteristics over others. We examined bee and plant communities in an Oregon riparian ecosystem. Our purpose was to describe bee-plant associations, determine which plants are most frequently visited by bees, identify plants that may be preferred by bees, and examine how a plant's native status, flower color, and floral morphology affect the types of bees visiting it. We found that many blooming plants received a diverse set of bee visitors, but some plants had a higher number and species richness of visiting bees than others. No plant species seemed limited to visitation by a small set of specialist bees. The number and type of visiting bees were not influenced by the plant's native status. However, flower morphology (but not color) significantly affected types of bees visiting plants. Bilaterally symmetrical and medium tubular flowers, with nectar and pollen typically more difficult to reach, were associated with larger bees with longer tongues, while smaller, easily accessible flowers attracted smaller bees with shorter tongues. Our results suggest that certain plants are particularly useful for supporting abundant and diverse bee communities, and increasing diversity in the morphology of blooming plants is a key factor to consider when restoring riparian areas for bee pollinators.

Keywords: bee preferences; pollination; floral morphology; riparian areas

Introduction

The Pacific Northwest boasts a wide diversity of native bees (Rao and Stephen 2010; Rao et al. 2011; Kimoto et al. 2012a, b; Roof and DeBano 2016), many of which are important pollinators of crops and garden plants, in addition to native plants. However, many species of bees are in decline around the world (NRC 2007), and one of the leading causes of this is the destruction and degradation of their habitat (Wilcove et al. 1998, Winfree et al. 2009, Potts et al. 2010, Koh et al. 2016). Forests and grasslands in the western United States that once provided bees with a wide variety of forages and nesting sites have since disappeared, replaced by pasturelands, agricultural fields, or urban/suburban areas (Rao and Stephen 2010). Riparian areas are of special concern because they support high levels of biodiversity, including floral diversity, and thus potentially provide key habitat for bees, both in natural and human-dominated landscapes (DeBano et al. 2003, 2016; DeBano and Wooster 2003; Williams 2011). Many riparian areas have been heavily influenced by human activities and thus are often the focus of restoration efforts (Hanula and Horn 2011, Williams 2011).

Effectively restoring or conserving bee habitat requires a better understanding of the complex relationship between bees and flowering plants (Menz et al. 2010). If scientists, conservationists,

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and land managers know which plants certain species of bees prefer, better management strategies can be developed to protect or create more suitable habitat for native bees (DeBano et al. 2016). Although lists that recommend planting certain flowers attractive to bees are available, many are based on anecdotal observations rather than rigorous scientific studies (Garbuzov and Ratnieks 2014, Bahlai and Landis 2016). As a consequence, some plants attractive to bees are not included in these lists, while some less attractive plants are, and often there is little correspondence among lists (Garbuzov and Ratnieks 2014). Of studies based on sound science, many only focus on pollinator interactions involving a few key plant species, rather than the larger plant community that comprises the potential plant-pollinator network (Pornon et al. 2016). Particularly lacking is data on plant-bee associations in florally diverse riparian areas, where this information is needed to guide restoration and management, including ungulate grazing (DeBano et al. 2016).

Although studied for centuries (Sprengel 1793), there is still much uncertainty about how species-specific plant characteristics affect a plant's attractiveness and use by bees. Corolla color (Heuschen et al. 2005, Raine and Chittka 2007), flower shape and complexity (Laverty 1994, Gegear and Laverty 1995, Gómez et al. 2008), and nectar and pollen quantity and quality (Somme et al. 2015, Brunet et al. 2015) are all examples of characteristics that can influence bee preferences. Bee species traits also play a role in plant selection. For example, evidence suggests that bees with longer tongues forage on plants with longer corollas, while bees with shorter tongues prefer plants with shorter corollas (Harder 1985, Inoue and Yokoyama 2006, Gonzalez et al. 2013, Tubbesing et al. 2014). However, past research on bee preferences has often focused on bumble bee (*Bombus*) species, and the relationship between the tongue length of other types of bees with flower morphology is less clear. Until recently, estimating tongue length was a time-consuming proposition and was seldom included in ecological studies; this has recently changed with the development of a model allowing the estimation of tongue length and body size from the intertegular distance, (i.e., the distance between the base of a bee's wings) (Cariveau et al. 2016). In addition, other factors, such as season, sex of the bee, and plant resource availability may further complicate foraging choices of bees (Ritchie et al. 2016). A bee's flower preference during a particular foraging trip, therefore, depends on characteristics of the flower, the bee, and the relationship between them.

There is also a lack of consensus about how the presence of introduced plants affects native bee abundance and richness (Salisbury et al. 2015, Albrecht et al. 2016). Some work suggests that native plants support greater bee abundance and species richness than do introduced plants, indicating that native bees prefer foraging on native plants (Morandin and Kremen 2013, Palladini 2013). Other studies suggest that introduced plants are equally or more attractive to many bees, and may have a neutral or even positive effect on native bee abundance and diversity (Tepedino et al. 2008, Matteson and Langellotto 2011). Introduced plant species may also extend the flowering season and provide more foraging options for late season bees (Salisbury et al. 2015).

The purpose of this study was to investigate flowering plant-native bee associations in a riparian system in a northeastern Oregon experimental forest by documenting which bee species are associated with which flowers. Specifically, this study examined: 1) which plants are commonly visited by bees and which bee species are visiting them, 2) which plants appear to have the greatest number of visiting bees relative to their blooming stem abundance, 3) whether the abundance and composition of bee visitors differ between native and introduced plants, and 4) whether other plant traits, including flower color and morphology, influence the types of bees visiting each plant species.

Methods

Study Area

We sampled 12 sites located in three riparian pastures directly adjacent to riparian areas of Meadow Creek at the United States Forest Service (USFS) Starkey Experimental Forest and Range (Starkey)

(Figure 1). These sites are part of a long-term study by the USFS researching the effects of restoration and ungulate grazing on stream and riparian areas. Starkey is located in the Blue Mountains of northeastern Oregon (Rowland et al. 1997, Wisdom 2005). Elevations range from 1130–1500 m and annual precipitation is approximately 50 cm, with the majority falling as snow (Skovlin 1991). The forest and rangeland habitats at Starkey were formally designated as a research site by the USFS in 1940 to evaluate how management actions and natural disturbance affect multiple resources in this ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson)/mixed conifer/native bunchgrass setting (Skovlin 1991). Beginning with the arrival of settlers on the Oregon Trail in the 1800s, much of Starkey and the surrounding landscape have been heavily degraded from grazing and logging (Skovlin 1991). In the 1980s, approximately 10 000 ha at Starkey were enclosed with game-proof fencing so that closed populations of wild elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) could be manipulated, and effects of management evaluated, in an experimental setting.

