USDA Forest Service
U.S. DEPARTMENT OF AGRICULTURE

Rocky Mountain Research Station | General Technical Report RMRS-GTR-429 | January 2022

Assessing Pollinator Friendliness of Plants and Designing Mixes to Restore Habitat for Bees

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Glenny, Will; Runyon, Justin; Burkle, Laura. 2022. **Assessing pollinator friendliness of plants and designing mixes to restore habitat for bees**. Gen. Tech. Rep. RMRS-GTR-429. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 52 p. https://doi.org/10.2737/RMRS-GTR-429.

ABSTRACT

The worldwide decline in bee populations is threatening the delivery of pollination services, thus leading to the development of pollinator restoration strategies. In the United States, one way to protect and restore bee populations is to use seed mixes composed of pollinator-friendly native plants to revegetate federal lands following disturbance. However, we lack information about which native plant species and mixes are best for bees. We assessed the attractiveness and use by bees of 24 native plant species that are standard for revegetation projects (focal plants) on national forest lands in western Montana. Focal plants that had the highest visitation rate, attracted the most bee species, supported specialist bee species, and bloomed for extended periods across the landscape were considered "pollinator-friendly." Our results suggest that *Salix bebbiana*, *Arctostaphylos uva-ursi*, *Lupinus sericeus*, *Rosa woodsii*, *Symphoricarpos albus*, *Erigeron speciosus*, *Symphyotrichum foliaceum*, and *Gaillardia aristata* could create a seed mix that is effective for pollinator restoration on public lands. Pollinator-friendliness score cards are provided to allow land managers to select plant species to include in restoration mixes that benefit pollinators. Identifying mixes of pollinator-friendly native plant species that are available for restoration will allow land managers to both revegetate disturbed habitats and restore bee communities on federal lands. The methods developed in this project can be used to design seed mixes for pollinator restoration on other public lands.

Keywords: *bees, pollinators, restoration, community ecology, Region 1*

COVER PHOTOS: ***Main photo***: A bumble bee (*Bombus nevadensis*) visits showy fleabane (*Erigeron speciosus*), a plant species used in revegetation projects on the Helena-Lewis & Clark National Forest. Credit: Will Glenny, Montana State University. **Small photos**: ***Upper right*** – A close view of a cuckoo bee (*Coelioxys* sp.) visiting western aster (*Symphyotrichum* sp.). Credit: Casey M. Delphia, Montana State University. ***Middle right*** – A digger bee (*Anthophora* sp.) inspecting flowers of scorpionweed (*Phacelia* sp.). Credit: Casey M. Delphia, Montana State University. ***Lower right*** – The Western bumble bee (*Bombus occidentalis*) visits a flower. Credit: Casey M. Delphia, Montana State University.

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ACKNOWLEDGMENTS

This project was funded by the Western Wildland Environmental Threat Assessment Center (WWETAC) and the USDA Forest Service's Northern Region (Region 1) Native Plant Program. We thank Justina Dumont (Forest Service) and Ted Snyder (Forest Service) of the Helena-Lewis and Clark National Forest in Helena, Montana, for assistance with initial site selection. Susan Rinehart (Forest Service) at the Native Plant Program in Missoula, Montana, is thanked for insightful discussions that guided early development of this project. We also thank Helen Smith (Forest Service) at the Missoula Fire Science Laboratory for coordinating access within the Tenderfoot Experimental Forest; Zab Reese (Montana State University), Dr. Casey Delphia (Montana State University), Skyler Burrows (Utah State University), and Dr. Terry Griswold (Forest Service's Agricultural Research Service) for bee species identification; Dr. Matt Lavin (Montana State University) for plant species identification and photos used in figure 13; and Jake Anton, Alissa Freeman, Jared Trilling, and Jessica Eggers for assistance in the field. We would like to thank Dr. Kasten Dumroese (Forest Service's Rocky Mountain Research Station in Moscow, Idaho) and Dr. Anthony Slominski (Montana State University) for providing valuable feedback on this general technical report.

