Floral Guilds of Bees in Sagebrush Steppe: Comparing Bee Usage of Wildflowers Available for Postfire Restoration

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ABSTRACT: Healthy plant communities of the American sagebrush steppe consist of mostly wind-pollinated shrubs and grasses interspersed with a diverse mix of mostly spring-blooming, herbaceous perennial wildflowers. Native, nonsocial bees are their common floral visitors, but their floral associations and abundances are poorly known. Extrapolating from the few available pollination studies, bees are the primary pollinators needed for seed production. Bees, therefore, will underpin the success of ambitious seeding efforts to restore native forbs to impoverished sagebrush steppe communities following vast wildfires. This study quantitatively characterized the floral guilds of 17 prevalent wildflower species of the Great Basin that are, or could be, available for restoration seed mixes. More than 3800 bees representing >170 species were sampled from >35,000 plants. Species of *Osmia*, *Andrena*, *Bombus*, *Eucera*, *Halictus*, and *Lasioglossum* bees prevailed. The most thoroughly collected floral guilds, at *Balsamorhiza sagittata* and *Astragalus filipes*, comprised 76 and 85 native bee species, respectively. Pollen-specialists dominated guilds at *Lomatium dissectum*, *Penstemon speciosus*, and several congenerics. In contrast, the two native wildflowers used most often in sagebrush steppe seeding mixes—*Achillea millefolium* and *Linum lewisii*—attracted the fewest bees, most of them unimportant in the other floral guilds. Successfully seeding more of the other wildflowers studied here would greatly improve degraded sagebrush steppe for its diverse native bee communities.

Index terms: Apoidea, Asteraceae, Great Basin, oligolecty, restoration

INTRODUCTION

The American sagebrush steppe grows across the basins and foothills over much of the Great Basin (Figure 1) and adjoining ecoregions of the US Intermountain West. This arid biome is characterized by cold winters and a spring growing season, followed by hot, generally dry summers and autumns (West 1983). Soil moisture largely comes from winter storms and melting snowpack. These climatic conditions give rise to similar plant associations elsewhere (e.g., the Iranian plateau) that are also dominated by mostly wind-pollinated shrubs (esp. *Artemisia* spp.) and perennial bunchgrasses (Takhtajan 1986), as well as many showy, bee-pollinated perennial wildflowers. Bee faunas of sagebrush steppe and their floral host relations are undercollected and poorly known relative to neighboring biomes, such as the Mojave Desert to the south (e.g., Cane et al. 2013) or the montane biota of the Rocky and Sierra Nevada Mountains to the east and west, respectively (Figure 1).

Fire regimes in the American sagebrush steppe have dramatically changed over the past century. They are fueled by the highly flammable Eurasian annual, cheatgrass (*Bromus tectorum* L.), and exacerbated by climatic shifts (Davies et al. 2011). Formerly, natural wildfire burned a given locale once every several decades to several centuries. Now, where cheatgrass is a dominant groundcover, fires burn once or twice a decade (Whisenant 1990). Massive wildfires are burning record acreages of the American West; two fires in 2007 together burned >500,000 ha of shrub-steppe and juniper woodlands across Idaho, Nevada, and Utah (Chambers and Pellant 2008). In some years (e.g., 2015), these have largely been dramatic forest fires, but usually these fires are burning at lower elevations in pinyon-juniper woodlands and adjoining shrub-steppe.

In the weeks following wildfire, federal land management agencies are required to seed burned acreages. Seed mixes are prescribed by Burned Area Emergency Response (BAER) teams. Their primary objective is to stabilize and vegetate bare soil surfaces. Until the past decade, these seed mixes comprised sagebrush and a small number of Eurasian grasses and forbs chosen because their seed is cheap and commercially plentiful, the plants are edible for livestock, and they establish reliably to withstand competition from cheatgrass. In recent years, more seed of native grasses and forbs are used in these postfire seed mixes. Information about propagating native forbs destined for seed production is compiled in Fact Sheets and Plant Guides issued by the USDA-NRCS Plant Materials Centers of the region (http://www.greatbasinnpp.org/plant-guides-nrcs). Nonetheless, the bulk of forbs seeded after Intermountain wildfires continue to be Eurasian species (reviewed in Gray and Muir 2013). The only two

Figure 1. Map of the hydrographically defined Great Basin and surrounding geographic ecoregions and features. Source with permission: Kmusser, own work, elevation data from Shuttle Radar Topography Mission (SRTM); all other features from the National Atlas of the United States. Rand McNally, The New International Atlas, 1993, used as reference.

commonly seeded native wildflowers are western yarrow (*Achillea millefolium*) and Lewis' flax (*Linum lewisii*). Yarrow and flax constituted 77% of the native wildflower seed bought during a recent BLM Consolidated Seed Buy (2014); the seed of other native wildflowers only constituted 3% of the 500,000 kg of all seed bought (shrubs, grasses, forbs).

More recently, an additional criterion was imposed for choosing among wildflower species to use in postfire rehabilitation. In April 2015, the White House issued a National Pollinator Health Strategy (Pollinator Health Task Force 2015). Among its many provisions, the Strategy directs federal land management agencies to enact or adapt programs that benefit native bees and managed honey bees. In response, the Bureau of Land Management (BLM) ad-

opted this goal: "A major emphasis is the use of at least one pollinator-friendly native plant in all post-fire re-vegetation efforts."

The "pollinator-friendliness" of different wildflowers can be compared by the relative abundance and diversity of wild bees visiting their flowers across plant communities of a region. For the Intermountain West, our knowledge about bees in these floral guilds has been largely fragmentary, anecdotal, or extrapolated from other regions, with few quantitative estimates of bees' relative abundances at bloom or their intensities of floral use. A floral guild is a list of animal species (in our case, bees), found visiting a particular plant species sampled across much of its range, akin to the definition for herbivore guilds (Hawkins and MacMahon 1989). To distinguish strays from regular visitors, some objective measure of abundance is needed, too. Although these guilds are sometimes called "pollinator guilds," that implies knowing that visitors do indeed pollinate the flowering species. Among the sagebrush steppe native wildflowers thus far available, or ready for inclusion, in rehabilitation seed mixes, most do indeed benefit from, or require, pollinating bees for fruit and seed set (Cane 2008). However, species-specific pollination efficacies of bee species in this fauna are rarely known.

