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RESEARCH ARTICLE

Feed the bees and shade the streams: riparian shrubs planted for restoration provide forage for native bees

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With evidence of pollinator declines and an increasing focus on restoration, interest is growing in investigating floral resources for native bees. Although native bees forage on shrubs, few studies have explored the pollinator communities of native shrubs and none have examined shrub-pollinator interactions in riparian areas of the northwestern United States. Life history traits of shrubs may make them particularly important resources for bees, especially in early spring—a key point in the lifecycle of many bee species. We conducted extensive hand-net surveys over 2 years in a large riparian restoration project in the Pacific Northwest to understand bee-flowering plant interactions with the aim of guiding future restoration efforts. Although forb blooming stem abundance and richness were higher than that of shrubs in spring, 57% of bees observed foraging were on willow (*Salix* spp.), a commonly planted riparian shrub. Season-long, bee community composition on shrubs differed from that of forbs. Bee species diversity was highest on wax currant (*Ribes cereum*) and willow in early spring (April) and on black hawthorn (*Crataegus douglasii*) and mallow ninebark (*Physocarpus malvaceus*) later (i.e., June – July). Some bees showed a strong preference for wax currant and black hawthorn, both of which are more resistant to ungulate herbivory than other shrubs. Our results suggest that riparian restoration practitioners could consider using shrubs that provide forage to a diverse community of pollinators and improve stream health by shading and stabilizing banks. Planting bee-friendly shrubs can help accomplish multiple restoration goals and leverage limited restoration funding.

Key words: biodiversity, conservation, insect ecology, Pacific Northwest, pollination, pollinator network

Implications for Practice

- Shrubs are frequently planted in riparian restorations for benefits provided to streams and stream-dwelling organisms, such as stabilizing streambanks and shading thermally stressed streams. Shrubs can provide forage for diverse bee communities, although this is seldom considered in riparian restoration.
- Bee and flower communities show strong phenological patterns throughout the growing season. Shrubs may be particularly important in spring when emerging bees require abundant floral resources. Considering phenology in pollinator-plant relationships is recommended when restoring structure and function of degraded systems.
- Wax currant and black hawthorn may be especially useful in riparian Pacific Northwestern, US restoration projects by providing forage to diverse native bees and exhibiting resistance to ungulate herbivory. Both are regionally used in riparian restoration.

Introduction

Recently, the fields of native bee conservation and restoration have rapidly expanded. One reason native bees are of conservation interest is their importance as pollinators in wildlands and croplands. Although honey bees are responsible for more pollination services in agroecosystems of the United States, native bees still contribute approximately $3.07 billion to crop pollination (Losey & Vaughan 2006; Klein et al. 2007; Reilly et al. 2020). This is likely an underestimate, given the challenges associated with valuing pollination services (Hanley et al. 2015; Melathopoulos et al. 2015). Moreover, native bees provide a majority of pollination services in wildlands (Aslan et al. 2016). Yet, remarkably little is known about many native bee species and knowledge gaps exist regarding species diversity, abundance, population trends, and life histories (LeBuhn et al. 2013). Observed declines in wild bee numbers (Potts et al. 2010; Colla et al. 2012) have intensified interest in managing and restoring habitat for wild bees (Winfree 2010; Hanula et al. 2016). However, effective restoration for pollinators requires understanding how landscape features and plant communities can benefit native bees.

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One habitat type of key interest among restoration practitioners in the western United States is riparian areas, which support diverse and abundant wildlife, including native bees, avifauna and other others (DeBano et al. 2004; Williams 2011; DeBano et al. 2016; Roof et al. 2018). Riparian areas connect habitat types across large geographic areas, leading to high levels of invertebrate and plant diversity (Naiman et al. 1993; DeBano et al. 2004; DeBano & Wooster 2004; Galindo et al. 2017). Historically, these systems have been degraded through land management practices including logging (Sweeney et al. 2004), livestock grazing (Schulz & Leininger 1990; Belsky et al. 1999), and stream channel alteration (Sweeney et al. 2004). Currently, 71% of US streams and rivers are in "poor-fair" condition and "lack of adequate vegetation" is a primary stressor (US EPA 2017). Interest is growing in restoring riparian ecosystem structure and function (Goodwin et al. 1997; Bernhardt et al. 2005; Wohl et al. 2015), including restoration for pollinator health (Williams 2011).

Riparian restoration often involves establishing vegetation, primarily shrubs and trees (Guillozet et al. 2014; Averett et al. 2017b) that are planted to improve stream condition by shading water (Wondzell et al. 2019), stabilizing banks (Hughes 2016), and connecting terrestrial habitats (Rockwell & Stephens 2018; Stanford et al. 2020). While riparian restoration objectives do not traditionally include improving pollinator habitat, pollinators may benefit from restoration that includes pollen- and nectar-producing plants (e.g., Golet et al. 2011; Williams 2011; de Araújo et al. 2018). However, for bees and other pollinators to benefit from riparian plantings, pollinator and plant life history traits, including phenology and pollinator floral preferences, should be considered.

Native bee communities include solitary and social species, many of which over-winter as adults or prepupae, emerging in spring or summer to establish nests, forage for pollen and nectar, and provision brood cells (Michener 2007). Interspecific variation in emergence time results in strong phenological patterns in bee communities, with different groups of bee species active throughout the year. Numerous studies have documented distinct changes in species composition of native bee communities throughout the season (Williams et al. 2001; Kimoto et al. 2012; DeBano et al. 2016; Smith DiCarlo et al. 2020).

Pollen and nectar availability at emergence depends on flowering plant phenology (Rathcke & Lacey 1985; DeBano et al. 2016; Hicks et al. 2016; Smith DiCarlo et al. 2020). Proximate cues for the onset of bloom are photoperiod, temperature, and moisture, with plant functional groups generally responding to different cues (Rathcke & Lacey 1985). In temperate systems, temperature is the most common cue for blooming in shrubs and some perennial forbs, whereas photoperiod is a common cue for annual forbs (Rathcke & Lacey 1985). These cues structure plant responses to selective factors; for example, wind-pollinated trees often flower before deciduous plants have leafed out, enabling easier pollen movement through the environment (Rathcke & Lacey 1985). The changing availability of pollen and nectar, driven by plant phenology, influences the varied native bee species that are active from early spring to late fall.

Early spring in temperate North America is hypothesized to be a time of great vulnerability for many native bee species emerging during this period. Weather conditions can be highly variable or extreme and may result in bees operating closer to the lower end of their thermal tolerances (Bale 2002; Weissel et al. 2011; Rotheray et al. 2017). In addition, bloom abundance, species richness, and total floral resource availability are often at their lowest levels in early spring (Hicks et al. 2016). During this time, floral resource availability and density are likely critical to providing bees with sufficient pollen and nectar for their brood cells (Mattila & Otis 2006), and their success in this high-risk environment has direct consequences for fitness (Williams et al. 2012; Crone 2013; Malfi et al. 2019). For example, in social bees (e.g., bumble bees), colony fitness of spring-emerging females depends on floral resource availability in early spring (Williams et al. 2012; Rotheray et al. 2017; Malfi et al. 2019). Solitary bee abundance has also been found to increase following years with higher floral abundance during emergence (Crone 2013).

In riparian areas, shrubs may play a key role during these periods because they often bloom early in the spring, providing valuable forage for bees during the critical time when many native bees are emerging (Dumroese & Luna 2016; Bentrup et al. 2019). Onset of shrub bloom and spring bee emergence are both tightly linked to temperature, such that shrub blooms likely become abundant when bees are emerging (Rathcke & Lacey 1985; White et al. 2009; Fründ et al. 2013). Several early-season shrubs [e.g., willow (*Salix* spp.)] are commonly planted in riparian restorations because they thrive near streams and rivers. In some communities, willows are one of few plant species blooming when bees first begin to emerge (Moquet et al. 2015). Many willows have sufficiently nutritious pollen and nectar to attract and feed bees (Roulston et al. 2000; Weiner et al. 2010; Saunders 2018), despite some being anemophilous.