CONTENTS

INTRODUCTION

The Importance of Pollinators and Widespread Pollinator Decline

Pollinators are essential for the maintenance of biodiversity and the functioning of ecosystems. Pollination services support healthy vegetation communities that increase soil stability, water quality, nutrient availability, the aesthetic value of landscapes, and habitat and food for many mammal, bird, and insect species (Wratten et al. 2012). Most plant species rely on animals including birds, bats, butterflies, flies, wasps, and, most importantly, bees, to transport pollen between individuals for successful reproduction (Ollerton et al. 2011). It is estimated that 60 to 80 percent of all flowering plant species require bees for reproduction (Ollerton et al. 2011). Additionally, almost 35 percent of food consumed by humans requires pollination services from bees, resulting in nearly U.S. $180 billion in annual revenue globally (Calderone 2012; Eilers et al. 2011; Gallai et al. 2009).

Bees (Hymenoptera: Apoidea) are premier pollinators because females actively visit many flowers to collect floral pollen and nectar to provide food for larvae and, in doing so, effectively transfer pollen between plants of the same species. Females of most bee species have specialized hairs on their legs and/or abdomen that form structures to acquire and transport pollen (e.g., pollen baskets). Bees are also highly diverse, with more than 4,000 species native to the United States (Kopec and Burd 2017). However, bee populations are declining in the United States and many other parts of the world. Climate change altered disturbance regimes, habitat loss, pathogens, and pollutants are implicated in the global decline of bee populations and threaten the delivery of pollination services (Biesmeijer et al. 2006; Burkle et al. 2013; Potts et al. 2010). Declining pollination services could threaten the persistence, abundance, reproduction, and ultimately population dynamics of plants in natural communities (Biesmeijer et al. 2006). Therefore, bees are critical for the maintenance of vegetation communities that support ecosystem function.

Recent bee declines have gained national attention, resulting in population assessments of several candidate species for federal protection under the Endangered Species Act (ESA). In 2017, the rusty patched bumble bee (*Bombus affinis*) in the eastern United States became the first bee species in the continental United States listed for protection under the ESA. Since then, four species in the western United States, including Franklin's bumble bee (*Bombus franklini*), the yellow-banded bumble bee (*Bombus terricola*), the western bumble bee (*Bombus occidentalis*), and Suckley's bumble bee (*Bombus suckleyi*), were petitioned for protection under the ESA. Notably, the western bumble bee (fig. 1) has undergone extensive range declines during the past 20 years (Cameron et al. 2011; Graves et al. 2020). The western bumble bee was once widely distributed from the Pacific Ocean to the Colorado plains and from Alaska to the border of

Figure 1—The western bumble bee (*Bombus occidentalis*) has undergone extensive range declines in the past 20 years and will be considered for inclusion under the Endangered Species Act. Courtesy photo by Casey Delphia, Montana State University.

Mexico but is now primarily restricted to high elevations in the northern extent of its range (Cameron et al. 2011; Graves et al. 2020). Currently, federally managed lands in Montana (U.S. Department of Agriculture, Forest Service, Region 1) remain a stronghold for populations of the western bumble bee and may serve as a refuge for this species against disturbances like climate change and habitat loss (Graves et al. 2020). Montana also contains populations of Suckley's bumble bee and the yellow-banded bumble bee (Dolan et al. 2017). If these or other pollinator species are listed under the ESA, information about restoring their habitat will be critical for the protection and recovery of these imperiled species.

Land Restoration Using Seed Mixes

Seed mixes are a combination of seeds from multiple plant species that are dispersed to establish vegetation cover of desired plant species. On federal lands, seed mixes are used to revegetate wildlands following disturbances such as roadsides, mining, and other resource extraction sites, slash piles and landings, skid trails, wildland fire rehabilitation, and grazing pastures. On National Forest System lands, seed mixes are primarily deployed to establish vegetative cover to minimize soil erosion, but also to reduce noxious weed invasion, improve soil health, and provide forage for grazing animals (Grant et al. 2011; Robichaud 2000). In particular, the Forest Service Burned Area Emergency Response (BAER) program relies heavily on seed mixes to revegetate slopes following wildfire and reduce surface soil erosion, reduce sediment input into streams, and maintain water quality. Seed mixes used by land managers are primarily composed of a third of each of nonnative grasses, native grasses, and native shrubs because seeds for these plants can be produced at commercial scale and, when used to revegetate landscapes, readily establish on affected areas (Maynard and Hill 1992; Monsen and Shaw 2001). Seed mixes are an increasingly important tool for land managers to maintain ecosystem health following disturbances on public lands.