Our objective here was to compare the floral guilds of bees at those native forbs whose seed is available for postfire rehabilitation following sagebrush steppe fire in the Great Basin and adjoining regions. Are currently seeded forbs "bee-friendly," and if not, which ones are superior among the available choices? We characterize a given wildflower's floral guild in terms of both the list of bee species visiting that species' flowers as well as each bee species' relative abundance at that wildflower species. Bee abundance at bloom is a comparative measure for the wildflower's attractiveness or "friendliness," measured as bees per 100 flowering plants surveyed. Knowing abundance allows us to sort strays from regular, frequent visitors in the lists of bees composing a particular floral guild. Most sites were sampled primarily for the purpose of evaluating the response of resident bee communities and native wildflowers to wildfires over a chronosequence of years, which we will be reporting in detail elsewhere.

METHODS

Sampling Protocols for Bees

Local guilds of floral visitors were sampled quantitatively along a "walking scan census" during which we individually netted bees at flowers of sequentially inspected plants at each site. This method is effective, systematic, sensitive, repeatable, and largely unbiased for experienced collectors (Cane et al. 2013). The prevalent wildflowers of the American sagebrush steppe are mostly spring-blooming herbaceous perennial plants. Spaced by their arid habitat, individuals are often discrete, making them easy to confidently count and their bees easy to see and then collect by net. We walked haphazard transects where conspecific plants were abundant, or sampled from every individual where they were sparse. Two experienced collectors usually walked a given site together, visiting and counting sequential flowering plants of the target floral host along different routes. We did not wait for bees to arrive at flowers, nor did we sample any plant twice. Repeatedly sampling the same site over the course of the day would have been desirable (as in Cane et al. 2013), but lingering at one site would have precluded scouting for and sampling others at widely scattered, often remote reaches of the Great Basin during the seasonally brief windows of periodically favorable weather for bee activity. Bees were netted at first viewing to yield a single "snapshot" of guild composition and relative abundance at each location.

Occasionally, irregularities required practical accommodation. On rare occasions, a bee escaped being netted. Our familiarity with these bee faunas usually allowed us to recognize the missed bee as to genus and appearance (e.g., small greenish *Osmia*). After the formal sample, we would then seek a similar-looking replacement individual, in this case a small greenish *Osmia*. The alternative was to ignore the missed bee and subtract some ill-defined number from the count of plants already examined. For 14% of our samples, bees were netted systematically, but without counting host plants. These cases were either trial samples from early in the project, or where counting plants proved impractical (e.g., shifting weather conditions, tiny plant populations). In a few cases, 2–3 floral hosts could be sampled concurrently at the same location, so there are more surveys than sites sampled.

We surveyed bees at multiple populations of 17 wildflower species (Table 1). Bees were taken from late April through June at 219 locations scattered over 340,000 km^2 (130,000 mi^2), an area the size of California. Plants are vouchered with the Intermountain Herbarium at Utah State University. We are not entirely confident of our plant identifications within the difficult genera *Lupinus* and *Sphaeralcea*, whose variable species in the sagebrush steppe are often ill-defined and apparently hybridize.

From experience, we expected few bees at yarrow and flax. However, sparse or depauperate local guilds could also reflect degraded plant or bee communities, or collecting during drought or poor weather. As a positive control, we always concurrently sampled bees at another co-flowering native forb at the same location, one known to attract bees. Depending on circumstances, these paired forbs were *Chaenactis douglasii, Crepis acuminata, Phacelia hastata,* or *Sphaeralcea* spp. By this approach, we could distinguish truly sparse guilds at yarrow or flax from unfavorable conditions for bee activity.

Bee Identification

Bees were identified to species using published keys and comparison with authoritatively identified specimens in the extensive collections at the USDA-ARS Pollinating Insect Research Unit in Logan, Utah, where our specimens are deposited. No comprehensive key exists for western *Osmia*, a taxonomically difficult yet often abundant and diverse bee genus at many Great Basin wildflowers. For another Great Basin denizen, *Eucera,* an illustrated key to species was developed and made public for this project (www.discoverlife.org). Single legs of some bee species were taken

Table 1. Summary of survey data from walking scan census method used to quantify bee density at each wildflower host. Taxa alphabetized by family, then genus name.

Wildflower Species	Bees Collected	Plant Count	No. Sites Surveyed	States Surveyed
Apiaceae				
Lomatium dissectum (Nutt.) Math. & Const.	82	295	5	ID,NV,UT, WY
Lomatium triternatum (Pursh) Coult. & Rose	133	1309	9	ID,OR,WY
Asteraceae				
Achillea millefolium L.	23	1628	5	ID,UT
Balsamorhiza hookeri Nutt.	204	2657	11	NV,UT
Balsamorhiza sagittata (Pursh) Nutt.	797	5513	41	T
Chaenactis douglasii (Hook.) H. & A.	25	427	4	ID,UT
Crepis acuminata Nutt.	28	580	3	ID,UT
Boraginaceae				
Phacelia hastata Dougl.	48	169	3	UT
Fabaceae				
Astragalus filipes Torr.	1097	11399	61	CA,ID,NV, OR,UT
Dalea ornata (Dougl.) Barneby, *D. searlsiae* (Gray) Barneby	103	751	4	ID,OR,UT
Lupinus argenteus Pursh	110	1624	7	NV,OR,UT
Linaceae				
Linum lewisii (Pursh) Eat. & Wright	70	2519	7	ID,UT
Malvaceae				
Sphaeralcea munroana (Dougl.) Spach, *S. grossularifolia* (H. & A.) Rydb.	639	4353	37	ID,NV,UT, WY
Plantaginaceae				
Penstemon radicosus A. Nels.	98	1623	7	ID,UT
Penstemon speciosus Dougl.	64	789	4	NV

for molecular bar-coding (International Barcode of Life, www.ibol.org) to identify conspecifics, to help sort through species complexes, and to contribute to the compilation of a robust molecular dataset of bees, especially *Osmia*, for the American West.