Other life history traits, beyond phenology, may make shrubs valuable to riparian bees. The pollen of some shrub species has relatively high protein content. For example, Roulston et al. (2000) reported average protein in willow pollen as 41.4%, which is high, given a range of 2.4–61.0% protein observed in pollen from >300 plant species. Roulston et al. (2000) found that protein content was highly conserved within genera and families, suggesting that the willow species present in Starkey likely have high protein content despite differing from the species considered by Roulston et al. (2000). In addition to potential differences in pollen quality, the growth form of shrubs typically results in higher densities of blooms per plant than for forbs, with some shrubs having tens of thousands of blooms per plant (Wender & Harrington 2004). Many bee species make foraging decisions based on density of floral resources and focus efforts on dense flower patches (Sih & Baltus 1987).

Although previous studies have shown that insect pollinators can benefit from some species of shrubs and trees (reviewed in Bentrup et al. 2019), most studies focused on timber production systems (e.g., Reddersen 2001), hedgerows in agroecosystems (e.g., Hannon & Sisk 2009; Kovács-Hostyánszki et al. 2013; Morandin & Kremen 2013), or on non-native honey bees (Bareke et al. 2017). To our knowledge, no studies have examined native bee communities associated with shrubs growing in riparian areas in the United States. By understanding bee-plant interactions in riparian habitats, restoration practices can be refined to not only restore stream health, meeting fish- and plant-focused restoration goals, but to also enhance pollinator habitat. Because riparian restoration is expensive (Nagle 2007; Bouwes et al. 2016; Silverman et al. 2018), annually costing over $1 billion (USD) in the United States (Bernhardt et al. 2005), and because financial and logistical support for restoration is limited (Holl & Howarth 2000; Iftekhar et al. 2017), combining restoration goals is a high priority for land managers (González et al. 2017). Although most restoration plans have not traditionally considered invertebrates, the scope of these plans is changing. Riparian restoration benefiting pollinators is especially pertinent given increasing conservation concerns about these taxa (Winfree 2010; Hanula et al. 2016). Refining plant selection to accomplish multiple objectives is a simple way to achieve more with limited financial resources. However, selecting shrubs that benefit pollinators and streams requires understanding how bees interact with flowering plants used in riparian restoration projects.

This study sought to determine which shrubs may be good candidates for simultaneously restoring riparian areas and enhancing pollinator habitat in the Pacific Northwest (PNW) by examining interactions between bees and shrubs. Many of the shrub species examined in this study occur across the western United States and are commonly used in riparian restoration projects (Hoag & Landis 2002). To understand the relationships between bees and flowering shrubs, we addressed the following questions: (1) How does bee visitation rate differ between shrubs and forbs early in the season? (2) When does richness of blooming shrub and forb species peak during the growing season? and (3) Do bee communities that interact with shrubs and forbs differ, and which bee species interact with particular blooming species?

We hypothesized that, due to interacting life history traits between bee and plant species in the context of seasonal variation in abiotic conditions, shrubs will play an important role in supporting native bees, especially early in spring. We predicted that blooming shrubs would receive more visitors relative to forbs in early spring, given their phenological availability, their abundant and nutritious floral rewards, and the high density of blooms on individual plants (Wender & Harrington 2004; Weiner et al. 2010). In addition, we predicted that many non-shrub floral resources available in spring would be small annual plants, unlikely to provide the resources necessary for nest initiation (Pywell et al. 2005). Finally, we predicted that abundance and species richness of blooming forbs would increase throughout the season while shrub abundance and diversity would decrease.

Methods

Study Area

This study was conducted in riparian meadows along 11 km of Meadow Creek, encompassing approximately 157 ha, at elevations of approximately 1,100 m (Averett et al. 2017a, 2017b) in the U.S. Forest Service (USFS) Starkey Experimental Forest and Range (Starkey) (Fig. 1). Average annual precipitation is 42 cm, mostly arriving between November and June (NOAA 2010). Climate and vegetation in Starkey are typical of forested riparian systems in the Blue Mountains of Oregon (Rowland et al. 1997).

Meadow Creek was part of a large-scale riparian restoration project implemented in 2012 and 2013 by the USFS that focused on restoring stream function for the benefit of Endangered Species Act (ESA)-listed salmonids (Averett et al. 2017a). During restoration, over 50,000 native trees and shrubs were planted in the riparian area, including flowering-shrubs such as willows,

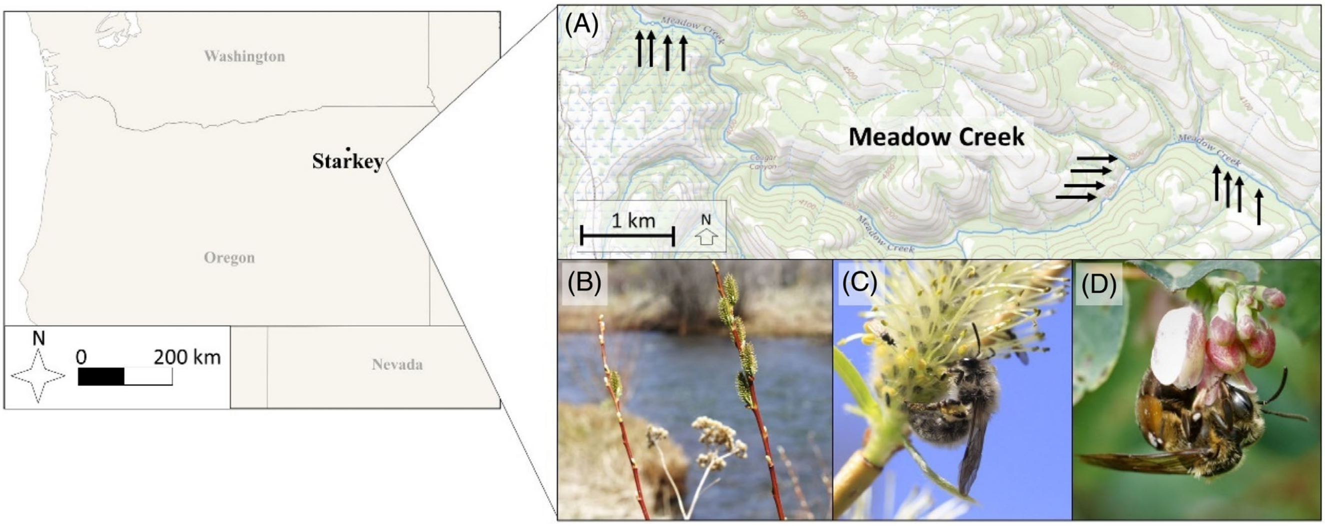

Figure 1. Study sites and native bees. (A) U.S. Forest Service Starkey Experimental Forest and Range: Meadow Creek, located in northeastern Oregon, with approximate sampling locations indicated. Black arrows indicate location of sites used in plant and bee sampling; several additional sites (not shown) were opportunistically sampled for bees. (B) Planted one-color willow (*Salix monochroma*) in bloom. (C) Bee (*Andrena* sp.) foraging on one-color willow in April. (D) Bee (*Andrena* sp.) foraging on common snowberry (*Symphoricarpos albus*) in July. All photos by S. Mitchell.

currants (*Ribes* spp.), and black hawthorn (*Crataegus douglasii*), which occur naturally in similar habitats throughout the western United States and are regionally good candidates for restoration (Hoag & Landis 2002). Sampling for this study occurred primarily at 12 sites that are part of a long-term study (Averett et al. 2017a) (Fig. 1). Cattle (*Bos taurus*), mule deer (*Odocoileus hemionus*), and elk (*Cervus canadensis*) occur in the study area. Cattle were not present until mid-June and stocking rates were low.

Plant and Bee Sampling

To understand how bee visitation rate differs between shrubs and forbs in spring, we conducted exhaustive searches of all shrub and forb blooming stems in 11 of 12 one-hectare sites (Fig. 1) in April 2018. During searches, we systematically walked sites, counting every blooming stem present and tallying (but not catching) every foraging bee observed, recording the plant species on which the bee was observed. Like other pollinator studies (e.g., Roof et al. 2018; Graham et al. 2021), blooming stems were defined as easily distinguishable individual flowers (e.g., *Viola adunca*, *Rosa spp.*) or tight clusters of flowers on a stem (e.g., *Noccaea fendleri*). Catkins (e.g., willow) and composite flowers (e.g., *Taraxacum officinale*) were counted as single units. Each survey took approximately 1 hour to complete and was conducted between 26 and 28 April 2018. This approach allowed us to calculate a visitation rate for each site (#bees/blooming stem/site) for shrubs and forbs. The 12th site was not sampled due to inclement weather (hailstorm), which obscured low-growing forb blooms and eliminated the possibility of observing foraging bees.