Commercial availability of native plant materials for habitat revegetation is provided through federally managed programs that collect and cultivate native plant species from wildlands. Collecting native plant seeds from natural populations ensures that germinants will be locally adapted and genetically diverse while reducing the risk of introducing maladapted traits (Erickson and Halford 2020). As a result, seeds used in restoration that have been cultivated from local wildland sources are adapted to native growing conditions and require minimal maintenance. Native plants can, however, be difficult and expensive to cultivate, and high demand from western land managers for rehabilitation projects further increases costs. For example, from 1999 to 2004, federal agencies distributed 6,500 metric tons of seeds to revegetate areas burned by wildfires in the Great Basin alone (Cane 2008). Therefore, federal initiatives like the National Seed Strategy for Rehabilitation and Restoration (Olwell and Riibe 2016) and the Forest Service National Nursery System are critical for providing affordable native plant materials to revegetation projects (Dumroese et al. 2005). As the demand for native plant materials increases into the future, seeds made available by federal programs are critical to accomplish restoration goals.

Designing Seed Mixes to Support Bee Communities

Despite the stated importance of restoration strategies for bees, little work has been accomplished to develop effective seed mixes for bee restoration. Recommended seed mixes are rarely evaluated empirically (Garbuzov and Ratnieks 2014). Without a science-based evaluation of plant species comprising seed mixes, large portions of the bee community can be neglected. For instance, only 37 percent of species from a bee community in the United Kingdom utilized plant species contained within a government-designed seed mix (Wood et al. 2015), and some seed mixes in the United States required up to 45 different plant species before restored plots recovered the number of bee species present on remnant habitats (Harmon-Threatt and Hendrix 2015). Examining the relationships between plant species, and the community of bees that visit them, could provide insights into how to best identify important plant species for seed mixes.

Bee Visitation Patterns

Bees demonstrate a range of foraging behaviors and preferences for different plant species, resulting in community-wide patterns of plant-bee interactions that determine the relative importance and roles of plant species for providing floral resources (fig. 2). Plants that are visited by many bee individuals can provide floral resources to maintain the metabolic rates of adults (nectar) and provision food for the development of larvae (nectar and pollen). Additionally, plants visited by many different bee species can provide floral resources to sustain large portions of bee communities. Including plants within seed mixes that receive many visitations from a wide range of bee species may provide valuable floral resources for more of the bee community. Furthermore, bee foraging behaviors can range from only foraging on one or a few flower species (specialist) to foraging on many flower species (generalist). Specialist bee species are often the most vulnerable to habitat loss and disturbances but are frequently neglected by recommended seed mixes (Bommarco et al. 2010; Nichols et al. 2019). The inclusion of plants that provide foraging resources specifically for specialist bee species could aid in the recovery of sensitive bee species following disturbances. Evaluating community-wide interactions between plants and bees can identify plants that provide the most resources for the bee community and support sensitive species.