Nonetheless, a few bees in this study were identified to genus but not species, sometimes because as a singleton, it represented the only species of that genus taken at a given host (e.g., *Melecta*), but more often, because of the sheer difficulty of the genus (e.g., *Osmia, Andrena*). Consequently, our species counts somewhat underestimate true faunal richness. More importantly, many of our guilds remain undersampled; additional surveys will undoubtedly extend the species list for many of these floral guilds (e.g., *Phacelia hastata*).

We treated one bee subgenus, *Micrandrena,* as separate from its genus *Andrena*, because those bees represent important and recognizable members of the floral guilds found only at *Lomatium* in our surveys. In addition, we included the solitary pollen wasp *Pseudomasaris vespoides* (Cresson) because it is an often abundant oligolectic pollinator of many *Penstemon* species.

RESULTS

From 2004 to 2015, we collected 3824 bees (and *Pseudomasaris* wasps) representing more than 170 species in 27 genera across the Intermountain West. Floral guilds were mostly sampled in sagebrush steppe habitat, sometimes in ecotones with pinyon-juniper woodlands, and rarely at higher elevations in forest openings (several *Lomatium* and *Lupinus* surveys). A total of 187 walking scan surveys were completed for the 17 plant species (range 3–61 surveys), sampling over 35,000 plants (range 169–11399 plants), and collecting 3500 bees to calculate bee density (Table 1, Figure 2). Plants at an additional 32 locations were sampled without counting individuals and added to the percentage representation of bee genera in each floral guild (Table 2).

We collected most widely and thoroughly at *Astragalus filipes*, *Balsamorhiza sagittata, B. hookeri,* and two species of *Sphaeralcea* (Table 1). Bee species and their abundances at *A. filipes, B. hookeri,* and *B. sagittata* are compiled in the Appendix. Pollination and pollinators of *Sphaeralcea* will be the subject of a later manuscript. These three

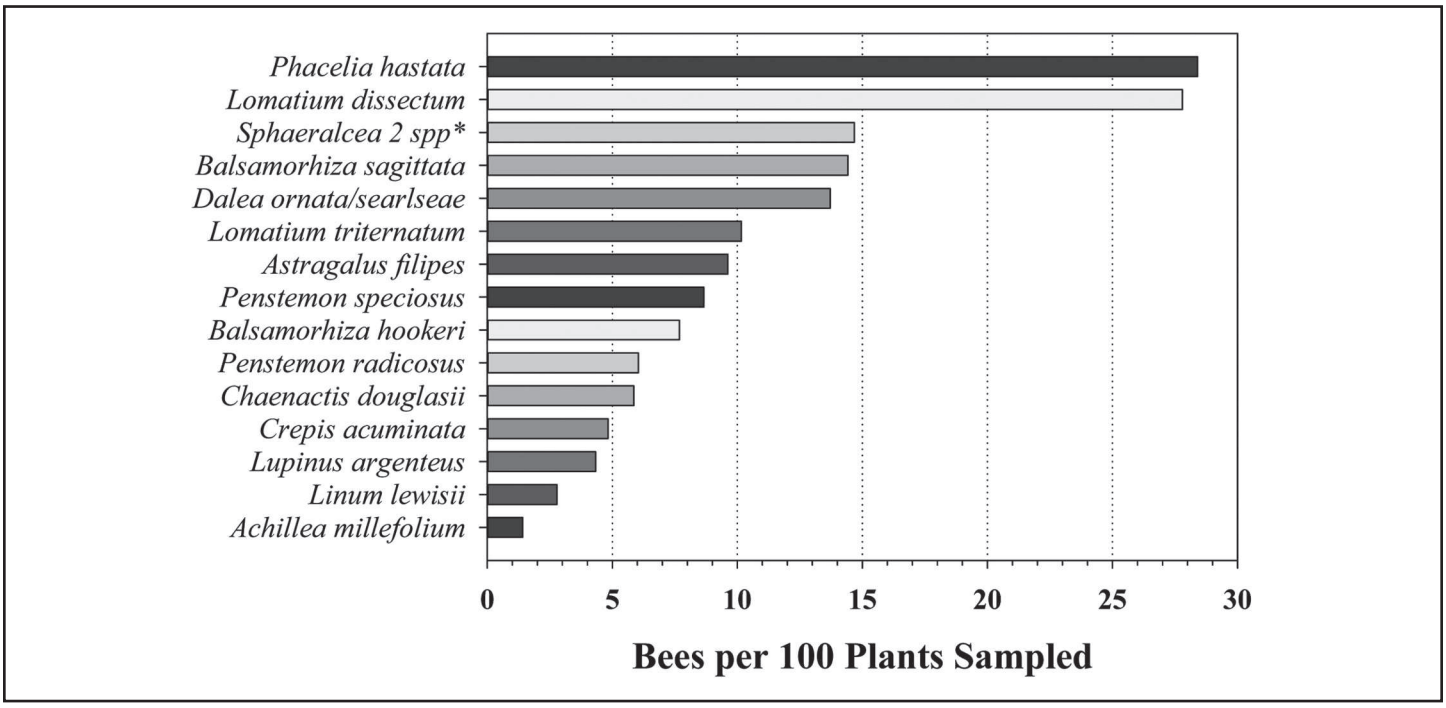

Figure 2. The average densities (bees / 100 plants) of all native bees visiting flowering individuals of each of the wildflower hosts sampled at two or more sites (refer to Table 2 for number of sites sampled). ****Sphaeralcea grossularifolia* **and ***S. munroana*****.**

taxa, being particularly common, widespread, and recognizable from a distance, were the focal species of our postfire studies of bee and wildflower communities (being reported elsewhere). Generic richness of bees was greatest at these three taxa (17, 15, and 19 bee genera, respectively), partly a consequence of our intensive sampling effort (68, 52, and 37 sites, respectively) (Table 2). Nonetheless, some other forb species that we sampled far less thoroughly also hosted many bee genera. For instance, *Phacelia hastata* was sampled at just seven sites, yet we found 14 genera of bees visiting its flowers (plus a pollen wasp, *Pseudomasaris*) (Table 2). Similarly, just eight surveys at two *Dalea* species yielded 13 bee genera (Table 2). Species lists of bees at these taxa will certainly grow with more collecting. Nine surveys at >2500 flax plants yielded 12 bee genera. The fewest genera of bees were taken at yarrow (three bee genera) and *Lomatium dissectum* (five genera) from five and 11 surveys, respectively (Table 2).