To understand the timing of peak richness of blooming shrubs and forbs, we conducted 20-min presence/absence surveys of blooming plant species throughout each of the 12 sampling sites once monthly in May, June, July, and September 2018. Here we defined richness as the total number of currently blooming species present at a site. Bloom richness in April was based on exhaustive search surveys as described above.

To understand how bee communities associated with shrubs and forbs differ and understand interactions between bee and blooming plant species, we sampled bees with hand-nets from April to September of 2018 and May to September of 2019. Bees were only collected when they appeared to be actively foraging on blooms. Collected specimens were euthanized with ethyl acetate, preserved for identification, and vouchered at Oregon State University's Hermiston Agricultural Research and Extension Center's Invertebrate Ecology Laboratory collection. Bees were identified by a taxonomic expert using methods described in Kuhlman and Burrows (2017). Because our objective was to describe bee communities for individual blooming plant species, we attempted to maximize the number of observations of bees for every blooming species of forb and shrub present in the study area during each sampling period. To do this, we conducted targeted netting on all common blooming shrubs in the area. There were many more forb species than shrubs during most sampling bouts, so we conducted hand-netting on forbs by walking through sites systematically for approximately the same duration spent netting on shrubs. We opportunistically sampled on less common plant species when encountered. Most bees were sampled in the 12 plant sampling plots, but some opportunistic sampling occurred immediately adjacent to the 12 sites (Fig. 1) in order to increase sample size on less common plants.

Statistical Analyses

Bee Visitation Rate. To examine how bee visitation rate differed between shrubs and forbs, we compared the bloom abundance, richness, and visitation rate of shrubs and forbs at each site in April 2018 using Wilcoxon rank sum tests (Zar 1998), conducted in R (R Core Team 2019). Visitation rate of bees to shrub blooms was calculated by dividing the total number of bees observed visiting shrub blooms (all species combined) in a site by the total number of shrub blooming stems (all species combined) counted in a site $\left(\frac{\#\text{of bees visiting shrubs}}{\#\text{of shrub blooms}}\right)$. Visitation rate to forb blooms was calculated similarly.

Seasonal Phenology. To understand the timing of peak richness of blooming shrubs and forbs, we used Poisson-distributed generalized linear mixed models (GLMMs) to determine if average richness of blooms in a site differed significantly among months for each plant type (forbs vs. shrubs). Pairwise comparisons of monthly means were made using Tukey contrasts (Tukey 1949). Poisson-distributed GLMMs and Tukey contrasts were conducted in R (R Core Team 2019) with the lme4 package (Bates et al. 2015), and results were visualized using the ggplot2 package (Wickham 2016).

Bee and Plant Interactions and Communities. To understand whether bee communities interacting with shrubs differ from those interacting with forbs, we ordinated bee communities foraging on shrub and forb blooms using non-metric multi-dimensional scaling procedures (NMDS) (Kruskall & Wish 1978). Multi-response permutation procedures (MRPPs) (McCune et al. 2002) were used to determine if bee communities differed between forbs and shrubs. For both NMDS and MRPP analyses, rare species were excluded by removing bee species with fewer than five specimens and plant species with fewer than five bee observations. This resulted in a matrix with 48 rows (plant species) and 58 columns (bee species). We ordinated bloom species in bee species space with the following options: Sorenson distance measure, maximum of 500 iterations, random starting coordinates, step length of 0.20 (McCune & Mefford 2006), 100 runs with real data, and 500 runs with randomized data to generate a final three-dimensional configuration. We used PC-ORD Version 7 (McCune & Mefford 2006) to conduct all multivariate analyses.

Table 1. Numbers of bees collected on each of 16 shrub species blooming in April 2018 and May, June, and July of 2018 and 2019.

Common Name	*Species Name*	*April*	*May*	*June*	*July*
Willow sp.	*Salix sp.*	23	20	-	-
Wax currant	*Ribes cereum*	6	167	3	-
Geyer's willow	*Salix geyeriana*	-	23	-	-
Onecolor willow	*Salix monochroma*	-	19	-	-
Lemmon's willow	*Salix lemmonii*	-	12	-	-
Shining willow	*Salix lasiandra*	-	3	-	-
Black hawthorn	*Crataegus douglasii*	-	-	101	-
Wild rose	*Rosa sp.*	-	-	46	5
Red-osier dogwood	*Cornus sericea*	-	-	40	3
Mallow ninebark	*Physocarpus malvaceus*	-	-	15	2
English hawthorn	*Crataegus laevigata*	-	-	2	-
Sticky currant	*Ribes viscosissimum*	-	-	1	-
Blue elderberry	*Sambucus nigra*	-	-	8	53
Common snowberry	*Symphoricarpos albus*	-	-	39	48
Thimbleberry	*Rubus parviflorus*	-	-	-	1
White spirea	*Spiraea betulifolia*	-	-	-	1
	Grand Total	*29*	*244*	*255*	*113*

We then examined bee and flower interactions by constructing pollinator networks using all data from both years. Bipartite networks allow for visualization of two node networks where box size of individual species is proportional to the number of observations of a species and the thickness of lines connecting plants to bees is proportional to the number observed interactions (Dormann et al. 2008). We conducted network analyses using the bipartite package in R (Dormann et al. 2008, 2009). Diet breadth of all common bee species ($n \geq 10$) was further explored visually.

Finally, we calculated the Shannon diversity (Shannon & Weaver 1949) of bee visitors for each shrub species to determine which shrubs provide forage for the highest diversity of bees. Shannon diversity was used instead of species richness because it accounts for the number and relative abundance of each species. This information is especially relevant to conservation because a shrub species that provides resources equally for multiple species is more likely to support a diverse bee fauna than one that is visited by an equivalent number of species, but only occasionally by most species. Shannon diversity was calculated in the bipartite package of R (Dormann et al. 2009).

Results

In 2018 and 2019, we collected 1,886 bees of 150 species or morphospecies on 16 shrub species (641 specimens, Table 1), 76 forb species (1,245 specimens), and one tree species (17 specimens) (Table S1). Of the 150 bee species collected, 30 were only observed on shrubs, 70 were only observed on forbs, and 50 were observed on both forbs and shrubs (Table S1). Approximately 20% of bee species were only observed once during the study (24 species on forbs, 13 on shrubs).

Bee Visitation Rate

In early season sampling (April 2018), we counted 20,831 blooming stems from 27 plant species (25 forb, two shrub) and observed 37 bees foraging on those blooms. Forb blooming stems were more abundant ($W = 120$, $p < 0.001$) and more species rich ($W = 121$, $p < 0.001$) than shrub blooming stems (Fig. 2). However, there was not a statistically significant difference in the number of bees per forb blooming stem versus shrub blooming stem in the 11 sites ($W = 76$, $p = 0.66$) (Fig. 2). Despite this finding, 57% of observed bees were visiting willow

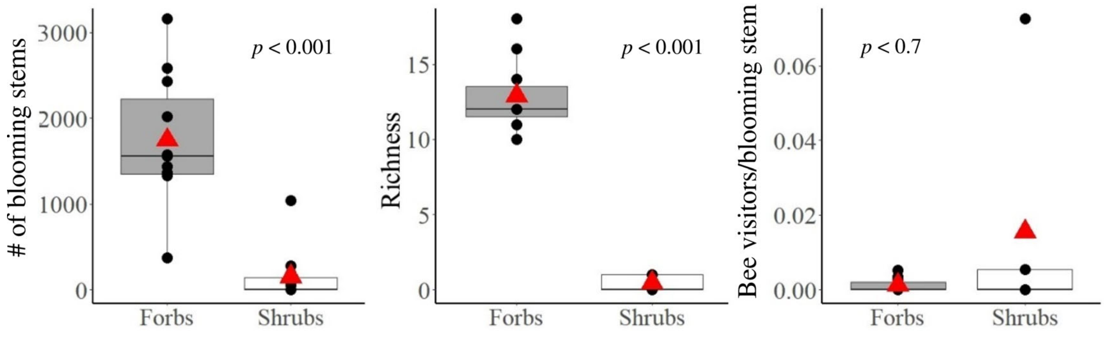

Figure 2. Boxplots displaying counts of blooming stem abundance, richness of blooming species, and number of bee visitors/blooming stem of forbs and shrubs ($n = 11$ sites). Red triangles show mean value. Comparisons were made using Wilcoxon rank sum tests.