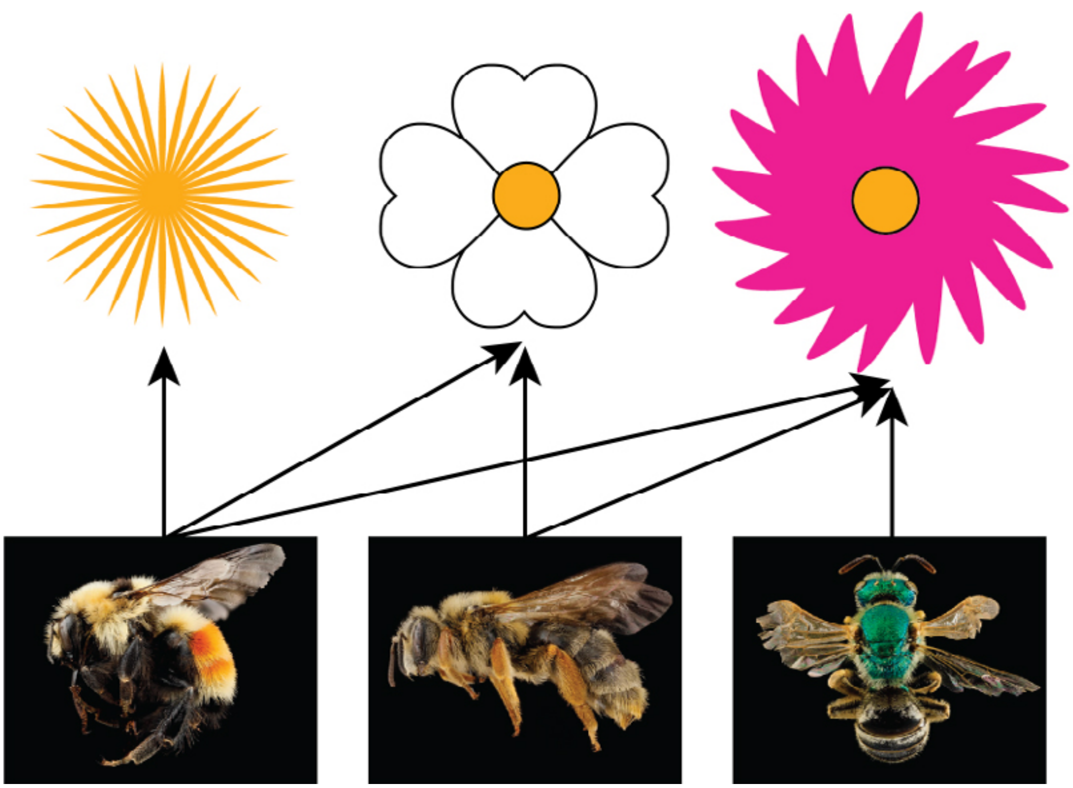

Figure 2—Species-specific foraging patterns of bees result in community-wide patterns of bee-flower interactions. Arrows indicate interactions between bees (bottom row) and focal plants (top row). Plants that attract many bee species (pink flower) are important for providing foraging resources for a large portion of the bee community, including specialist bees (green bee) that might exclusively collect floral resources from a single source. U.S. Geological Survey photos from the Native Bee Inventory and Monitoring Lab.

Temporal Availability of Resources

Bee communities exhibit substantial variation across the growing season because individual bee species are active and abundant at different times during the year (Petanidou et al. 2008; Williams et al. 2001). To ensure floral resources are available to pollinator communities that are active at different times of the growing season, seed mixes are composed of plants that have complementary bloom periods (Havens and Vitt 2016). Additionally, periods of resource scarcity can occur during the beginning and end of the growing season when ephemeral plant species are emerging or senescing, and immediately following disturbances when most flowers have been removed from the landscape (Havens and Vitt 2016). Seed mixes that include plant species to fill these bottlenecks in floral resource availability can provide foraging resources during periods of resource scarcity (Dixon 2009; Menz et al. 2011) (fig. 3).

Context-Dependent Roles of Plant Species

Context-dependent interactions between plants and bees might alter the functional role of plants for bee restoration in seed mixes. Variation in plant and bee community composition (Petanidou et al. 2008; Williams et al. 2001) (fig. 4), the influence of co-occurring plant species (Glenny et al. 2018), and changing environmental conditions (Burkle et al. 2016; Simanonok and Burkle 2014) alter interaction patterns between plants and bees in different habitat contexts. As a result, the value of plant species for pollinator communities is context-dependent and may change across space and time. This is especially important to consider when designing seed mixes for public lands, which contain a diversity of habitat types that are continuously shaped by natural and anthropogenic disturbances. Seed mixes containing plant species that consistently supply foraging resources to pollinators across the season and habitats are important for wide application across public lands.

The Role of Federal Land Management Agencies in Pollinator Conservation

Federal agencies can play an essential role in restoring and conserving pollinators because federal agencies manage more than one-quarter of the land area, and most habitat types, in the United States. Federally managed lands include areas with the highest known bee species richness per square kilometer in the United States and are especially important for the conservation of bees (Koh et al. 2016; Meiners et al. 2019; Wilson et al. 2018). Most public lands are managed, however, for a balanced combination of “outdoor recreation, range, timber, watershed, and wildlife and fish purposes” (Multiple Use and Sustained Yield Act, 1960), which can be a challenge for land managers to maintain and improve the health of public lands. Natural disturbances including wildfire, extreme drought, wind, and flooding, and anthropogenic disturbances such as logging, grazing, invasive species, and recreation, frequently degrade wildlands. As a result, restoration of multiple-use lands following disturbances is often necessary to recover ecological health and function.