Two bee genera serve to illustrate the extent of sharing of floral hosts. In the Great Basin bee fauna, *Bombus* and *Eucera* are widespread, often abundant, polylectic bee genera. Their species are readily identified, unlike *Osmia* and *Andrena*. We compiled their data from all net samples (including two samples from *Hedysarum boreale* Nutt.) at both wildland and several cultivated populations (Tables 3, 4). Ten bumble bee species were collected visiting 11 wildflower species (Table 3). Specifically, *B. centralis*, *B. huntii,* and *B. fervidus* were found visiting nearly half of the 17 forb species sampled. Two legumes, *Astragalus filipes* and the two *Dalea* species, hosted the most bumble bee species (8 and 7, respectively). So-called "long- horned" bees (*Eucera*) were collected from 10 wildflower species (Table 4). Specifically, *E. actuosa* and *E. edwardsii* were collected from nearly half of the 17 forb species sampled. The species *E. frater* was most commonly found visiting *A. filipes* (200 of the 217 individuals collected) and was this plant's most common *Eucera* visitor (200 of 273 *Eucera* individuals collected) (Appendix).

Honey bees were absent from all but a few sites. Feral colonies do not persist in these regions, and managed apiaries either are absent or mostly placed out later in the summer after the forbs surveyed here have finished blooming.

DISCUSSION

Membership patterns among pollinator guilds are comparatively discussed using various conceptual frameworks. Traits commonly used to characterize plant-pollinator interactions include: seasonality, bee and flower morphologies, and floral host specialization, as well as floral reward characteristics and phylogenetic history (Linsley 1958; Real 1983). Our research was motivated by conservation objectives for bee and wildflower communities of the American sagebrush steppe. Consequently, our discussion is organized around comparative diversities and abundances of wild bees of the 17 wildflowers that we surveyed. Bee diversity and abundance together define the degree to which a given wildflower species is "pollinator-friendly," which is the mandate of the new Presidential directive. In practical terms, Great Basin land managers cannot restore entire plant communities through reseeding, but must choose to buy from among a small set of commercially available seed species. All 17 wildflowers have been cultivated and many are commercially available. Among the floral guilds that we surveyed, some were populous; others were not. Some

Table 2. Percentages of bee genera comprising floral guilds at target wildflower species. To aid visual comparisons, greater abundance values are color-coded by darker shading, grouped within a floral guild into five incrementing bins, as shown in the legend. Formal surveys and net samples are included. An empty cell indicates that no individuals of that bee genus were collected from that particular floral host. The subgenus *Micrandrena* is treated at the generic level (refer to methods). The genus *Pseudomasaris* consists of pollen-collecting wasps (Vespidae).

Plant Species / Bee Genus	*Achillea millefolium*	*Astragalus filipes*	*Balsamorhiza hookeri*	*Balsamorhiza sagittata*	*Chaenactis douglasii*	*Crepis acuminata*	*Dalea ornata*, *D. searlsiae*
Number Sample Sites	(*n* = 5)	(*n* = 68)	(*n* = 12)	(*n* = 52)	(*n* = 9)	(*n* = 14)	(*n* = 8)
Agapostemon		0.5	1.0	3.5	5.9	7.7	2.4
Andrena	34.8	0.8	20.8	16.5	5.9	10.6	15.2
A. (*Micrandrena*)							
Anthidium		2.6					12.0
Anthophora		1.9					0.8
Apis		0.1		1.0			3.2
Ashmeadiella		0.2		0.1			0.8
Bombus		13.5	1.9	0.7	1.5	10.6	16.0
Ceratina				3.2	13.2		
Colletes	4.3		0.5			2.9	9.6
Diadasia							
Dianthidium					1.5		
Dufourea							
Epeolus							
Eucera		32.8	29.5	14.6		1.9	28.0
Habropoda		0.1		0.2			
Halictus	60.9	1.9	2.4	7.8	16.2	9.6	1.6
Hoplitis		3.3		0.7		3.8	0.8
Hylaeus							
Lasioglossum		1.7	6.8	7.8	19.1	7.7	7.2
Megachile		0.1		0.2	7.4	1.9	2.4
Melecta		0.4	0.5	0.6			
Melissodes							
Nomada		0.3	0.5	6.4		2.9	
Osmia		39.7	36.2	36.7	29.4	40.4	
Panurginus							
Perdita		0.1					
Pseudomasaris							
Shade legend:	≤ 5%	>5–10%	>10–25%	>25–50%	> 50%		

were taxonomically diverse; others were depauperate. Some featured prevalent oligoleges, others attracted only floral generalists. Most combinations of these states are exemplified by these 17 floral guilds. We discuss flax and yarrow last, as they proved to be the least friendly to pollinators despite their prevalence in postfire seeding mixes used today.

Table 2 (*Continued*). Percentages of bee genera comprising floral guilds at target wildflower species. To aid visual comparisons, greater abundance values are color-coded by darker shading, grouped within a floral guild into five incrementing bins, as shown in the legend. Formal surveys and net samples are included. An empty cell indicates that no individuals of that bee genus were collected from that particular floral host. The subgenus *Micrandrena* is treated at the generic level (refer to methods). The genus *Pseudomasaris* consists of pollen-collecting wasps (Vespidae).