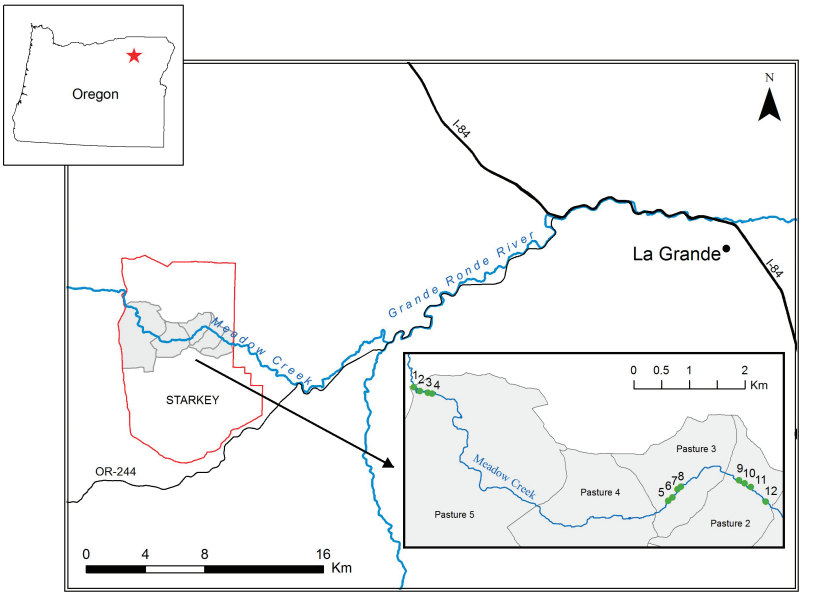

Figure 1. Location of the USFS Starkey Experimental Forest and Range in Oregon and the 12 study sites sampled for native bee and floral resources along Meadow Creek. Site 1 was the furthest upstream and Site 12 was the furthest downstream.

Our study sites were located along a 13-km reach of Meadow Creek, a major tributary of the upper Grande Ronde River that flows through Starkey (Figure 1). Discharge in Meadow Creek varies within and across years, with severe scouring by ice and high flows often occurring in spring (Filip et al. 1989). Dominant riparian shrubs include willow (*Salix* spp. L.), black hawthorn (*Crataegus douglasii* Lindl.), thinleaf alder (*Alnus incana* [L.] Moench subsp. *tenuifolia* [Nutt.] Breitung), black cottonwood (*Populus balsamifera* L. subsp. *trichocarpa* [Torr. & A. Gray ex Hook.] Brayshaw), and common snowberry (*Symphoricarpos albus* [L.] S.F. Blake). Scattered ponderosa pine, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and western larch (*Larix occidentalis* Nutt.) are also found in the riparian corridor. Herbaceous vegetation includes a variety of forbs (Roof et al. 2018) as well as sedges (*Carex* spp. L.), rushes (*Juncus* spp. L.), common spikerush (*Eleocharis palustris* [L.] Roem. & Schult.), creeping bentgrass (*Agrostis stolonifera* L.), and fowl mannagrass (*Glyceria striata* [Lam.] Hitch.). Upland habitat consists of mixed coniferous forest with Douglas-fir and grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.), along with lodgepole (*P. contorta* Douglas ex Loudon) and ponderosa pine.

Because of legacies associated with past land uses (e.g., logging, livestock grazing, planting exotic forage) in the riparian corridor (Skovlin 1991, USFS 2012), the USFS began actively restoring approximately 11 km of Meadow Creek in 2013, including planting approximately 40 000 native shrubs and conifers along the stream, placing boulders and large woody debris throughout

the reach, and developing upland water sources and fencing to support a deferred rotation grazing system for cattle (USFS 2012). In addition, research exclosures were built in three pastures along Meadow Creek to evaluate effects of ungulate herbivory on restoration plantings, fish habitat, and other variables within the riparian system, including bee pollinators. Nine study sites were located in the research exclosures. Of these, six excluded deer and elk. None of the study sites were grazed by livestock during the course of the study.

Bee Sampling

Bees visiting flowers were sampled with a hand-net at all 12 sites and throughout the day between 0800–2000 hours from May to September during four sampling periods in 2014 and three sampling periods in 2015 (Table 1). All individuals involved in hand-netting were trained in proper hand-netting techniques in an effort to reduce biases. Hand-netting occurred as part of our normal field sampling, in which we collected bees observed on any species of blooming flowers for 15–20 min at each site throughout the day. In addition, in July 2015, we focused an additional 240 min of extra sampling effort on 12 particular plant species in order to compare abundance of bee visitors on native and introduced species to specifically address our third objective. These focal plants included six native species: *Achillea millefolium* L., *Mentha arvensis* L., *Potentilla gracilis* Douglas ex Hook., *Solidago missouriensis* Nutt., *Symphyotrichum spathulatum* (Lindl.) G. L. Nesom, and *Trifolium wormskioldii* Lehm., and six introduced plants: *Cirsium arvense* (L.) Scop., *Cirsium vulgare* (Savi) Ten., *Hypericum perforatum* L., *Trifolium pratense* L., *Trifolium repens* L., and *Verbascum thapsus* L. Because of the difficulty of distinguishing between *T. pratense* and *T. repens,* they were combined into one group (*T. pratense/repens*) for analyses. We selected these species because they were the most common species during the sampling period that had also been reported in the literature as being pollinated by bees. Collectors counted the number of blooming stems and bees observed and collected on each plant species. Targeted sampling was only conducted during the July 2015 sampling period because we determined that July had the highest abundance and richness of bees and native and introduced plant species at Starkey in 2014 (DeBano et al. 2016). After collection, bees were brought back to the laboratory and placed in a freezer until they could be pinned. Bees were identified to species and bee voucher specimens are stored at the Oregon State University Hermiston Agricultural Research and Extension Center (OSU HAREC) Invertebrate Ecology Laboratory and the US National Pollinating Insect Collection in Logan, Utah.