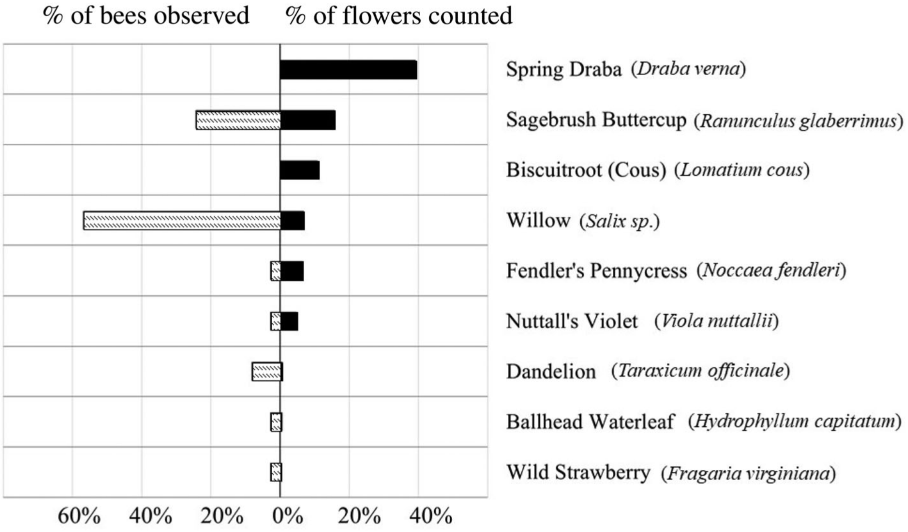

Figure 3. Percentages of total bees observed (left) and of total blooming stems counted (right) in 11 sites during exhaustive searches conducted in April 2018. Plant species with no observed bee visits and constituting less than 5% of the total count of blooming stems are not shown. Willow (*Salix* sp.) is the only shrub species displayed.

blooms, even though willow blooming stems were less than 7% of total observed blooming stems (Fig. 3).

Seasonal Phenology

Blooming shrub species richness peaked in May, with richness in that month and June statistically higher than April or September (Fig. 4). Blooming forb richness peaked in June and was significantly higher that month than in April, May, and September (Fig. 4). Bees were collected on blooming shrubs in April–July in 2018 and 2019 (Table 1). Because no shrubs were observed blooming after July, all bees collected in August or September were collected from forbs (Fig. 5, species key in Table S2).

The phenology of blooming shrubs and bee visitors varied strongly by season (Table 1; Fig. 5). In April and May, most bees were collected on willow and wax currant. In June, most bees were collected on black hawthorn, wild rose (*Rosa sp.*), red-osier dogwood (*Cornus sericea*), and common snowberry, but also infrequently on five other, less common shrubs. In July, most bees were collected on blue elderberry and common snowberry and less frequently on other species. The proportion of bees collected on shrubs versus forbs was highest in May and declined in June and July (Fig. 5). Bee and plant species turnover was high across months (Fig. 5; Table S2).

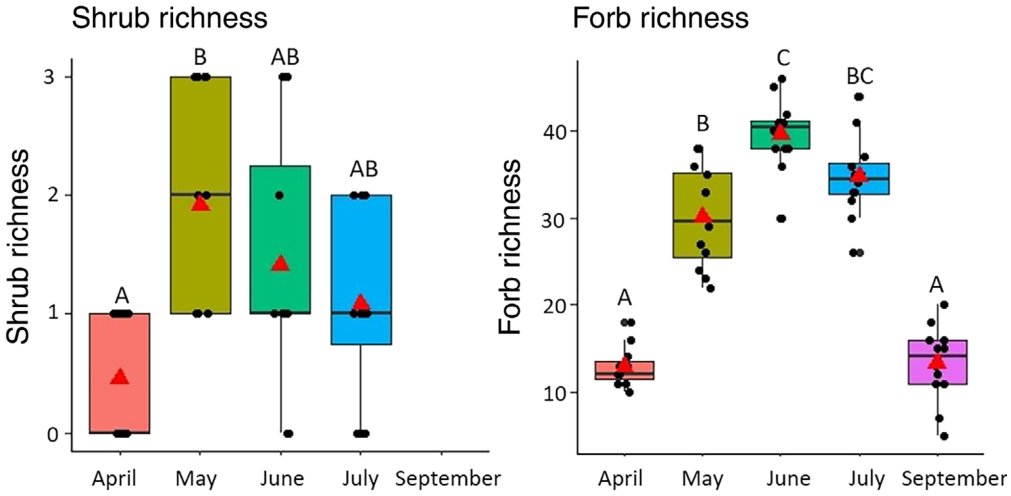

Figure 4. Seasonal variation in blooming forb and shrub species richness at 12 sites along Meadow Creek in 2018. Statistically significant differences among months (Poisson-distributed GLMM, multiple comparisons of means Tukey contrasts, $p < 0.05$) are indicated by different letters above boxplots. Dots show counts from individual sites ($n = 12$), red triangles show mean values. No shrub blooms were detected at any sites in September.

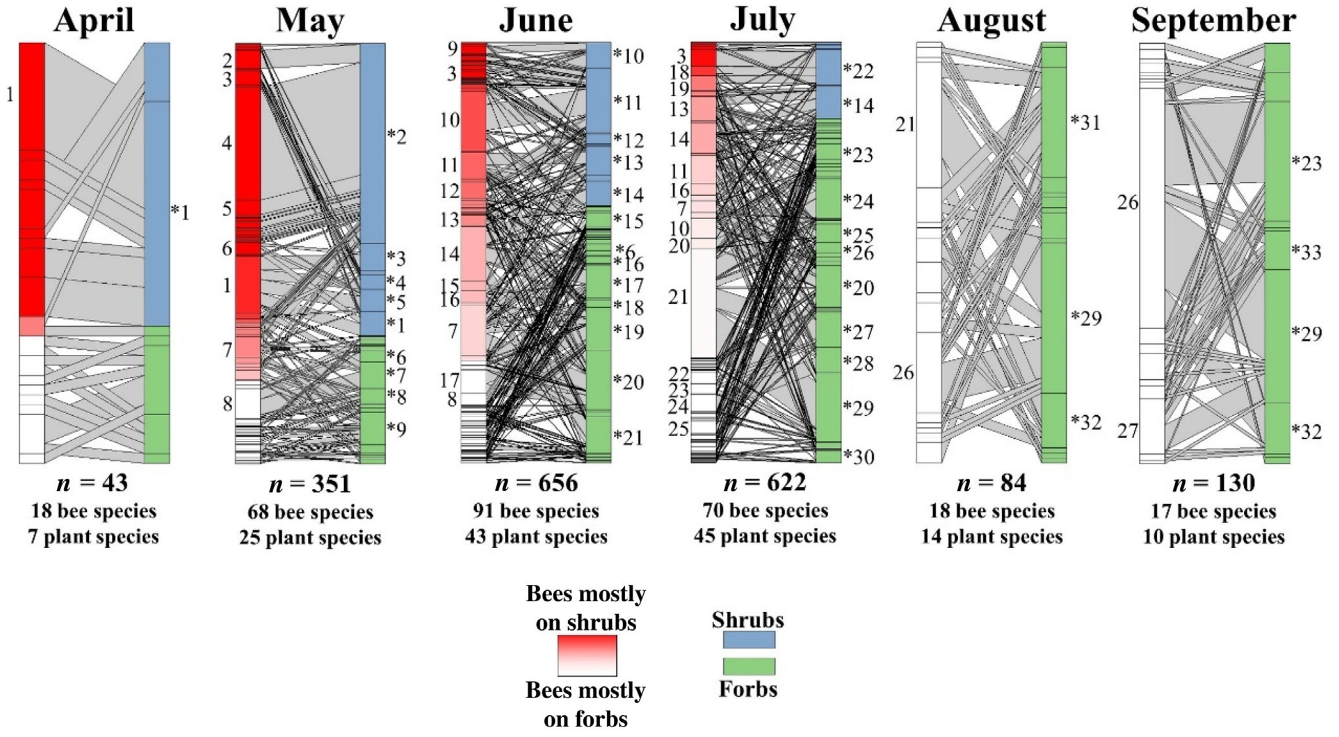

Figure 5. Monthly plant and bee networks (2018 and 2019 sampling combined). The number of interactions and bee and plant species represented by each network are given below each graph. The left-side of each network displays bee species and the right-side plant species. Bee species for which more than 10 specimens were collected are labeled with numbers. Plant species for which more than 10 bees were collected on are labeled with numbers and asterisks (see table S2 for key to bee and plant species). Box segment height corresponds to the number of observations for a species and line width to number of observed interactions between two connected species.