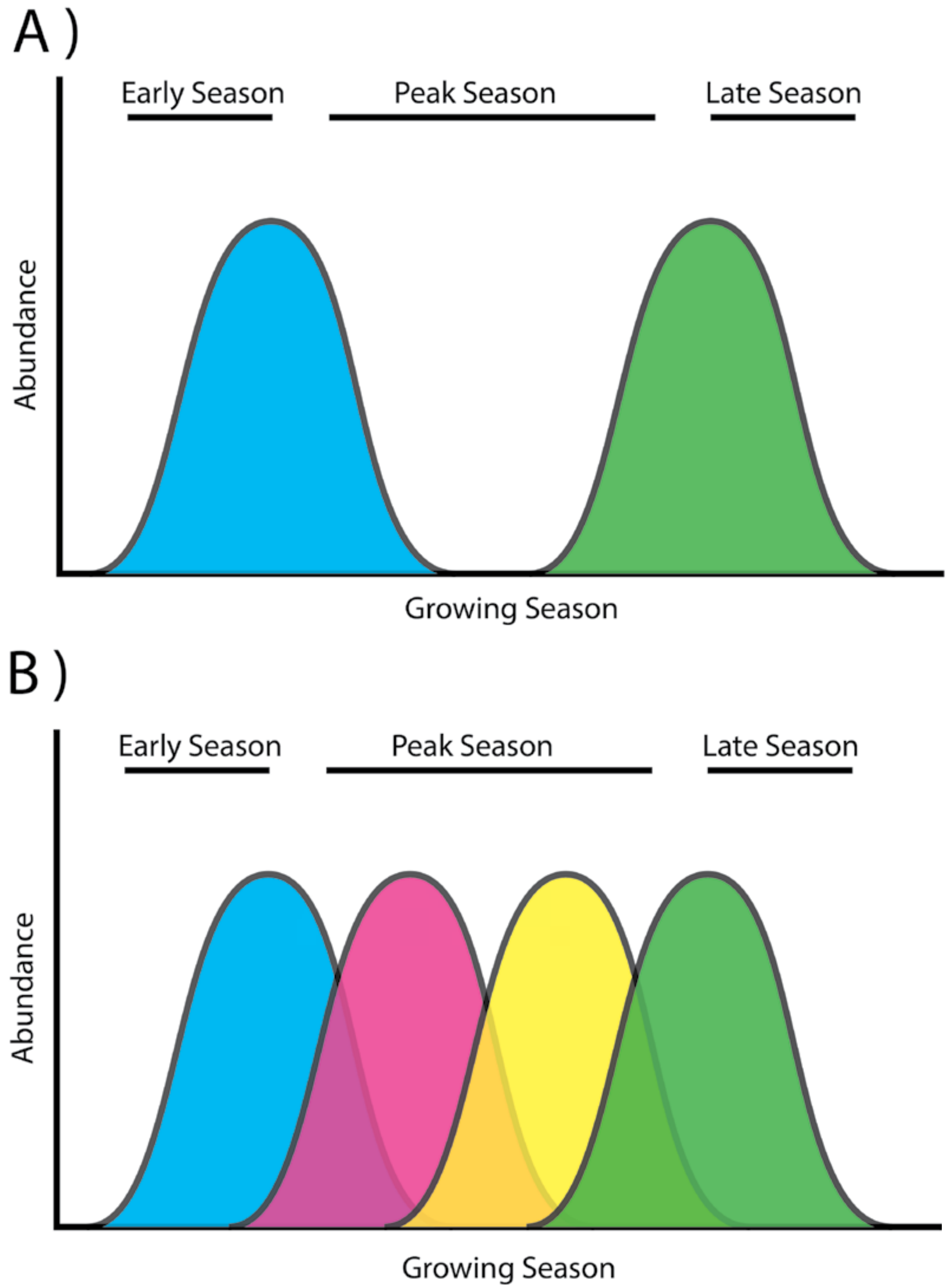

Figure 3—Seed mixes containing species with complementary bloom times are necessary to provide bee foraging resources for the whole growing season. Plant species (colored curves) have a bloom duration (x-axis) when floral resources are available for bees (y-axis). A): Plant communities missing plant species could result in resource bottlenecks when no foraging resources are available. B): Seed mixes containing plants with complementary bloom times can provide constant foraging resources for bees throughout the growing season.