Plant Sampling

To address our second objective of determining which plants have the greatest number of visiting bees relative to their blooming stem abundance, we sampled plants at each of the 12 sites in the summers of 2014 and 2015 (Table 1) along five parallel, 20-m-long, 0.3-m-wide belt transects, separated by 10 m, and oriented perpendicular to Meadow Creek. Along each transect the species and number of blooming stems of each forb or shrub species were counted and recorded. Blooming stems were defined as single flowers or clusters of flowers arranged on a stem. Plant voucher specimens are stored at the OSU HAREC Invertebrate Ecology Laboratory (Hermiston, OR).

Quantifying Plant-Bee Associations

To address our first objective, bee abundance and species richness associated with each plant species from all hand-netting efforts were used to provide information on flowering riparian plants that were commonly visited by bees. To investigate patterns that may indicate pollinator specialization by the plant (e.g., identify plants with a high abundance of visitors but few species of bees), we compared total bee abundance and bee richness for each plant species with linear regression using SYSTAT, Version 12.0 (SPSS Inc., San Jose, CA).

To address our second objective of determining which plants have the greatest number of visiting bees relative to their blooming stem abundance, we considered flowering plants preferred by bees as those which were visited at higher rates than

TABLE 1. Sampling dates of bees and plants at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon.

Sampling	2014				2015		
Bees	May 25–26	June 28–July 1	July 31–Aug. 1	Sep. 20–22	June 17–25	July 24–29	Sep. 3–8
Plants	May 24–26	July 1	July 31–Aug. 1	Sep. 20–22	June 13–16	July 25–26	Sep. 3–5

expected given their abundance in the environment. To determine which species had the highest visitation rates per blooming stem, we compared bee abundance data from all hand-netting efforts for each plant species with the stem count data from the plant transect sampling.

Bee Visitor Community Composition Relative to Flowering Plant Species

To examine whether different plant species had different types of bee visitors, we used nonmetric multidimensional scaling (NMS) ordination to characterize bee visitor community composition for plant species using all hand-netting data. We used PC-Ord, Version 5.0 (MjM Software Design, Gleneden Beach, OR), for all multivariate analyses (McCune and Mefford 2006) with a relative Sorenson's distance measure, and all counts were transformed (log(X+1)) before analyses. For the ordination analysis, we examined all plant species with at least six visitors (mean = 34.8 bees per species) resulting in 43 bee species used in an ordination of the 17 most visited plant species. The best solution was determined through 250 runs of randomized data, and dimensionality was determined by evaluating the relationship between final stress and the number of dimensions. We used Pearson's correlation coefficients to quantify relationships between bee species abundance and ordination axis scores (McCune and Mefford 2006).

Effect of Plant Native Status

To determine if bees prefer native or introduced flowering plants, we compared the number of bees collected per blooming stem for the targeted hand-netting data on the 12 focal plants only. We focused on using the targeted hand-netting data in this case because the number of bees collected per blooming stem could be better compared between plant species, as bees and available stems were both counted for all plant species. We used an *F*-test to examine whether variation in the number of bees visiting native and introduced plant species differed. Because abundance data did not meet the assumptions of parametric statistics, a Mann-Whitney *U* test was used to determine whether bee abundance differed significantly between native and introduced plants (SYSTAT, Version 12.0, SPSS Inc., San Jose, CA).

We used multi-response permutation procedures (MRPP) in PC-Ord, Version 5.0 (MjM Software Design, Gleneden Beach, OR), to determine whether differences in the community of bees visiting the 17 common plant species analyzed in the ordination were related to the native status of the plant. MRPP is a multivariate, nonparametric procedure for testing the hypothesis of no difference between two or more groups. MRPP calculates the mean within-group distance and generates an expected distance through permutation (McCune and Mefford 2006). The *P* value generated by the test is the probability of observing a within-group distance smaller than the observed distance due to chance alone. MRPP tests also provide a measure of the effect size (*A*), which is one minus the ratio of the observed mean within-group distance to the expected within-group distance. An effect size of 1 indicates that all items within each group are identical (i.e., the within-group distances are zero), a value of 0 indicates that the heterogeneity within groups is no different from that expected by chance, and a negative effect size indicates there is more heterogeneity within groups than expected by chance (McCune and Grace 2002). We used a relative Sorensen's distance measure in all MRPP analyses. All hand-netting data were used for this analysis because the focus was on community composition, not abundance.

Influence of Flower Color and Morphology

To determine whether traits of blooming plant species explained variation in the types of bees visiting each plant species, we grouped each of the 17 plant species analyzed in the ordination by flower color and morphology, and used MRPP on all hand-netting data to examine whether community composition of bee visitors differed among groups. Flower color was categorized by our own perception of corolla color and included: white, *A. millefolium* and *Eriogonum heracleoides* Nutt.; pink, *Sidalcea oregana* (Nutt. ex Torr. & A. Gray) A. Gray, *T. pratense/repens,* and *T. wormskioldii;* purple, *C. vulgare, Mentha arvensis, Monardella odoratissima* Benth., *Symphyotrichum spathulatum* (categorized by its ray floret color), and *Vicia cracca* L.; and yellow, *Grindelia nana* Nutt., *H. perforatum, Lotus corniculatus* L., *P. gracilis, Senecio serra* Hook., *Sedum stenopetalum* Pursh, and *Solidago missouriensis*.

Floral morphology was categorized by each plant species' basic floral shape and size, using floral shapes adapted from those described in Willmer (2011) (Figure 2). First, bilaterally symmetric flowers, including *L. corniculatus, T. pratense/repens, T. wormskioldii,* and *V. cracca*, were separated from radially symmetric flowers. Next, composite flowers in the family Asteraceae were separated from other radially symmetric flowers. Of the composites, we considered *A. millefolium*, *G. nana*, *Solidago missouriensis*, *Senecio serra*, and *Symphyotrichum spathulatum* as having medium-length disk florets, and *C. vulgare* as having long-length disk florets. *Sedum spathulatum* was also categorized as having medium-length disk florets. Of the non-composites, we categorized *H. perforatum, Sidalcea oregana,* and *Sedum stenopetalum* as simple, fully-open flowers, and *E. heracleoides, Mentha arvensis,* and *Monardella odoratissima*, as being medium-length tubular, or bowl-shaped flowers. Because *C. vulgare* was the only species in the long disk floret category, it was excluded from the MRPP analysis. Because the same data were used for three separate MRPP analyses (native status, flower color, and flower morphology), we used a Bonferroni correction to compensate for testing multiple hypotheses, resulting in an adjusted α of 0.017.