Linum lewisii	*Lomatium dissectum*	*Lomatium triternatum*	*Lupinus argenteus*	*Penstemon radicosus*	*Penstemon speciosus*	*Phacelia hastata*	*Sphaeralcea grossularifolia*
							S. munroana
(*n* = 9)	(*n* = 11)	(*n* = 10)	(*n* = 12)	(*n* = 7)	(*n* = 8)	(*n* = 7)	(*n* = 37)
1.3			2.2			1.1	12.1
7.8	55.2	32.1	5.6	2.0		2.2	0.3
	40.3	51.1					
						7.7	0.3
			1.1	4.1	2.7	2.2	0.8
1.3							0.2
1.3			47.2	1.0	8.1	14.3	0.3
1.3		0.7			0.9		0.6
							10.3
2.6							36.8
						17.6	
							0.2
5.2			9.0	15.3		11.0	7.4
				2.0			
28.6	0.7	4.4	6.7	1.0	11.7	1.1	9.9
			6.7	4.1	1.8	6.6	
						3.3	
22.1	2.2	8.0	12.4		3.6	1.1	12.7
3.9			1.1			2.2	1.9
							0.2
							3.3
2.6	1.5	1.5					0.6
22.1		0.7	7.9	68.4	51.4	15.4	0.9
		1.5					
							1.4
				2.0	19.8	14.3	

Table 3. Compilation of collected individual bees representing species of bumblebee (*Bombus*) netted at the different floral hosts reported here. Numbers represent the sum of individuals from all collections, with more intensive collecting efforts often represented by more bees. A floral host or bee species represented by a single bee individual is not reported. "c" denotes collections at cultivated plants only (no counts available).

Floral Host	*Bombus* Species										Sum
	bifarius	*californicus*	*centralis*	*fervidus*	*griseocollis*	*huntii*	*insularis*	*morrisoni*	*nevadensis*	*rufocinctus*	
Astragalus filipes	2	2	19	9		53	1		18	6	110
Balsamorhiza hookeri			1			2	1				4
Balsamorhiza sagittata				1			2				3
Crepis acuminata	6		1								7
Dalea ornata/searlseae	5		2	5	3	1		5	c		21
Hedysarum boreale			3			5		c	1		9
Lupinus argenteus	5		5			2					12
Penstemon radicosus				1							1
Penstemon speciosus			c	c	c	c					
Phacelia hastata	8				1					2	11
Sphaeralcea sp.				1		2					3
Sum	26	2	29	17	3	65	4	5	19	8	140

"c" = taken at cultivated plants only

Table 4. Compilation of collected individual bees representing species of *Eucera* bee netted at the different floral hosts reported here. Counts of males and females are combined. Details as in Table 3.

Floral Host	*Eucera* Species					Sum
	actuosa	*edwardsii*	*frater*	*fulvitarsis*	*lutziana*	
Astragalus filipes	2	46	200	25		273
Balsamorhiza hookeri	15	38	8			61
Balsamorhiza sagittata	16	33	5	4		58
Dalea ornata		2				2
Linum lewisii				4		4
Lupinus argenteus	1	4	3			8
Penstemon radicosus	1	7	1	3		12
Phacelia hastata	6	4				10
Phlox longifolia				7		7
Sphaeralcea sp.	2	25			4	31
Sum	43	159	217	43	4	466

Taxonomic Diversity of Guilds

Guilds with Few Bee Genera

Among surveyed wildflowers, *Achillea, Lomatium,* and *Penstemon* attracted bees representing the fewest genera (Table 2, Figure 3). In each case, >50% of the floral visitors belong to a single bee genus (Table 2) represented by only a few species. These plant hosts fall into two contrasting groups. The bees at *Lomatium* and *Penstemon* consist largely of sometimes abundant taxonomic pollen specialists (oligoleges) restricted to those genera. In contrast, *Achillea* was sparsely visited, and only by broad taxonomic generalists (polyleges).

Four species of *Lomatium* hosted bees of the Holarctic genus *Andrena*. They predominated numerically at both *L. dissectum* (95% of bees caught) and *L. triternatum* (84% of bees), often in great abundance (Figures 2, 3). These *Andrena* likewise prevailed at a sampled population each of *L. ambiguum* (Nutt.) Coult. & Rose and *L. nudicaule* (Pursh) Coult. & Rose. From five samples at *L. grayi* Coult & Rose, several species of sweat bees (*Halictus, Lasioglossum*) were also common. Both *Bombus* and *Osmia* bees were absent. *Andrena* is the largest genus of bees (1526 named species), consisting entirely of nonsocial, ground-nesting species. Most species are vernal with a single annual generation (univoltine) (Linsley 1958). Several species of one *Andrena* subgenus, *Micrandrena*, particularly *A. microchlora*, composed 45% of the *Andrena* fauna at *L. dissectum* (Table 2). These particular *Micrandrena* seem to be oligoleges for *Lomatium* (Ribble 1968), a difficult contention to prove. Nonetheless, these small bees were rarely absent from surveyed *Lomatium* sites, a remarkable ubiquity given that these sites are often widely separated by mountain ranges or desert basins. Like *Lomatium*, *Micrandrena* are endemic to the western United States. Such pollinators are important for *L. dissectum*, as without bee visitation, it rarely sets any seed (J. Cane, unpubl. data). Where cultivated for seed production, we have only seen abundant honey bees and sometimes sweat bees visiting *L. dissectum* and *L. grayi*, followed by good seed sets (Shock et al. 2012). We have experimental evidence that individual *L. dissectum* plants readily survive the heat of sagebrush steppe wildfires (Love and Cane 2016), as should its fauna of entirely ground-nesting bees (Cane and Neff 2011). As a consequence, both bee and plant should survive wildfire to reproduce the following spring. Given the genus' shared pollinator fauna, we expect that where one *Lomatium* species already exists, any additional seeded congenerics will be pollinated by resident *Andrena*.

The two sampled species of *Penstemon* were likewise visited by a few species of mostly specialist bees (and one pollen wasp) (Table 2). The genus *Penstemon* has more species than any other genus endemic to North America. Unlike *Lomatium,* penstemons collectively present a great variety of flower sizes and colors (Nold 1999). Hence, there is no one universal pollinator for the genus. Two species of bee are oligoleges of some penstemons, *Osmia brevis* and the less common *O. penstemonis* Ckll., as is a pollen wasp, *Pseudomasaris vespoides* (e.g., Tepedino et al. 1999). All three visited *P. speciosus*. At the few sites where we sampled *P. radicosus*, *O. brevis* was likewise, a common visitor.