Black hawthorn had the highest observed diversity of bees, followed by mallow ninebark (*Physocarpus malvaceus*). Among shrubs blooming in April and May, wax currant was visited by a higher diversity of bees than any willow species (Fig. 6).

Bee and Plant Interactions

Community analyses of blooming plants in bee community space revealed that bee communities on forbs and shrubs were distinct from each other (MRPP: $A = 0.02$, $p < 0.001$; Fig. 7). Final stress of the three-dimensional ordination was 12.6. Axis 1 explained 23% of the variation present in the data, axis 2 explained 13%, and axis 3 explained 11%. NMDS ordination showed some separation between shrub and forb species on axis 1 and on axis 3, indicating that bee communities differed between shrubs and forbs (Fig. 7). Shrub species were associated with positive values on axis 1, indicating association with several *Andrena* and *Osmia* species, and negative values on axes 2 and 3, indicating association with several *Bombus*, *Lasioglossum*, and *Osmia* species (Fig. 7, Table S3). Forb species were negatively associated with axis 1 and positively with axes 2 and 3 and were associated with several species of *Melissodes*, *Lasioglossum*, and *Halictus*.

Network analyses suggested that bees exhibited a mix of foraging patterns, with some species displaying preferences for certain plants (oligolectic) and others visiting many plants (polylectic). The five most specialized bee species (of 35 species, $n \geq 10$, labeled in Fig. 8) were *Andrena porterae* (15 specimens, 100% on wax currant), *A. flocculosa* (13 specimens, 100% on red osier dogwood), *Anthophora pacifica* (104 specimens, 97% on wax currant), *Diadasia nigrifrons* (25 specimens, 92%

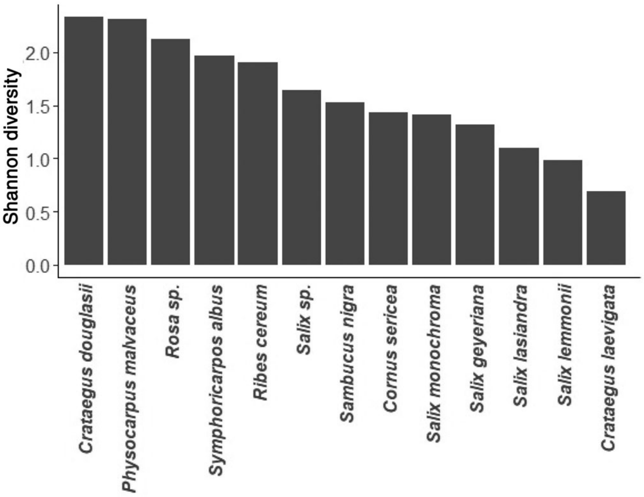

Figure 6. Shannon diversity of bee visitors to shrub species occurring at Meadow Creek. Shrubs with only one observed visitor were excluded.

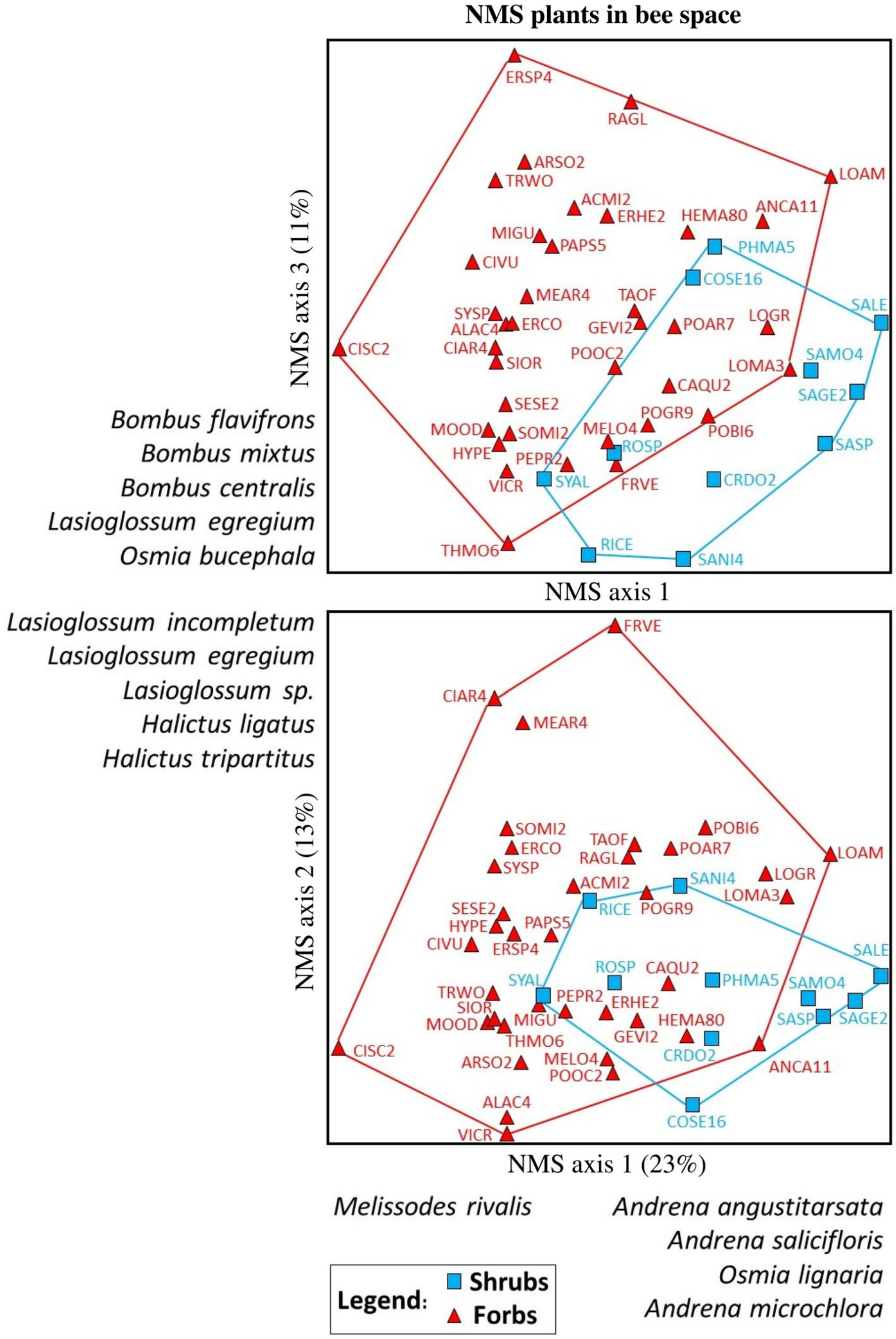

Figure 7. Blooming plant species in bee community space (top panel is axis 1 vs. axis 3, bottom panel is axis 1 vs. axis 2). Percent of variation explained by each axis is shown on the axis label. Symbols are plant species labeled with codes from the USDA NRCS database (https://plants.sc.egov.usda.gov/java/). Bee communities observed foraging on shrubs versus forbs were significantly different ($A = 0.02$, $p < 0.001$). Bee species with $r > 0.1$ correlation to each axis are shown. All data were combined from 2018 and 2019 sampling.