When MRPP revealed significant differences in bee community composition relative to flower morphology, we examined the relationship of body size and tongue length of bee visitors among groups. We used the BeeIT R package described in Cariveau et al. (2016) to estimate total tongue length (including the glossa and prementum) and body mass for each bee species from their measured intertegular distances (the distance between wing bases). Up to 10 specimens per species were measured to calculate an average intertegular distance that was used in BeeIT to estimate tongue length and body mass. To determine whether bees visiting different flower morphologies varied in the size of those characters, we calculated a weighted average of estimated tongue length and body mass of all bee visitors for each plant species. We used SYSTAT, Version 12.0 (SPPSS Inc., San Jose, CA) for an analysis of variance (ANOVA) and a Fisher's LSD test to determine whether tongue length and body mass of bee visitors for each flower species varied among flower groups and to compare means.

Results

Plant-Bee Associations

We collected 692 native bees (160 in 2014 and 532 in 2015), in 84 species and 23 genera, and identified 92 species of flowering forbs and shrubs during the two years of sampling (Roof et al. 2018; Table S1 available online). Of these plants, 70 species were native, 19 were introduced, and the status of three could not be determined, as they were only identified to the genus level. Most flowering plant species (54) had no observations of bee visitors, but 541 bees in 23 genera were observed visiting 29 species of native plants, and 151 bees in 11 genera were observed visiting nine species of introduced plants. There was no evidence that any plant species relied on a small subset of bee species for pollination. Plants with more bee visitors had a higher number of species visiting ($r^2 = 0.81$, $P < 0.01$), and there were no plant species that received a high number of

Figure 2. Floral morphology categories used in MRPP analyses of plant and bee associations along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon (from top left clockwise): long disk florets (*Cirsium vulgare)*, medium disk florets (*Symphyotrichum spathulatum)*, simple (*Hypericum perforatum)*, medium tubular (*Monardella odoratissima)*, bilateral symmetry (*Lotus corniculatus)*.

bee visitors that also had low species richness of visitors (Figure 3).

The 17 most commonly visited flowering plant species had distinctive communities of bee visitors; the NMS ordination yielded a three-dimensional solution that explained 82.6% of the variation (Figure 4). Axis 1 described 52.8% of the variation, axis 2 described 23.9%, and axis 3 described 5.9%. The bee species correlated with axes 1 and 2 are listed in Table 2.

There were 14 commonly visited plants in the riparian system (those with 10 or more bee visitors), 11 of which were native and three of which were introduced (Table 3). The four plant species that had the greatest number of bees observed visiting them were native *Solidago missouriensis* (149 bees), native *Potentilla gracilis* (118 bees), native *Symphyotrichum spathulatum* (54 bees), and introduced *Cirsium vulgare* (54 bees). The plants with the highest species richness of bee visitors were *P. gracilis* (31 species), *Solidago missouriensis* (20 species), *C. vulgare* (14 species), and the introduced *V. cracca* (14 species).

Bee Visitation Relative to Plant Abundance

To quantify the attractiveness of plant species to bees while controlling for variation in blooming plant abundance, we calculated visitation rates (number of visits per blooming stem) for each plant species. Plants exhibited a wide range of visitation rates (Table S1). *Cirsium vulgare* had the highest number of bee visitors per blooming stem with a visitation rate of 13.5 visits/bloom. The natives *Epilobium ciliatum* Raf. and *Mimulus guttatus* DC. had the next highest visitation rates, with 2.0 and 1.5 bees collected per blooming stem, respectively. Of the 92 plant species identified on transects and/or on which bees were collected, 54 were never observed to have a bee visitor during any sampling period. In addition, six species on which bees were observed did not occur on transects, and a visitation rate could not be calculated.

Effect of Plant Native Status

During 240 minutes of targeted sampling we observed 7236 blooming stems and 115 visiting bees, with 72 on native plants, and 43 on introduced plants. Although the average abundance of bee visitors between native and introduced plants used in targeted sampling was not statistically different ($U = 12.00$, $P = 0.58$), the variances were significantly different ($F = 250.27$, $DF = 4,5$, $P < 0.01$), with more variation in the number of bees observed per flower among introduced species than for native species. For example, the introduced *C. vulgare* had the highest number of bees observed per bloom for targeted hand-netting bouts, while the introduced *C. arvense* was never observed to have a bee visitor (Figure 5). Differences in the community composition of bees visiting different plant species were not explained by the native status of the plant ($A = 0.02$, $P = 0.12$) (Figure 4).

Influence of Flower Color and Morphology

Corolla color did not explain variation in the bee community associated with each plant species

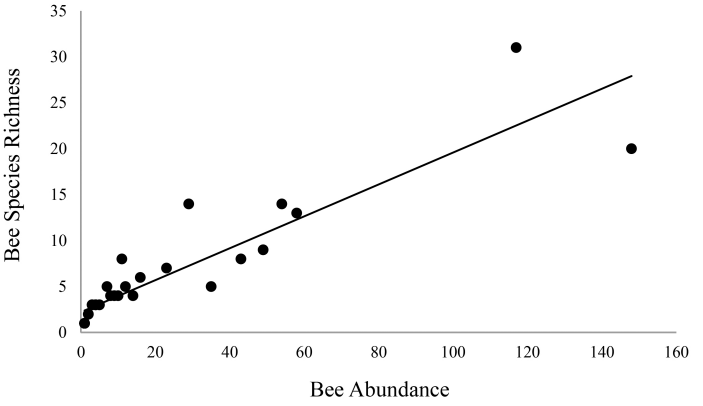

Figure 3. Abundance and richness of bee visitors for each plant species visited by bees at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon ($r^2 = 0.81$, $P < 0.001$, $n = 37$).