Nesting habits of these two oligolectic *Osmia* are unknown, but they probably nest in the ground (Cane et al. 2007). If true, then they are free to nest in the treeless sagebrush steppe where *P. speciosus* grows. However, the typically shallow nests of *Osmia* (Cane et al. 2007) may be susceptible to soil heating by wildfires (Cane and Neff 2011), as would be true for the surface nests of *P. vespoides*.

Only in our laboratory's common garden did we encounter bumblebees at *P. speciosus*, where workers of four species avidly visited its flowers (Table 3). In one commercial seed field, numerous *Anthophora* bees were seen at its flowers too. All of these polylectic bees sonicated the flowers for pollen. Foragers from a hive of honey bees placed amid rows of *P. speciosus* on one farm never visited its flowers. Pollinators are necessary for reproduction; without bees (or manual pollination), *P. speciosus* sets capsules with little or no seed (Cane, unpubl. data).

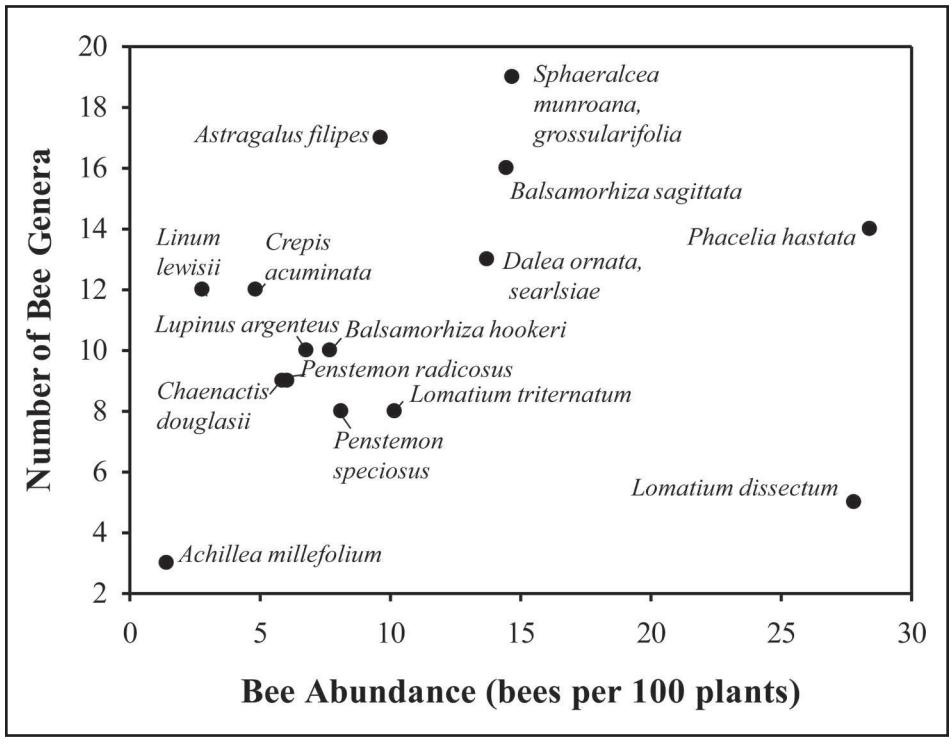

Figure 3. Scatterplot summarizing abundances of bees at flowers and the richness of bee genera attracted, mapped by floral guild. Note that evenness is not portrayed, but can be seen in Table 2.

Populous, Diverse Floral Guilds

Other common, widespread forbs of the American sagebrush steppe attract diverse bees in abundance, particularly arrowleaf and Hooker's balsamroots (*Balsamorhiza sagittata* and *B. hookeri*, respectively), basalt milkvetch (*Astragalus filipes*) and *Phacelia hastata* (Table 2, Figure 2, Appendix). These four forb species are widespread and locally frequent. Both *B. sagittata* and *A. filipes* require pollinators for seed set (Cane 2005; Watrous and Cane 2011), and each species is visited by a remarkably rich fauna of bees (Appendix). Species of *Astragalus* outnumber those of any other flowering genus in the Intermountain ecoregion (156 species) (Barneby 1989). Bee taxa we found visiting *A. filipes* match those of the several other studied species (Green and Bohart 1975; Clement et al. 2006). Bees visiting *A. filipes* represent 23% ($n = 32$) of all 139 named species of *Osmia* bees in the United States (Cane et al. 2007), plus six more unnamed species (Appendix), an extraordinary diversity for any one wildflower. The genus *Osmia* itself is remarkably diverse, ubiquitous, and frequent in many floral guilds of the Great Basin, particularly at papilionaceous legumes. The few species of *Balsamorhiza*, all endemic to the western United States, support several western *Osmia* species (*O. californica* and *O. montana*) (Rust 1974; Cane 2005). They are mesolectic (sensu Cane and Sipes 2007), meaning that these bees are associated with a single large plant family, in this case the Asteraceae (Rust 1974; Cripps and Rust 1989).

We expect that some of our undercollected forb species will also be valuable bee plants. From only 169 plants, we collected a diverse and abundant guild of bees visiting *P. hastata* (Table 2, Figure 2), including multiple species of *Bombus* (Table 3) and *Eucera* (Table 4). Diverse *Osmia* species, including *O. bruneri*, provision their nests with pollen taken from *Phacelia*, including *P. hastata* (Rust 1974; Cripps and Rust 1989). We found *O. bruneri* foraging at *P. hastata*, *A. filipes,* and *Lupinus argenteus*. Collectively, *P. hastata* shares native bee species with most of the wildflower species reported here.

Pollinator Sharing among Floral Guilds

Members of the same genus or even family of wildflower attracted some of the same dominant genera or species of bee. This was most evident for forbs attracting mostly oligolectic bees, notably *Lomatium* and *Penstemon*. Some of the same polylectic species of *Bombus, Osmia,* and *Eucera* found visiting *A. filipes* (Appendix) are reported in limited bee collections from five other *Astragalus* species in the region (Green and Bohart 1975; Geer et al. 1995). At the family level, *B. hookeri, B. sagittata*, *Crepis acuminata* and *Chaenactis douglasii* (all Asteraceae) were all visited by foraging *O. californica* and *O. montana.* These results illustrate that, through pollinator sharing, multiple related forb species can benefit from the bee fauna supported by any one abundant congeneric or even shared family member. For instance, where another like-flowered *Astragalus* is resident (e.g., *A. beckwithii* Torr. & Gray), seeded *A. filipes* will have a ready-made pollinator fauna, a useful consideration when choosing forbs to seed after fire. Conversely, only one of the 16 species of *Andrena* bees taken at the four *Lomatium* species was found visiting *Balsamorhiza* (Appendix), despite the two plant genera being intermingled and often flowering concurrently at multiple sample sites. This complete segregation of *Andrena* by floral host is consistent with the oligolectic nature of many *Andrena* species (Linsley 1958).