on Oregon checker-mallow), and *Bombus vosnesenskii* (10 specimens, 80% on bull thistle). The most generalist species were *B. mixtus* (101 bees on 25 plant species), *A. salicifloris* (13 bees on seven plant species), *B. flavifrons* (141 bees on 38 plant species), *Hoplitis fulgida* (12 bees on eight plant species), and *B. centralis* (55 bees on 21 plant species). Some species appeared to primarily visit plants of particular genera and thus could be considered oligolectic (specializing on closely related plants). One example was *A. angustitarsata*. Although collected on 11 plant species, 78% of specimens were caught on one of four willow species, suggesting some level of oligolecty on willows (see Fig. S1 for diet breadth of the 35 most commonly sampled bee species). *A. salicifloris* was also potentially oligolectic on willow with 46% of specimens collected on one of three

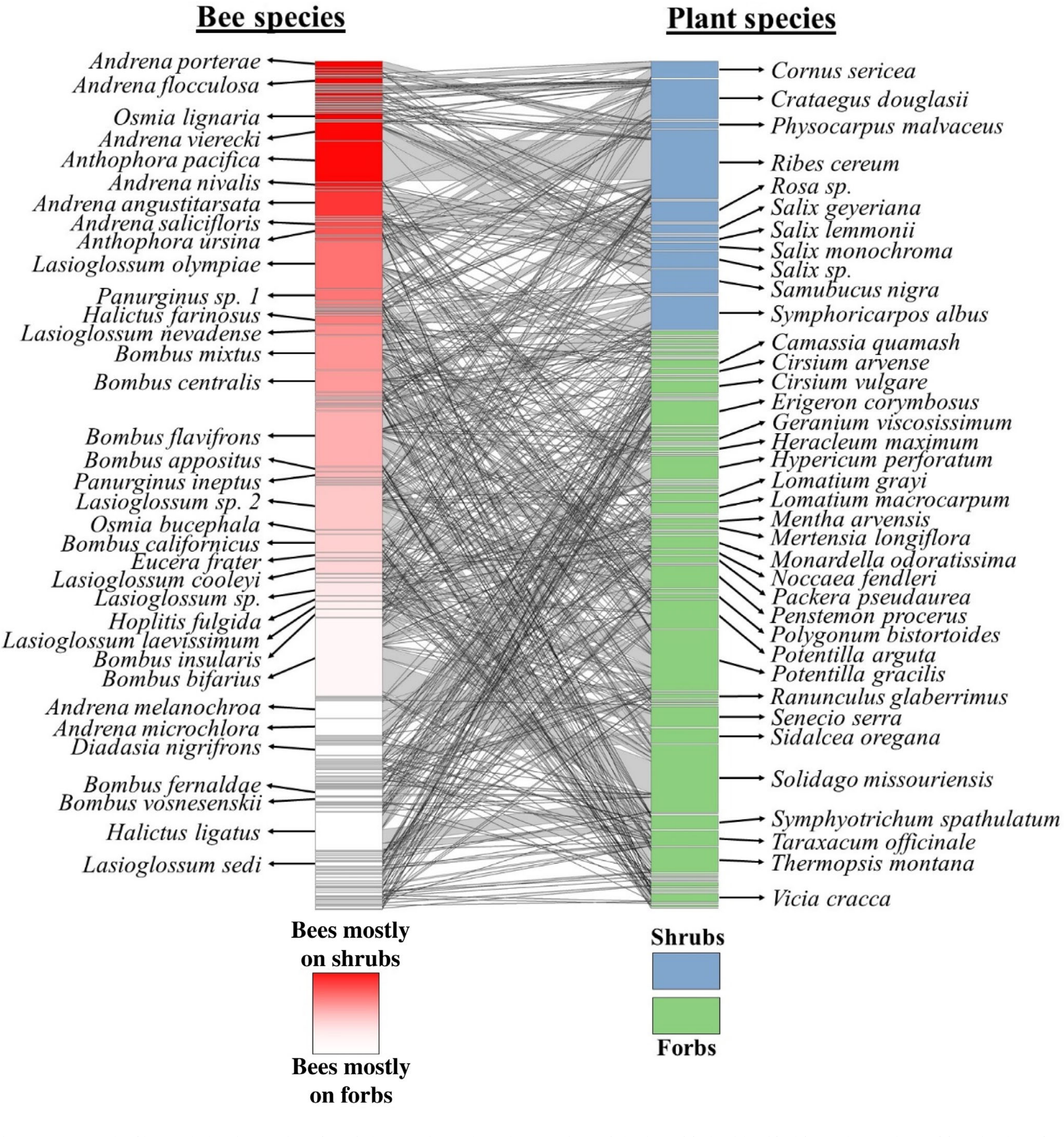

Figure 8. Network of bee and plant interactions for 150 bee species and 92 plant species (16 shrubs, 76 forbs) identified from observations of foraging bees from April to September, 2018–2019, at Meadow Creek. Names of bee and plant species with 10 or more observations are displayed. Box height and lines connecting bee and plant species are proportional to the number of observations.

willow species and the remaining 54% collected on four other plant species.

Discussion

While other studies have explored relationships between native bees and shrubs in agricultural contexts (Reddersen 2001; Hannon & Sisk 2009; Kovács-Hostyánszki et al. 2013), this study is the first to explore in-depth relationships between native bees and shrubs in U.S. riparian areas. As predicted, our results indicated that species-rich communities of native bees forage on a diverse community of plants in restored riparian areas planted with commonly selected shrub species. As other studies have found in agricultural contexts and as we hypothesized, shrubs appear to play an important role in supporting native bee communities, especially in spring. We found that a diverse and distinct community of bees visited shrubs, with several species of *Andrena* exhibiting specialist interactions with willows. Another striking and unexpected case of apparent specialization in this study was that of Pacific digger bees (*A. pacifica*) and wax currant. Of the 104 specimens captured, 101 were collected on wax currant. This case of apparent specialization was unexpected because this species has been documented visiting many plant species from over 15 plant families (Ascher & Pickering 2020).

The diversity of floral resources varied through the season. As predicted, and perhaps most importantly, we found that while shrubs were less abundant than forbs in the early season, some shrub species like willow were visited at high rates, especially by certain bee species. In fact, most bees observed during the earliest part of the year (April) were found foraging on willow. Willow distribution was patchy but when present, willow had a high concentration of blooms, likely attracting a high number of bees with abundant nectar and pollen. Dominant blooming forb species in April included many small annuals such as spring draba (*Draba verna*) and blue-eyed Mary (*Collinsia parviflora*), which likely provide minimal nectar or pollen for bees (Pywell et al. 2005) due to their size. Given the dominance of less beneficial small annual forbs in April and the relatively high protein content of willow compared to other plant species (Roulston et al. 2000; Weiner et al. 2010), this genus may be an appealing resource for bees. Later in the season, shrubs such as currants, hawthorns, and common snowberry supported diverse bee fauna. Future studies could compare the pollen nutrition, nectar volume, and sugar content of early spring blooming forbs with willow species to further explore the relative value of willows to native bees.

Some of the shrubs we examined, such as willows and red osier dogwood, are more common in riparian areas or are riparian obligates, while others, such as wax currant (*Ribes cereum*), common snowberry (*Symphoricarpos albus*), elderberry (*Sambucus nigra*), mallow ninebark, wild rose, and black hawthorn, occur in both upland and riparian areas. It may be particularly important to include riparian obligates in riparian restoration projects, given their importance to bees and the high biodiversity of riparian areas.

When considering restoration in riparian areas, land managers should also consider the palatability of planted species to ungulates. Ungulates such as mule deer and elk can depress shrub establishment and growth in riparian areas, as seen at Starkey (Averett et al. 2017a, 2019). Additionally, because the plants bees visit may overlap significantly with ungulate diets (particularly forbs), unpalatable but site-suitable native shrubs, such as hawthorn and currants (Holechek et al. 1982), can be a useful component of restoration projects (DeBano et al. 2016). These less palatable species exhibit higher survival in riparian restoration projects in the presence of ungulate herbivory (Averett et al. 2017b), lending support to their value in riparian restoration plantings to benefit both native bees and riparian communities overall. In the early season, 30 species of bees were collected on wax currant, and later in the season 24 species on black hawthorn. In total, 50 bee species (one-third of total observed species richness) were collected on these two shrubs. Both plant species provision a high diversity of bee species, especially when compared to other shrubs blooming at the same time. Since both shrubs are long-lived, resistant to ungulate herbivory, and provide forage to a diverse community of bees, they are prime candidates for riparian restoration projects where suitable. When used in conjunction with other shrubs and forbs, they may be highly successful in revegetating riparian areas and providing forage to pollinators. In riparian areas with particularly intense ungulate herbivory, a multi-pronged management approach utilizing techniques such as virtual or temporary fencing may be necessary.