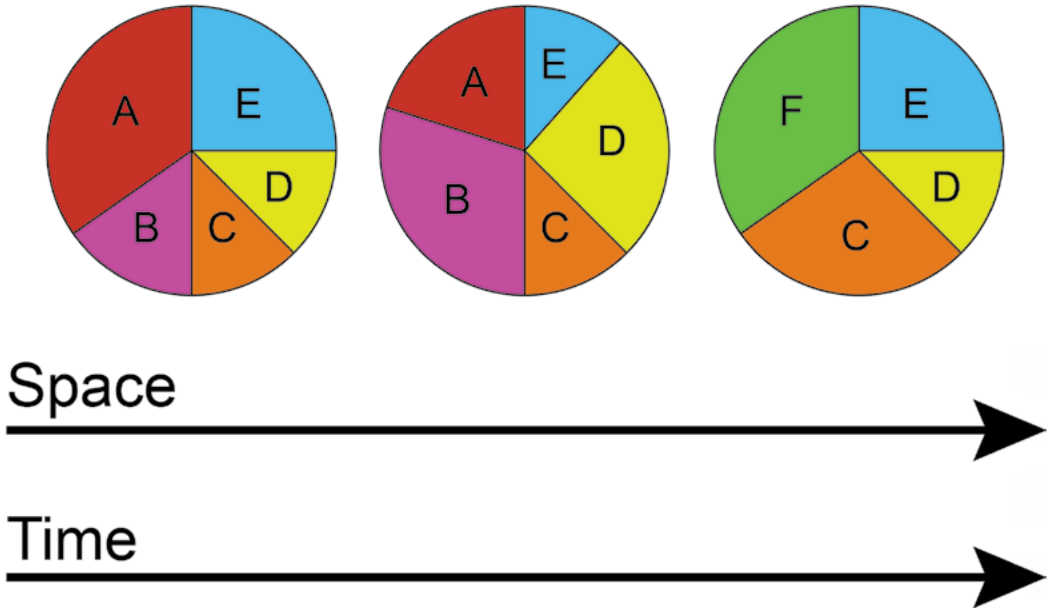

Figure 4—Theoretical description of how bee community composition changes across time and space, emphasizing the need for broadly applicable seed mixes. Pie charts represent a bee community, colors and letters are bee species, and the proportion of each color indicates the relative abundance of species in a bee community. Across space and time, bee species abundance and richness changes, resulting in altered species composition.

Recently, federal land management agencies were tasked with promoting bee health across the United States in a Presidential Memorandum (Obama 2014) and many agencies are incorporating strategies for bee habitat restoration into revised management plans. The Presidential Memorandum designated a pollinator health taskforce and called for a unified strategy to promote the health of bees on federal lands. Bee experts from multiple federal land management agencies (Forest Service, BLM, USFWS) drafted the Pollinator Research Action Plan (Pollinator Health Task Force Report 2015), which outlined bee habitat improvement as a major step required for bee recovery and conservation. Land managers, however, lack information and guidance for implementing practical solutions to meet the management goals of restoring bee habitats. Additionally, the 2012 Planning Rule (https://www.fs.usda.gov/detail/planningrule/home/?cid=stelprdb5359471) requires land managers to revise forest management plans to maintain and restore ecological integrity while fulfilling the multiple-use objectives for the plan area. Several national forests (NFs) within the USDA Forest Service National Forest System (NFS) have included desired conditions and goals for maintaining and restoring bee habitat in their revised forest plans (e.g., Helena-Lewis and Clark NF, Montana; Flathead NF, Montana; Grand Mesa, Uncompahgre, and Gunnison NF, Colorado; Manti-La Salle NF, Utah; and Pisgah NF, North Carolina). Additionally, bee species continue to be identified as species of conservation concern (SCC) on national forests (e.g., *B. occidentalis* on many western forests). Information is needed on how to preserve and restore populations of SCCs, and bees more broadly, to aid in the recovery of these potentially endangered species. Land managers can therefore incorporate the best available science, including knowledge from research into pollinator restoration across the United States, to meet the goals designated by the Presidential Memorandum.

Seed Mixes as a Tool for Pollinator Habitat Restoration

Seed mixes deployed on public lands can be improved to meet multiple management objectives, including pollinator habitat restoration. While the seed mixes that are currently deployed on federal lands emphasize plants that can outcompete invasive plant species and limit soil erosion, these plants provide minimal value for bees. Seed mixes are primarily composed of grasses that offer little to no floral resources for bees and typically contain less than 0.5 percent of seeds that are native forbs (herbaceous flowering plants) (Cane 2008). Additionally, the forbs that are included within seed mixes are generally not preferred by bees. For example, *Achillea millefolium* and *Linum lewisii*, the two forb species most frequently used for revegetation in the Great Basin, received the lowest abundance and diversity of bee visitors of 17 Great Basin forb species examined (Cane and Love 2016). Evaluating bee visitation patterns to the plants that are cultivated at Forest Service nurseries could be a method to identify plants that are important sources of nectar and pollen for bees and improve seed mixes deployed on public lands for bee habitat revegetation.