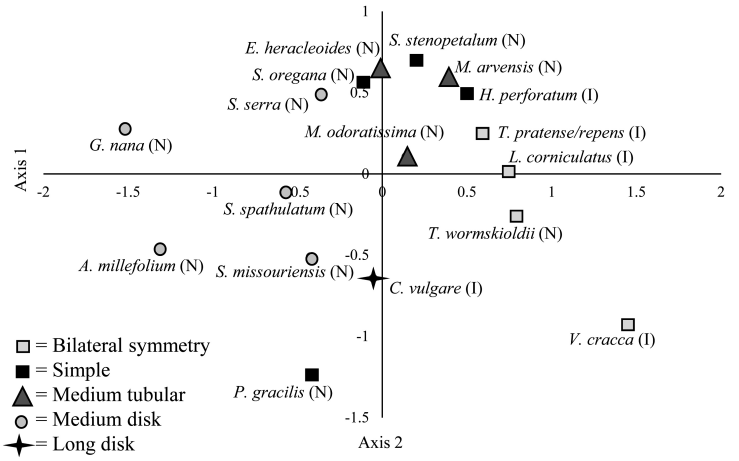

Figure 4. NMS ordination of 17 plant species associated with 43 bee species at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon. Symbols represent each plant species in bee species space, coded by flower morphology. Axis 1 described 52.8% of the variation, and axis 2 described 23.9% of the variation. Axis 3, describing only 5.9% of the variation, is not presented. Letters in parentheses designate native status: N = native, I = introduced.

($A = -0.04$, $P = 0.92$). However, flower morphology did ($A = 0.14$, $P < 0.01$); groups differentiated along axis 1, with plant species with medium disks associated with negative values of axis 1, species with bilateral symmetry associated with positive values of axis 1, and species with simple and medium tubular flowers of intermediate values (Figure 4). The weighted body size and tongue length of bee visitors differed significantly among flower morphology groups ($F = 6.12$, $DF = 3,12$, $P < 0.01$; $F = 4.57$, $DF = 3,12$, $P = 0.02$; Figure 6). Bee species visiting medium disk and simple flowers were smaller with shorter tongues than those visiting medium tubular and bilaterally symmetrical flowers (Figure 6).

Discussion

Plant-Bee Associations

We found that riparian areas in this region of northeastern Oregon support an abundant and diverse community of bees and flowering plants, and that plant species varied both in the number and types of bees visiting them. Over the two-year duration of the study, we observed 84 bee species in 23 genera visiting 38 species of flowering forbs and shrubs (Table S1, available online). Some common plants appeared to support a wide variety of bee genera and species. For example, 31 different bee species in 11 genera were observed visiting slender cinquefoil (*P. gracilis*). Other common plants with a high number of observed visitors were bull thistle (*C. vulgare*), Missouri goldenrod (*Solidago. missouriensis*), western mountain aster, (*Symphyotrichum spathulatum*), several species of clover (*T. pratense*, *repens*, and *wormskioldii*), and bird vetch (*V. cracca*). These plants, due to their commonness and frequent visitation, may play particularly important roles in supporting bees in riparian areas in eastern Oregon. Unlike other work in the region (Tubbesing et al. 2014), we found no indication that any single plant taxon

TABLE 2. Bee species at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon that were correlated with nonmetric multidimensional scaling ordination axes 1 and 2 for 17 commonly visited plant species. Significant correlations ($P < 0.05$) are denoted with an *.

Axis 1	Axis 2
Positive:	**Positive:**
Osmia albolateralis, r = 0.63*	*Bombus occidentalis*, r = 0.35
Bombus vosnesenskii, r = 0.58*	*Osmia californica*, r = 0.25
Eucera frater, r = 0.51*	*Diadasia nigrifrons*, r = 0.24
Osmia densa, r = 0.51*	*Dianthidium subparvum*, r = 0.12
Osmia nigrifrons, r = 0.51*	*Bombus bifarius*, r = 0.09
Osmia raritatis, r = 0.49*	*Osmia pusilla*, r = 0.08
Bombus centralis, r = 0.36	
Bombus flavifrons, r = 0.34	**Negative:**
Anthidium utahense, r = 0.27	*Halictus confusus*, r = –0.60*
Bombus occidentalis, r = 0.22	*Lasioglossum olympiae*, r = –0.59*
Bombus californicus, r = 0.17	*Lasioglossum sisymbrii*, r = –0.59*
Bombus bifarius, r = 0.13	*Bombus flavifrons*, r = –0.56*
Bombus fervidus, r = 0.09	*Andrena angustitarsata*, r = –0.55*
Osmia pusilla, r = 0.09	*Andrena cyanophila*, r = –0.55*
Bombus mixtus, r = 0.04	*Andrena miranda*, r = –0.55*
	Bombus centralis, r = –0.55*
Negative:	*Hylaeus basalis*, r = –0.55*
Halictus ligatus, r = –0.67*	*Lasioglossum cooleyi*, r = –0.55*
Dianthidium subparvum, r = –0.52*	*Lasioglossum* sp. 2, r = –0.55*
Osmia californica, r = –0.48	*Panurginus torchio*, r = –0.55*
Halictus farinosus, r = –0.50	*Perdita wyomingensis*, r = –0.55*
Lasioglossum sp., r = –0.38	*Halictus ligatus*, r = –0.50*
Lasioglossum sisymbrii, r = –0.29	*Hylaeus wootoni*, r = –0.49*
Megachile perihirta, r = –0.29	*Lasioglossum egregium*, r = –0.46
Lasioglossum olympiae, r = –0.29	*Lasioglossum* sp., r = –0.44
Melissodes microsticta, r = –0.25	*Hylaeus episcopalis*, r = –0.44
Halictus confusus, r = –0.21	*Eucera frater*, r = –0.40
Hylaeus wootoni, r = –0.21	*Osmia nigrifrons*, r = –0.40
Lasioglossum egregium, r = –0.20	*Osmia densa*, r = –0.40
Bombus insularis, r = –0.17	*Megachile perihirta*, r = –0.39
Osmia coloradensis, r = –0.16	*Osmia albolateralis*, r = –0.38
Hoplitis fulgida, r = –0.15	*Bombus insularis*, r = –0.30
Hylaeus modestus, r = –0.15	*Halictus farinosus*, r = –0.30
Panurginus torchio, r = –0.14	*Bombus appositus*, r = –0.28
Andrena cyanophila, r = –0.14	*Bombus fervidus*, r = –0.28
Hylaeus basalis, r = –0.14	*Agapostemon virescens*, r = –0.28
Andrena angustitarsata, r = –0.14	*Bombus mixtus*, r = –0.27
Andrena miranda, r = –0.14	*Osmia coloradensis*, r = –0.24
Lasioglossum cooleyi, r = –0.14	*Bombus californicus*, r = –0.23
Lasioglossum sp. 2, r = –0.14	*Hylaeus modestus*, r = –0.22
Perdita wyomingensis, r = –0.14	*Melissodes microsticta*, r = –0.18
Hylaeus episcopalis, r = –0.14	*Osmia raritatis*, r = –0.17
Agapostemon virescens, r = –0.11	*Anthidium utahense*, r = –0.11
Diadasia nigrifrons, r = –0.04	*Hoplitis fulgida*, r = –0.08
Bombus appositus, r = –0.02	*Bombus vosnesenskii*, r = –0.07

we sampled relied on just a few species of bee pollinators; no plant species had a high abundance but low richness of bee visitors. One advantage of a generalist strategy from a plants' perspective is that having a greater diversity of pollinators increases the plant's likelihood of being pollinated (Balamurali et al. 2015).