Our study represents an initial assessment of the value of plants used in riparian restoration plantings for supporting native bee communities and suggests that shrubs should be an integral component of such plantings (Bentrup et al. 2019). Future work should assess pollinator communities pre- and post-restoration to determine if shrub plantings increase bee richness and diversity or merely enhance resources for existing populations. More in-depth studies of bee-shrub interactions would help identify additional shrubs that support specialist bees. In addition to documenting foraging behavior of bees through observation, pollen load analyses using microscopy or metabarcoding will be helpful in determining which plant species are used as pollen sources for presumed bee specialists (Smith et al. 2019; Arstingstall et al. 2021). Using such approaches is particularly valuable in pollinator-plant interactions studies because pollen analyses can reveal cryptic interactions in networks, not detected by observations of bee foraging behavior (Arstingstall et al. 2021). Finally, future studies could explore the non-floral benefits (e.g., oils, nesting substrate) that woody plants can provide to native bees and explore how to incorporate these into restoration plans.

The woody shrubs examined by this study are widely distributed across the PNW and should support similar bee communities in other areas. In particular, the most common shrubs in Starkey (willows, black hawthorn, wax currant, elderberry, roses, and dogwood) occur across the PNW US and surrounding regions (e.g., northern California) and are thus good candidates for jointly accomplishing pollinator and river restoration goals across a broad area. Billions of dollars have been spent on river restoration projects in the United States since 1990 (Bernhardt et al. 2005), highlighting the importance of pursuing projects that can accomplish multiple restoration goals without adding significant cost to projects. With >50,000 trees and shrubs planted along this stream and hundreds of similar projects being initiated in the PNW US annually (primarily for ESA-listed fish), selecting plants that accomplish multiple goals could aid in native bee resilience on broad spatial scales. Explicitly incorporating bee-friendly shrubs, such as the ones examined in this study, into riparian restoration projects is one approach to extend restoration dollars by enhancing pollinator habitat while addressing traditional riparian restoration goals.

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LITERATURE CITED

Arstingstall KA, DeBano SJ, Xiaoping L, Wooster DE, Rowland MM, Burrows S, Frost K (2021) Capabilities and limitations of using DNA metabarcoding to study plant-pollinator interactions. Molecular Ecology. https://doi.org/10.1111/mec.16112

Ascher JS, Pickering J (2020) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). https://www.discoverlife.org/mp/20q?search=Anthophora+pacifica (accessed 28 Aug 2020)

Aslan CE, Liang CT, Galindo B, Hill K, Topete W (2016) The role of honey bees as pollinators in natural areas. Natural Areas Journal 36:478–488

Averett JP, Endress BA, Rowland MM, Naylor BJ, Wisdom MJ (2017a) Wild ungulate herbivory suppresses deciduous woody plant establishment following salmonid stream restoration. Forest Ecology and Management 391:135–144

Averett JP, Wisdom MJ, Endress BA (2019) Livestock riparian guidelines may not promote woody species recovery where wild ungulate populations are high. Rangeland Ecology and Management 72:145–149

Averett JP, Wisdom MJ, Naylor BJ, Rowland MM, Endress BA (2017b) Data and analyses of woody restoration planting survival and growth as a function of wild ungulate herbivory. Data in Brief 14:168–174

Bale JS (2002) Insects and low temperatures: from molecular biology to distributions and abundance. Transactions of the Royal Society of London B 357:849–862

Bareke T, Addi A, Wakjira K (2017) Screening of potential shrubs for bee forage development. Journal of Plant Science 5:160–164

Bates D, Maechlet M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48

Belsky AJ, Matzke A, Uselman S (1999) Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419–431

Bentrup G, Hopwood J, Adamson NL, Vaughan M (2019) Temperate agroforestry systems and insect pollinators: a review. Forests 10:981–1001

Bernhardt ES, Palmer MA, Allan JD, Alexander G, Barnas K, Brooks S, et al. (2005) Synthesizing U.S. river restoration efforts. Science 308:308–309

Bouwes N, Weber N, Jordan CE, Saunders WC, Tattam IA, Volk C, Wheaton JM, Pollock MM (2016) Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). Scientific Reports 6:28581

Colla SR, Gadallah F, Richardson L, Wagner D, Gall L (2012) Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. Biodiversity and Conservation 21:3585–3595

Crone EE (2013) Responses of social and solitary bees to pulsed floral resources. The American Naturalist 182:465–473

de Araújo GJ, Monteiro GF, Messias MC, Antonini Y (2018) Restore it, and they will come: trap-nesting bee and wasp communities (Hymenoptera: Aculeata) are recovered by restoration of riparian forests. Journal of Insect Conservation 22:245–256

DeBano LF, DeBano SJ, Wooster DE, Baker MB (2004) Linkages between surrounding watersheds and riparian areas. Pages 77–98. In: Baker MB, Ffolliott PF, DeBano LF, Neary DG (eds) Riparian areas of the southwestern United States: hydrology, ecology, and management. CRC Press, Washington, D.C.

DeBano SJ, Roof SM, Rowland MM, Smith LA (2016) Diet overlap of mammalian herbivores and native bees: implications for managing co-occurring grazers and pollinators. Natural Areas Journal 36:458–477

DeBano SJ, Wooster DE (2004) Chapter 10: Insects and other invertebrates: ecological roles and indicators of riparian and stream health. Pages 215–237. In: Baker MB, Ffolliott PF, DeBano LF, Neary DG (eds) Riparian areas of the southwestern United States: hydrology, ecology, and management. CRC Press, Washington, DC

Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. The Open Ecology Journal 2:7–24

Dormann CF, Gruber B, Fründ J (2008) Introducing the bipartite package: Analysing ecological networks. R News 8:8–11

Dumroese RK, Luna T (2016) Growing and marketing woody species to support pollinators: an emerging opportunity for forest, conservation, and native plant nurseries in the northeastern United States. Tree Planters 59:49–60

Fründ J, Zieger SL, Tscharntke T (2013) Response of wild bees to overwintering temperatures. Oecologia 173:1639–1648

Galindo V, Calle Z, Chará J, Armbrecht I (2017) Facilitation by pioneer shrubs for the ecological restoration of riparian forests in the Central Andes of Colombia. Restoration Ecology 25:731–737

Golet GH, Gardali T, Hunt JW, Koenig DA, Williams NM (2011) Temporal and taxonomic variability in response of fauna to riparian restoration. Restoration Ecology 19:126–135

González E, Felipe-Lucia MR, Bourgeois B, Boz B, Nilsson C, Palmer G, Sher AA (2017) Integrative conservation of riparian zones. Biological Conservation 211:20–29

Goodwin CN, Hawkins CP, Kershner JL (1997) Riparian restoration in the western United States: overview and perspective. Restoration Ecology 5:4–14

Graham M, Ates S, Melathopoulos AP, Moldenke AR, DeBano SJ, Best LR, Higgins CW (2021) Partial shading by solar panels increases floral abundance, delays blooms for pollinators during the late-season in a dryland, agrivoltaic ecosystem. Scientific Reports 11:7452

Guillozet P, Smith K, Guillozet K (2014) The rapid riparian revegetation approach. Ecological Restoration 32:113–124

Hanley H, Breeze TD, Ellis C, Goulson D (2015) Measuring the economic value of pollination services: principles, evidence and knowledge gaps. Ecosystem Services 14:124–132

Hannon LE, Sisk TD (2009) Hedgerows in an agri-natural landscape: potential habitat value for native bees: potential habitat value for native bees. Biological Conservation 142:2140–2154

Hanula JL, Ulyshen MD, Horn S (2016) Conserving pollinators in North American forests: a review. Natural Areas Journal 36:427–439

Hicks DM, Ouvrard P, Baldock KCR, Baude M, Goddard MA, Kunin WE, et al. (2016) Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows. PLoS One 11:158117

Hoag JC, Landis TD (2002) Plant materials for riparian vegetation. Pages 33–43. In: Dumroese RK, Riley LE, Landis TD (eds) National proceedings: forest and conservation nursery associations – 1999, 2000, and 2001. U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station, Ogden, Utah