Description of Study

We evaluated pollinator visitation to 24 plant species (focal plants) that are commercially available for use in USDA Forest Service Region 1 to identify the most effective plants to include in seed mixes for bee habitat restoration. Plant species that are cultivated by the Native Plant Program at the Forest Service Coeur d'Alene Nursery with proven effectiveness for revegetation could be leveraged to produce readily available, pollinator-focused seed mixes (table 1). These plant species were arranged by the Region 1 Native Plant Program into mixes for revegetation of dry (table 2), moist (table 3), high elevation (table 4), riparian (table 5), and highly disturbed habitat sites (table 6). However, the value of these plant species for bees is unknown.

To assess the value of these plant species for bees, we observed bee visitation to naturally occurring focal plant species in as many locations as possible across the Helena-Lewis and Clark National Forest (HLCNF, Region 1). The total number of bee individuals per flower per minute of observation (visitation rate), the number of bee species (richness), and the number of specialist bees visiting each plant species were compared among focal plants. Additionally, average bloom duration and spatial occurrence frequencies were compared among focal plant species to design seed mixes that contain plants that provide floral resources at different time periods (early, middle, and late) and in a range of habitat types.

Table 1—Focal plant species evaluated in this study for pollinator friendliness, including scientific names, common names, the six-letter abbreviation, and availability from the Coeur d'Alene nursery (number of seeds/lb or plants/acre). (See https://www.fs.usda.gov/detail/ipnf/about-forest/districts/?cid=stelprdb5085769).

Forb and shrub species	Common name	Six-letter abbreviation	Seeds/lb. or plants/acre
Antennaria microphylla	Small flowered pussytoes	ANTMIC	Variable
Antennaria rosea	Rosy pussytoes	ANTROS	Variable
Achillea millefolium	Yarrow	ACHMIL	2,835,000
Penstemon procerus	Small flowered penstemon	PENPRO	Variable
Penstemon attenuatus/albertinus	Taper leaf penstemon	PENATT/PENALB	Variable
Eriogonum umbellatum	Sulphur buckwheat	ERIUMB	217,000
Lupinus sericeus	Silky lupine	LUPSER	Variable
Anaphalis margaritacea	Pearly everlasting	ANAMAR	11,000,000
Erigeron speciosus	Showy fleabane	ERISPE	Unknown
Phacelia hastata	Silverleaf scorpion weed	PHAHAS	2,182,576
Gaillardia aristata	Blanket flower	GAIARI	438,719
Hedysarum boreale	Boreal sweetvetch	HEDBOR	3,968,320
Spiraea betulifolia	Birchleaf spiraea	SPIBET	2,200
Rosa woodsii	Wood's rose	ROSWOO	2,200
Symphoricarpos albus	Snowberry	SYMALB	1,450
Artcostaphylos uva-ursi	Kinnikinnick	ARCUVA	6,329
Berberis repens	Oregon grape	BERREP	1,200
Eurybia conspicua	Showy aster	EURCON	Variable
Senecio triangularis	Arrowleaf groundsel	SENTRI	2,204,622
Cornus sericea	Red osier dogwood	CORSER	3,031
Salix bebbiana	Bebb's willow	SALBEB	3,250
Symphyotrichum foliaceum	Smooth aster	SYMFOL	1,014,000
Solidago canadensis	Canada goldenrod	SOLCAN	9,700,339

Table 2—Standard revegetation seed mix developed by Region 1 Native Plant Program appropriate for low to middle elevation (< 6,500 ft) sites with low water availability, high potential for noxious weeds, and longer growing seasons. Typically, these sites can support sagebrush/grassland, limber pine, ponderosa pine, Douglas-fir, and some lodgepole pine habitat types.