Notably, no bees were collected on over half of the flowering forbs and shrubs identified in the study area. Plants such as pale agoseris (*Agoseris glauca* (Pursh) Raf.), Gardner's yampah (*Perideridia gairdneri* (Hook. & Arn.) Mathias), and slender phlox (*Microsteris gracilis* (Hook.) Greene) all had over 400 blooming stems counted, but no observed bee visitors. This suggests that these species have limited utility in supporting native bees. However, these plant species may play key roles in supporting other insect pollinators (e.g., Diptera, Coleoptera, and Lepidoptera) and managers should realize that focusing only on plants that are beneficial to bees may have negative impacts on non-bee pollinators.

Although some common plants, such as slender cinquefoil, supported large numbers of native bees, their high number of observed visitors may be partially due to their ubiquity; more than 1600 blooming slender cinquefoil stems were counted during the course of the study. To identify species that may actually be preferred by bees, we examined visitation rates relative to floral abundance. The plant species with the highest visitation rate was the introduced *C. vulgare*, with more than 13 bees observed per blooming

TABLE 3. The 14 plant species* at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon with the highest number of bees collected on them during the 2014 and 2015 sampling periods. For each plant, all bee species collected are listed, along with the number of bees and the percentage of that species compared to all bee species collected on that plant.

Plants and Associated Bee Species	Number of Bees	Relative Abundance (%)
Achillea millefolium		
Andrena pallidifovea	1	4
Ashmeadiella cubiceps	1	4
Halictus farinosus	3	13
Halictus ligatus	15	65
Lasioglossum olympiae	1	4
Lasioglossum sisymbrii	1	4
Megachile perihirta	1	4
Cirsium vulgare		
Agapostemon virescens	3	6
Bombus appositus	5	9
Bombus bifarius	8	15
Bombus californicus	7	13
Bombus centralis	4	7
Bombus fervidus	6	11
Bombus flavifrons	6	11
Bombus insularis	6	11
Bombus mixtus	2	4
Halictus ligatus	2	4
Lasioglossum sp.	2	4
Megachile perihirta	1	2
Melissodes rivalis	1	2
Osmia coloradensis	1	2
Eriogonum heracleoides		
Bombus bifarius	11	79
Bombus insularis	1	7
Colletes fulgidus	1	7
Hylaeus episcopalis	1	7
Grindelia nana		
Ashmeadiella cubiceps	1	9
Dianthidium subparvum	3	27
Halictus ligatus	2	18
Hoplitis bucconis	1	9
Lasioglossum sp.	1	9
Lasioglossum titusi	1	9
Osmia californica	1	9
Osmia montana	1	9
Mentha arvensis		
Agapostemon femoratus	1	3
Bombus bifarius	31	89
Bombus occidentalis	1	3
Bombus rufocinctus	1	3
Bombus vosnesenskii	1	3
Monardella odoratissima		
Anthophora bomboides	1	10
Bombus bifarius	3	30
Bombus californicus	5	50
Bombus fervidus	1	10
Potentilla gracilis		
Andrena angustitarsata	4	3
Andrena cupreotincta	1	1
Andrena cyanophila	11	9
Andrena miranda	4	3
Andrena sp. 1	1	1
Andrena birtwelli	1	1
Andrena thaspii	1	1
Anthidium mormonum	1	1
Bombus bifarius	11	9
Bombus flavifrons	1	1
Bombus mixtus	1	1
Ceratina acantha	1	1
Halictus confusus	2	2
Halictus ligatus	5	4
Halictus rubicundus	1	1
Halictus tripartitus	1	1
Hoplitis albifrons	2	2
Hoplitis fulgida	2	2
Hylaeus basalis	8	7
Hylaeus episcopalis	13	11
Hylaeus wootoni	1	1
Lasioglossum cooleyi	4	3
Lasioglossum egregium	1	1
Lasioglossum olympiae	7	6
Lasioglossum sisymbrii	6	5
Lasioglossum sp.	4	3
Lasioglossum sp. 2	1	1
Osmia juxta	2	2
Osmia montana	1	1
Panurginus torchio	15	13
Perdita wyomingensis	3	3
Senecio serra		
Bombus bifarius	8	67
Halictus ligatus	1	8
Osmia californica	1	8
Osmia subaustralis	1	8
Sphecodes arvensiformis	1	8

TABLE 3. *Continued*

Plants and Associated Bee Species	Number of Bees	Relative Abundance (%)
Sidalcea oregana		
Bombus bifarius	6	38
Ceratina nanula	1	6
Diadasia nigrifrons	5	31
Hoplitis fulgida	1	6
Lasioglossum sp.	2	13
Stelis sp. 01	1	6
Solidago missouriensis		
Bombus bifarius	59	40
Bombus fernaldae	1	1
Bombus flavifrons	1	1
Bombus insularis	10	7
Bombus vosnesenskii	1	1
Halictus confusus	1	1
Halictus farinosus	2	1
Halictus ligatus	27	18
Halictus rubicundus	1	1
Halictus tripartitus	1	1
Hylaeus affinis	1	1
Hylaeus episcopalis	4	3
Hylaeus modestus	4	3
Hylaeus wootoni	2	1
Lasioglossum egregium	3	2
Lasioglossum glabriventris	1	1
Lasioglossum sp.	23	16
Megachile perihirta	2	1
Melissodes microsticta	3	2
Sphecodes arvensiformis	1	1
Symphyotrichum spathulatum		
Agapostemon virescens	1	2
Bombus bifarius	25	43
Bombus insularis	1	2
Ceratina nanula	1	2
Halictus ligatus	16	28
Hoplitis fulgida	1	2
Lasioglossum sp.	3	5
Megachile perihirta	1	2
Melissodes confusa	1	2
Melissodes microsticta	5	9
Osmia coloradensis	1	2
Osmia pusilla	1	2
Stelis montana	1	2
Trifolium pratense/repens		
Bombus bifarius	30	70
Bombus flavifrons	2	5
Bombus mixtus	2	5
Bombus vosnesenskii	1	2
Osmia pusilla	3	7
Osmia raritatis	3	7
Osmia simillima	1	2
Osmia trevoris	1	2
Trifolium wormskioldii		
Anthidium mormonum	1	2
Anthidium utahense	2	4
Bombus bifarius	17	35
Bombus californicus	5	10
Bombus fervidus	1	2
Bombus flavifrons	6	12
Bombus vosnesenskii	11	22
Osmia albolateralis	5	10
Osmia trevoris	1	2
Vicia cracca		
Bombus centralis	1	3
Bombus flavifrons	2	7
Bombus nevadensis	2	7
Bombus vosnesenskii	1	3
Eucera frater	3	10
Hoplitis hypocrita	2	7
Osmia albolateralis	7	24
Osmia bucephala	1	3
Osmia densa	2	7
Osmia longula	1	3
Osmia nigrifrons	4	14
Osmia raritatis	2	7
Osmia simillima	1	3
Osmia sp. 2	1	3