Seasonal Limits to Pollinator Sharing

The distinctive bee fauna at summer-blooming *Sphaeralcea* illustrates the importance of seasonality and community turnover for understanding membership in pollinator guilds. Bee guilds of early spring species (e.g., *Lomatium*) overlapped little with those of *Sphaeralcea* (Table 2), which flower seven or more weeks later. That time period exceeds the 2–3 week lifespans of active adult univoltine solitary bees (Linsley 1958), the prevalent bees found in our surveys. Moreover, different genera often predominate in different seasons; for instance, many *Andrena* fly early in the spring, whereas species of *Diadasia*, including the four oligoleges at *Sphaeralcea*, are summer bees (Sipes and Tepedino 2005). The exceptions in the sagebrush steppe are the primitively eusocial bees, whose nests last through much of the growing season (e.g., *Bombus, Halictus,* many *Lasioglossum*) (Linsley 1958). For example, *H. tripartitus* was frequent at both *Balsamorhiza* and *Sphaeralcea*. Their queens and workers are polylectic and have access to all of the forbs that we sampled over the growing season, which explains why these social species are frequent elements in many of the guilds that we surveyed, although not always the same species (Tables 2, 3).

Least Visited Forbs

In our surveys, yarrow and flax were the least attractive forbs for bees (Figures 2, 3). At each survey site for these two forbs, we concurrently surveyed bees at an available flowering species known to attract bees. Bees were 2–26x (median 6x) less abundant at flax than at the paired forbs; this shortfall was even more pronounced at yarrow (median 15x sparser bees, range 3–68x fewer bees at yarrow than paired forb). We doubt that either yarrow or flax could support populations of any native bee of the American sagebrush steppe, inasmuch as they attracted only a smattering of broad generalists and stray specialists of other forb species. The halictid bees that make up the majority of their floral guilds are all social; their small underground colonies require pollen for many weeks before and after the bloom of these two forbs. We saw no *Osmia* at 1628 flowering yarrow plants, and only 15 *Osmia* at 2519 flowering flax plants. Bumblebees were absent from both wildflowers (Table 3) as were species of *Eucera* bees (Table 4), although all three genera are important for most other Great Basin forbs (Table 2).

CONCLUSION REGARDING YARROW, FLAX, AND BEES

Among the diverse widespread Intermountain native forbs considered here, only two native species are seeded after most large fires in the Intermountain West, western yarrow and Lewis' flax. Much more seed

of nonnative forbs is still used (e.g., alfalfa, small burnet, forage kochia). Yarrow and flax attracted few bees, mostly social *Halictus* (Table 2), which are versatile broad floral generalists. Flax and yarrow do have other virtues that merit their inclusion in rehabilitation seed mixes for the Great Basin and adjoining ecoregions. They are easily grown commercially, and partly as a consequence, their seed is affordable. Both species are widely adapted and establish well in postfire wildland seedings. Also, yarrow seems to endure invasion by cheatgrass (Leffler et al. 2014). The bright blue flowers of flax are attractive and colorful, and in the absence of other bloom, some native bees forage at its flowers, at least for self-maintenance. Adults of small-bodied wasps and flies that parasitize other insects sometimes feed at *A. millefolium,* at least to some degree (Colley and Luna 2000), but one experimental study found its floral scent repellent to some biocontrol agents (Wäckers 2004). Some forbs evaluated here are prominently represented in diets of sage-grouse chicks (e.g., *Astragalus, Crepis*, *Phlox,* and to lesser extent, *Lomatium*) (Klebenow and Gray 1968; Drut et al. 1994), although in poorer range, sage-grouse reportedly eat small amounts of yarrow, too (Klebenow and Gray 1968). Seeded yarrow and flax can have substantial practical advantages, but their ecological benefits are limited. Every one of the 15 other wildflower species reported here, all of them either in cultivation or poised for seed farming, are better choices for feeding native bee communities of the American sagebrush steppe.

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Jim Cane has studied the nesting and pollination ecologies of native nonsocial bees of North America and elsewhere for 30 years. He has worked with pollination and pollinators of alfalfa, cranberries, blueberries, squashes, almonds, raspberries, and native seed crops used for restoration. He is currently multiplying three species of native Osmia bees for these applications. Since 1998, he has worked for the USDA-ARS Pollinating Insect Research Unit in Logan, Utah. Prior to that, he was on the faculty of Auburn University in Alabama and a postdoc at Berkeley following a PhD from the University of Kansas.

Byron Love is a PhD student at Utah State University studying the response of bees to wildfire in Great Basin sagebrush steppe. His Master's thesis at Sacramento State University in California compared the influence of urban and agricultural land uses on bee communities living in seminatural habitat along river corridors. He is also a biological technician with the USDA-ARS Pollinating Insect Research Unit in Logan, Utah, assisting Dr. Cane with his research.

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Appendix. Bee taxa collected visiting *Astragalus filipes* (ASFI), *Balsamorhiza hookeri* (BAHO) and *B. sagittata* (BASA).