Holechek JL, Vavra M, Skovlin J, Krueger WC (1982) Cattle diets in the Blue Mountains of Oregon II forests. Journal of Range Management 35:239–242

Holl KD, Howarth RB (2000) Paying for restoration. Restoration Ecology 8: 260–267

Hughes AO (2016) Riparian management and stream bank erosion in New Zealand. New Zealand Journal of Marine and Freshwater Research 50:277–290

Iftekhar MS, Polyakov M, Ansell D, Gibson F, Kay GM (2017) How economics can further the success of ecological restoration. Conservation Biology 31:261–268

Kimoto C, DeBano SJ, Thorp RW, Rao S, Stephen WP (2012) Investigating temporal patterns of a native bee community in a north American bunchgrass prairie. Journal of Insect Science 12:1–23

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings: Biological Sciences 274: 303–313

Kovács-Hostyánszki A, Haenke S, Batáry P, Jauker B, Báldi A, Tscharntke T, Holzschuh A (2013) Contrasting effects of mass-flowering crops on bee pollination of hedge plants at different spatial and temporal scales. Ecological Applications 23:1938–1946

Kruskall JB, Wish M (1978) Multidimensional scaling. Sage Publications, Beverly Hills, California

Kuhlman M, Burrows S (2017) Checklist of bees (*Apoidea*) from a private conservation property in west-Central Montana. Biodiversity Data Journal 5:1–26

LeBuhn G, Droege S, Connor EF, Gemmill-Herren B, Potts SG, Minckley RL, et al. (2013) Detecting insect pollinator declines on regional and global scales: detecting pollinator declines. Conservation Biology 27:113–120

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. Bioscience 56:311–323

Malfi RL, Crone E, Williams N (2019) Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies. Oecologia 191:377–388

Mattila HR, Otis GW (2006) Influence of pollen diet in spring on development of honey bee (Hymenoptera: Apidae) colonies. Journal of Economic Entomology 99:604–613

McCune B, Grace JB, Urban DL (2002) Analysis of ecological communities. 1st edition. Gleneden Beach, Oregon: MjM Software Design

McCune B, Mefford MJ (2006) PC-ORD: multivariate analysis of ecological data. MjM Software, Gleneden Beach, Oregon

Melathopoulos AP, Cutler GC, Tyedmers P (2015) Where is the value in valuing pollination ecosystem services to agriculture? Ecological Economics 109:59–70

Michener CD (2007) The bees of the world. 2nd edition. Johns Hopkins University Press, Baltimore, Maryland

Moquet L, Mayer C, Michiz D, Jacquemart AL (2015) Early spring floral foraging resources for pollinators in wet heathlands in Belgium. Journal of Insect Conservation 19:1–12

Morandin LA, Kremen C (2013) Bee preference for native versus exotic plants in restored agricultural hedgerows. Restoration Ecology 21:26–32

Nagle G (2007) Evaluating 'natural channel design' stream projects. Hydrological Processes 21:2539–2545

Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212

National Water Quality Inventory: Report to Congress (2017) EPA 841-R-16-011) National water quality inventory. Environmental Protection Agency, Washington, D.C.

NOAA (1981- 2010) National Climatic Data Center https://catalog.data.gov/dataset/u-s-hourly-climate-normals-1981-2010 (accessed 18 Dec 2019)

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution 25:345–353

Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennett D, Wright A, Critchley CNR, Sherwood A (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 121: 479–494

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing, R. Vienna, Austria. https://www.R-project.org/

Rathcke B, Lacey EP (1985) Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179–214

Reddersen J (2001) SRC-willow (*Salix viminalis*) as a resource for flower-visiting insects. Biomass and Bioenergy 20:171–179

Reilly JR, Artz DR, Biddinger D, Bobiwash K, Boyle NK, Brittain C, et al. (2020) Crop production in the USA is frequently limited by a lack of pollinators. Proceedings of the Royal Society B 287:1–8

Rockwell SM, Stephens JL (2018) Habitat selection of riparian birds at restoration sites along the Trinity River, California. Restoration Ecology 26:767–777

Roof SM, DeBano SJ, Rowland MM, Burrows S (2018) Associations between blooming plants and their bee visitors in a riparian ecosystem in eastern Oregon. Northwest Science 92:119–135

Rotheray EL, Osborne JL, Goulson D (2017) Quantifying the food requirements and effects of food stress on bumble bee colony development. Journal of Apicultural Research 56:288–299

Roulston TAH, Cane JH, Buchmann SL (2000) What governs protein content of pollen: pollinator preferences, pollen–pistil interactions, or phylogeny? Ecological Monographs 70:617–643

Rowland MM, Bryant LD, Johnson BK, Noyes JH, Wisdom MJ, Thomas JW (1997) Starkey project: history, facilities, and data collection methods for ungulate research USFS PNW-GTR-396. United States Forest Service, Washington, D.C.

Saunders ME (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. Insect Conservation and Diversity 11:13–31

Schulz TT, Leininger WC (1990) Differences in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43:295–299

Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana, Illinois

Sih A, Baltus M-S (1987) Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology 68:1679–1690

Silverman NL, Allred BW, Donnelly JP, Chapman TB, Maestas JD, Wheaton JM, White J, Naugle DE (2018) Low-tech riparian and wet meadow restoration increases vegetation productivity and resilience across semiarid rangelands. Restoration Ecology 27:269–278

Smith C, Weinman L, Gibbs J, Winfree R (2019) Specialist foragers in forest bee communities are small, social or emerge early. Journal of Animal Ecology 88:1158–1167

Smith DiCarlo LA, DeBano SJ, Burrows S (2020) Arid grassland bee communities: associated environmental variables and responses to restoration. Restoration Ecology 28:A54–A64

Stanford B, Holl KD, Herbst DB, Zavaleta E (2020) In-stream habitat and macroinvertebrate responses to riparian corridor length in rangeland streams. Restoration Ecology 28:173–184

Sweeney BW, Bott TL, Jackson JK, Kaplan LA, Newbold JD, Standley LJ, Hession WC, Horwitz LJ (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proceedings of the National Academy of Sciences 101:14132–14137

Tukey JW (1949) Comparing individual means in the analysis of variance. Biometrics 5:99–114

Weiner CN, Hilpert A, Werner M, Linsenmair KE, Blüthgen N (2010) Pollen amino acids and flower specialisation in solitary bees. Apidologie 41:476–487

Weissel N, Mitesser O, Poethke HJ, Strohm E (2011) Availability and depletion of fat reserves in halictid foundress queens with a focus on solitary nest founding. Insectes Sociaux 59:67–74

Wender BW, Harrington CA (2004) Flower and fruit production of understory shrubs in western Washington and Oregon. Northwest Science 78:124–140

White J, Son Y, Park Y-L (2009) Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) adults. Journal of Economic Entomology 102:2026–2032

Wickham H (2016) Ggplot2: elegant graphics for data analysis. Springer-Verlag, New York. https://ggplot2.tidyverse.org

Williams NM (2011) Restoration of nontarget species: bee communities and pollination function in riparian forests. Restoration Ecology 19:450–459

Williams NM, Minckley RL, Silveira FA (2001) Variation in native bee faunas and its implications for detecting community changes. Conservation Ecology 5:1–21.

Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93:1049–1058

Winfree R (2010) The conservation and restoration of wild bees: wild bee conservation. Annals of the New York Academy of Sciences 1195:169–197

Wohl E, Lane SN, Wilcox AC (2015) The science and practice of river restoration. Water Resources Research 51:5974–5997

Wondzell SM, Diabat M, Haggerty R (2019) What matters most: are future stream temperatures more sensitive to changing air temperatures, discharge, or riparian vegetation? Journal of the American Water Resources Association 55:116–132

Zar JH (1998) Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey

Supporting Information

The following information may be found in the online version of this article:

Table S1: Number of bees of each species collected on forbs, shrubs, and trees in 2018 and 2019.
Table S2: Key to bee and plant species identified in monthly plant and bee networks as depicted in Figure 5.
Table S3: Bee species correlated with plant ordination axes 1, 2, and 3 (species with $r^2 > 0.10$ are highlighted in grey); non-metric multidimensional scaling (NMDS) ordinations are shown in Figure 7.
Figure S1: Foraging habits of 35 bee species represented by 10 or more individuals.

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