* Flowering species were identified using *Flora of the Pacific Northwest* (Hitchcock and Cronquist 1973). Contemporary name changes and the native status of all plants were determined using the United States Department of Agriculture PLANTS database (2017).

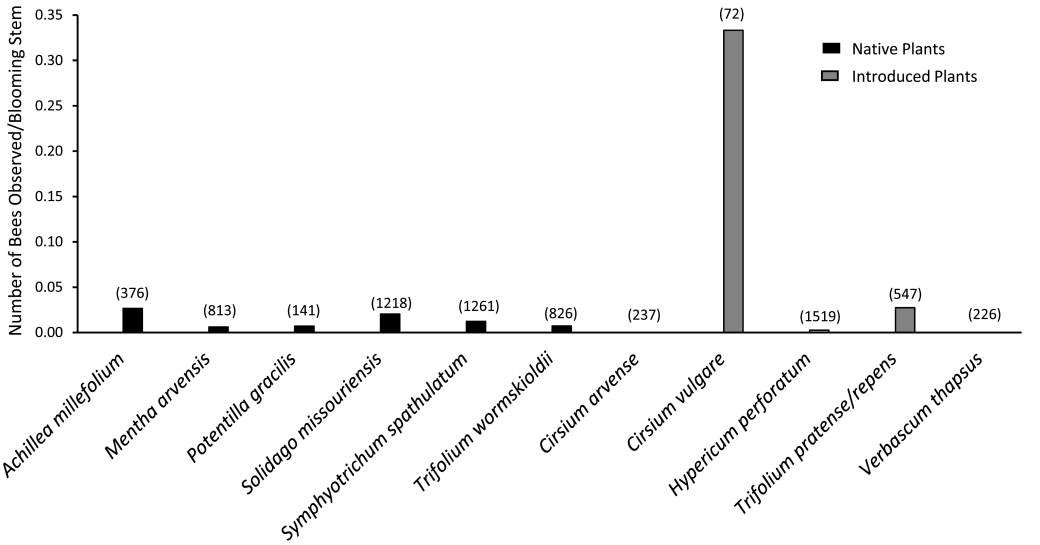

Figure 5. The number of bees observed on each plant species per blooming stem counted during targeted hand-net sampling of 11 native and introduced plant taxa at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon. Numbers in parentheses refer to the number of blooming stems counted for each plant.

stem. The popularity of *C. vulgare*, particularly among bumble bees, has been documented in other systems as well (Plowright et el. 1999, Goulson et al. 2005). Other plants with high visitation rates included fringed willowherb (*E. ciliatum*) and seep monkeyflower (*M. guttatus*). While seep monkeyflower is used by bumble bees (Carr et al. 2014) and fringed willowherb is visited by some sweat and bumble bees (Parker et al. 1995), our visitation rates for these species are based on low counts of both bees and blooming stems. Thus, further work is needed to confirm their attractiveness to bees. However, other estimates based on higher counts of bee abundance and/or blooming stems indicate that bird vetch (*V. cracca*), cows clover (*T. wormskioldii*), Oregon checkerbloom (*Sidalcea oregana*), and Missouri goldenrod (*Solidago missouriensis)* are species preferred by bees in this area. These preferred species could be planted in restoration areas or in gardens of eastern Oregon to enhance pollinator habitat. However, the use of *C. vulgare* and *V. cracca*, while potentially beneficial for bees, may negatively affect other aspects of a system not considered here (e.g., competing with native plant species for pollinators and other resources).

Although *C. vulgare* and *V. cracca* had high visitation rates, we found no statistically significant difference in the number of bees visiting native and introduced plants overall. *Cirsium vulgare* was unusual among introduced plants in having a large number of bees observed per blooming stem; most other introduced plant species had considerably lower visitation rates, including common mullein (*V. thapsus*) and Canada thistle (*C. arvensis*), on which no bee visitors were observed. Thus, variability in the number of bees visiting introduced plant species was much higher than for native plants. Williams et al. (2011) found similar results, with the average number of bees visiting introduced plants in California mainly influenced by a few highly visited and abundant plant species, while other introduced species were not visited at all. However, the literature is equivocal about how a plant's native status influences bees. Some work suggests that native plants may be more frequently visited by bees (Morandin and Kremen 2013, Salisbury et al. 2015), while others suggest that introduced plants may be equally or more attractive to bees (Tepedino et al. 2008, Vilà et al. 2009). In fact, the relationship is probably influenced by several