Bee Family	Bee Species	*Astragalus filipes*	*Balsamorhiza hookeri*	*Balsamorhiza sagittata*
Andrenidae	*Andrena amphibola* Viereck			1
	Andrena candidiformis Viereck & Cockerell			6
	Andrena lawrencei Viereck & Cockerell		30	16
	Andrena lupinorum Cockerell			1
	Andrena merriami Cockerell			1
	Andrena nigrocaerulea Cockerell			1
	Andrena nothocalaidis Cockerell		3	
	Andrena pallidifovea Viereck		6	11
	Andrena piperi Viereck			1
	Andrena prunorum Cockerell	1		1
	Andrena sladeni Viereck			2
	Andrena sola Viereck			3
	Andrena sp.	8	3	90
	Andrena transnigra Viereck		1	2
	Perdita wyomingensis Cockerell	1		
Apidae	*Anthophora bomboides* Kirby	5		
	Anthophora edwardsii Cresson	1		
	Anthophora pacifica Cresson	1		
	Anthophora sp.	2		
	Anthophora urbana Cresson	8		
	Anthophora ursina Cresson	6		
	Apis mellifera Linnaeus	11		8
	Bombus appositus Cresson	1		
	Bombus bifarius Cresson	2		
	Bombus californicus Smith	3		
	Bombus centralis Cresson	33	1	1
	Bombus fervidus Fabricius	15		1
	Bombus huntii Greene	68	2	1
	Bombus insularis Smith	1	1	2
	Bombus nevadensis Cresson	26		
	Bombus rufocinctus Cresson	6		
	Bombus sp.	2		1
	Bombus vosnesenkii Radoszkowski	2		
	Ceratina neomexicana Cockerell			1
	Ceratina pacifica Smith		1	26
	Eucera actuosa Cresson	5	15	18
	Eucera edwardsii Cresson	57	39	94
	Eucera frater Cresson	251	8	5
	Eucera fulvitarsis Cresson	28		4
	Eucera sp.	28		
	Eucera speciosa Cresson			1
	Eucera territella Cockerell			1

Continued

Appendix (*Continued*). Bee taxa collected visiting *Astragalus filipes* (ASFI), *Balsamorhiza hookeri* (BAHO) and *B. sagittata* (BASA).

Bee Family	Bee Species	*Astragalus filipes*	*Balsamorhiza hookeri*	*Balsamorhiza sagittata*
	Habropoda cineraria Smith	1		2
	Melecta pacifica Cresson	3		1
	Melecta separata Cresson		1	
	Melecta sp.	3		4
	Nomada sp.	3	1	53
Colletidae	*Hylaeus* sp.	1		
Halictidae	*Agapostemon femoratus* Crawford	2	1	9
	A. angelicus (Cockerell) / *texanus* Cresson)	5	1	20
	Halictus confusus Smith			1
	Halictus farinosus Smith			4
	Halictus ligatus Say			8
	Halictus rubicundus Christ	5	2	3
	Halictus tripartitus Cockerell	18	3	50
	Lasioglossum albohirtum Crawford	2		3
	Lasioglossum diatretum Vachal			1
	Lasioglossum incompletum Crawford		7	12
	Lasioglossum nevadense Crawford			5
	Lasioglossum obnubilum Sandhouse			1
	Lasioglossum pacatum Sandhouse			1
	Lasioglossum prasinogaster Gibbs	1		2
	Lasioglossum pruinosum Robertson			2
	Lasioglossum punctatoventre Crawford	1		
	Lasioglossum sedi Sandhouse			1
	Lasioglossum sisymbrii Cockerell	2		
	Lasioglossum sp.	15	4	32
	Lasioglossum titusi Crawford		2	
	Lasioglossum trizonatum Cresson		1	2
Megachilidae	*Anthidium atripes* Cresson	21		
	Anthidium emarginatum Cockerell	5		
	Anthidium sp.	10		
	Anthidium utahense Swenk	3		
	Ashmeadiella sculleni Michener	2		
	Ashmeadiella sp.			1
	Hoplitis albifrons Kirby	3		
	Hoplitis hypocrita Cockerell	32		6
	Hoplitis sp.	11		
	Megachile sp.	4		2
	Osmia aff. cyanopoda Cockerell	1		
	Osmia aff. hurdi White	6		
	Osmia albolateralis Cockerell	13		1
	Osmia alpestris Rust and Bohart	1		1
	Osmia atrocyanea Cockerell	8		2

Continued

Appendix (*Continued*). Bee taxa collected visiting *Astragalus filipes* (ASFI), *Balsamorhiza hookeri* (BAHO) and *B. sagittata* (BASA).

Bee Family	Bee Species	*Astragalus filipes*	*Balsamorhiza hookeri*	*Balsamorhiza sagittata*
	Osmia bella Cresson	1		3
	Osmia brevis Cresson	7		4
	Osmia bruneri Cockerell	36		50
	Osmia bucephala Cresson			8
	Osmia californica Cresson		1	69
	Osmia calla Cockerell	12	5	26
	Osmia coloradensis Cresson		1	11
	Osmia cyanella Cockerell	1		2
	Osmia cyanopoda Cockerell	4		
	Osmia densa Cresson	1		
	Osmia ednae Cockerell	2		1
	Osmia granulosa Cockerell	1		
	Osmia grinnelli Cockerell		1	8
	Osmia hurdi White	5		
	Osmia integra Cresson	19		1
	Osmia kincaidii Cockerell			2
	Osmia longula Cresson	12		
	Osmia marginipennis Cresson		3	15
	Osmia montana Cresson		3	31
	Osmia n. sp. 1 nr. *sladeni* Sandhouse	6		
	Osmia n. sp. 2 nr. *sladeni Sandhouse*	1		
	Osmia nanula Cockerell	1		
	Osmia nemoris Sandhouse	5	48	10
	Osmia nifoata Cockerell	17	5	2
	Osmia nigrifrons Cresson	49		
	Osmia physariae Cockerell	12		
	Osmia pusilla Cresson	1		2
	Osmia raritatis Michener	15		
	Osmia rawlinsi Sandhouse	6		
	Osmia regulina Cockerell	3		
	Osmia sanrafaelae Parker	12		
	Osmia simillima Smith	1		
	Osmia sladeni Sandhouse	2		
	Osmia sp. 3	1		
	Osmia sp. 4	1		
	Osmia sp.	200	6	24
	Osmia subaustralis Cockerell			1
	Osmia trevoris Cockerell	15	1	27
	Osmia unca Michener	5		
	Osmia vandykei Sandhouse			1
	Total Bees	**1208**	**207**	**828**
	Total Species	**85**	**32**	**76**