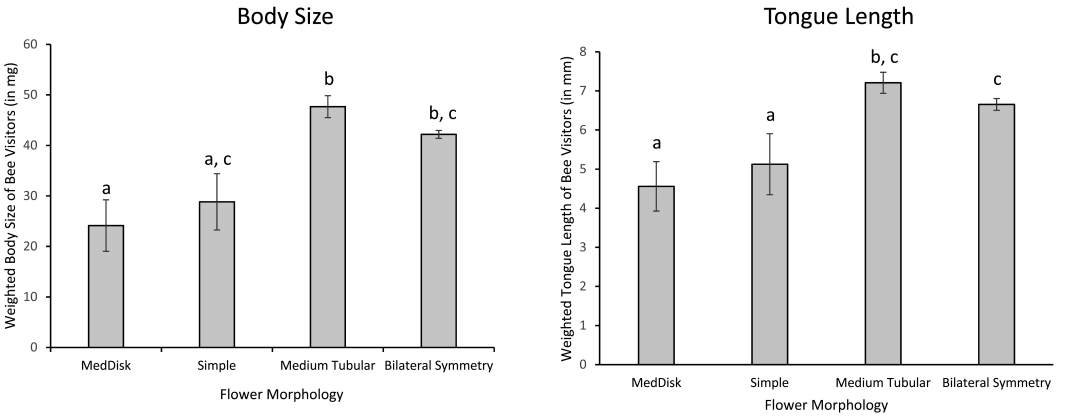

Figure 6. Weighted average of body size and tongue length of bees visiting plants in four categories of flower morphology at riparian sites along Meadow Creek in the USFS Starkey Experimental Forest and Range in Oregon. Different letters denote averages that differ significantly according to Fisher's LSD test.

factors, including the identity of species making up each group, and the larger context of the plant community (Kremen et al. 2007, Tubbesing et al. 2014). Our data indicates that selecting plants to attract bee pollinators simply based on their native status would likely be ineffective.

Factors Influencing Types of Bees Visiting Flowering Species

Plant species not only varied in the number of bee visitors they received, but also in the types of species visiting (Figure 4). One potential driver of this pattern is the native status of the plant. Differences in the species composition of bees visiting native and introduced plant species has been hypothesized for several reasons, including "invasive mutualisms" (Barthell et al. 2001) and the co-evolution of oligolectic bees and their plant hosts (Armbruster 2017). While some studies have found evidence consistent with these theories (e.g., McIver and Erickson 2012, Morandin and Kremen 2013), we found no evidence that the native status of a plant species influenced its visiting bee species composition. One explanation for this lack of effect of native status is that other factors (e.g., flower morphology) are more important in influencing the types of bees visiting a plant species, and that these factors vary within the introduced and native categories of plants.

Surprisingly, corolla color also did not explain observed patterns in bee community composition among plant species. Some studies suggest species-specific preferences for particular flower colors (e.g., Gumbert 2000, Heuschen et al. 2005, Willmer 2011), and the hypothesis that different species of bees are attracted to different colors of flowers forms the basis of using different colors of traps to sample bee communities (Westphal et al. 2008). Indeed, many studies have demonstrated differential capture rates of species (and even sexes) based on trap color (e.g., Leong and Thorp 1999, Toler et al. 2005). One reason that we may not have found an effect of flower color on species composition of visiting bees is that while bees may have innate color preferences, individual bees can learn through experience which flowers produce the greatest rewards (Raine and Chittka 2007). Experienced bees have been found to base their preferences on how productive flowers are, rather than their color, although color may then be used to help identify preferred flowers (Gumbert et al. 1999, Raine and Chittka 2007).

Unlike flower color or native status, flower morphology did describe variation in the types of bees visiting plants. Axis 1 was significantly positively correlated with two apid species, *Bombus vosnesenskii* and *Eucera frater* and four megachilid species of the genus *Osmia*. Both the Apidae and

Megachilidae families are generally considered to be long-tongued bees (Michener 2007). These bees may be strongly associated with bilaterally-shaped flowers, such as *V. cracca,* because nectar is located deeper within these longer-length flowers and would be difficult for short-tongued bees to reach (Salisbury et al. 2015). Foraging on long corolla flowers may give long-tongued bees an advantage as they have less competition with other bees (Willmer 2011). Bilaterally symmetrical flowers often require specialized handling methods that bees learn and remember through experience (West and Laverty 1998). Bees that choose flowers they already know how to handle increase their efficiency when there are abundant foraging options available (Geslin et al. 2014). This may explain why bee species in our study that were positively correlated with Axis 1 would chose bilaterally symmetrical flowers, rather than the more easily accessible radially symmetric flowers, such as Idaho gumweed (*G. nana*) or common yarrow (*A. millefolium*). Bee body size is closely related to tongue length (Harder 1985), and in our study both bee tongue length and body size differed significantly among plant morphology categories.

Species with medium-length disc florets in the family Asteraceae were significantly correlated with *Halictus ligatus* and *Dianthidium subparvum.* The genus *Halictus* comprises short-tongued bees (Michener 2007) and broad floral generalists (Cane and Love 2016), and would likely prefer foraging on small and easily accessible composite flowers. In our study, *H. ligatus* was strongly associated with *G. nana* and *A. millefolium* in particular. Cane and Love (2016) also found *Halictus* to be the major genus visiting *A. millefolium* with no *Bombus, Eucera*, or *Osmia* reported on the plant. The megachilid, *D. subparvumm*, was unusual among bees associated with composite flowers in our study because both its predicted tongue length and body mass were larger than other bee species found visiting those flowers and might be expected to be more strongly associated with simple or tubular-shaped flowers. This suggests that while bees in general may prefer floral morphology that best corresponds to their tongue length and size, other factors influence bee-flower associations.

Conclusions

This study found that many plants in a riparian system in northeastern Oregon are visited by a variety of bee species, and that some plant species appear to be particularly important to bees because they are common and/or preferred. Although introduced plants may have other negative impacts in an ecosystem, bees at Starkey did not show obvious avoidance of introduced plants as a group, and actually preferred certain introduced species, such as *C. vulgare*. Bee choices of plants may depend on a variety of factors, including floral resources available and the individual bee, but neither native status nor corolla color of a plant (in the visible spectrum) had a detectable impact on the types of bees visiting it. Floral morphology, however, was a key character explaining variation in the types of bees visiting different plant species. Bees with longer tongues and larger body sizes tended to be associated with larger, more complex flowers, while bees with shorter tongues and smaller body sizes tended to be associated with smaller, simpler flowers. This has implications for management and restoration work, as a diverse bee community will likely be better supported by a morphologically diverse plant community. Continued work aimed at incorporating the role of seasonal variation in flowering plants and the nutritional quality of pollen and nectar (Somme et al. 2015, Brunet et al. 2015, Vaudo et al. 2016) will likely further enhance our understanding of plant preferences of native bees.

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Data Accessibility

Data associated with this paper have been deposited in the Dryad repository: https://doi.org/10.5061/dryad.p5633 (Roof et al. 2018).

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