Forb and shrub species	Common name	Six-letter abbreviation
Erigeron speciosus	Showy fleabane	ERISPE
Gaillardia aristata	Blanket flower	GAIARI
Lupinus sericeus	Silky lupine	LUPSER
Penstemon albertinus	Alberta penstemon	PENALB
Penstemon attenuatus	Taper leaf penstemon	PENATT
Penstemon procerus	Small flowered penstemon	PENPRO
Phacelia hastata	Silverleaf scorpion weed	PHAHAS
Rosa woodsii	Wood's rose	ROSWOO
Spiraea betulifolia	Birchleaf spiraea	SPIBET
Symphoricarpos albus	Snowberry	SYMALB
Antennaria rosea	Rosy pussytoes	ANTROS
Antennaria microphylla	Small flowered pussytoes	ANTMIC
Achillea millefolium	Yarrow	ACHMIL
Eriogonum umbellatum	Sulphur buckwheat	ERIUMB
Anaphalis margaritacea	Pearly everlasting	ANAMAR

Table 3—Standard revegetation seed mix developed by Region 1 Native Plant Program appropriate for low to middle elevation sites (< 6,500 feet) with more available moisture and moderate temperature regimes. Typically, these sites support Engelmann spruce, lodgepole pine, subalpine fir, and some Douglas-fir habitat types.

Forb and shrub species	Common name	Six-letter abbreviation
Lupinus sericeus	Silky lupine	LUPSER
Rosa woodsii	Wood's rose	ROSWOO
Spiraea betulifolia	Birchleaf spiraea	SPIBET
Symphoricarpos albus	Snowberry	SYMALB
Antennaria rosea	Rosy pussytoes	ANTROS
Antennaria microphylla	Small flowered pussytoes	ANTMIC
Solidago canadensis	Canada goldenrod	SOLCAN
Berberis repens	Oregon grape	BERREP
Achillea millefolium	Yarrow	ACHMIL
Arctostaphylos uva-ursi	Kinnikinnick	ARCUVA
Anaphalis margaritacea	Pearly everlasting	ANAMAR

Table 4—Standard revegetation seed mix developed the Region 1 Native Plant Program appropriate for middle to high elevation sites (<6,500 ft) with more available moisture and moderate temperature regimes. Typically, these sites support Engelmann spruce, lodgepole pine, subalpine fir, and some Douglas-fir habitat types.

Forb and shrub species	Common name	Six letter abbreviation
Lupinus sericeus	Silky lupine	LUPSER
Phacelia hastata	Silverleaf scorpionweed	PHAHAS
Symphyotrichum foliaceum	Smooth aster	SYMFOL
Eurybia conspicua	Showy aster	EURCON
Antennaria rosea	Rosy pussytoes	ANTROS
Antennaria microphylla	Small flowered pussytoes	ANTMIC
Solidago canadensis	Canada goldenrod	SOLCAN
Anaphalis margaritacea	Pearly everlasting	ANAMAR

Table 5—Standard revegetation seed mix developed by Region 1 Native Plant Program appropriate for riparian or streamside vegetation communities. These sites can vary widely in elevation and temperature regimes. Typically, riparian areas are immediately adjacent to streams where tree establishment is slow and might be undesirable.

Forb and shrub species	Common name	Six-letter abbreviation
Cornus sericea	Red osier dogwood	CORSER
Salix bebbiana	Bebb's willow	SALBEB
Symphoricarpos albus	Snowberry	SYMALB
Symphyotrichum foliaceum	Smooth aster	SYMFOL
Eurybia conspicua	Showy aster	EURCON
Solidago canadensis	Canada goldenrod	SOLCAN
Senecio triangularis	Arrowleaf groundsel	SENTRI

Table 6—Standard revegetation seed mix developed by Region 1 Native Plant Program developed for areas with a high degree of soil disturbance including road decommissioning, timber sale landings, fire, and restoration projects at a variety of elevations.

Forb and shrub species	Common name	Six letter abbreviation
Penstemon albertinus	Alberta penstemon	PENALB
Penstemon attenuatus	Taper leaf penstemon	PENATT
Penstemon procerus	Small flowered penstemon	PENPRO
Phacelia hastata	Silverleaf scorpion weed	PHAHAS
Rosa woodsii	Wood's rose	ROSWOO
Spiraea betulifolia	Birchleaf spiraea	SPIBET
Symphoricarpos albus	Snowberry	SYMALB
Antennaria rosea	Rosy pussytoes	ANTROS
Antennaria microphylla	Small flowered pussytoes	ANTMIC
Achillea millefolium	Yarrow	ACHMIL
Eriogonum umbellatum	Sulphur buckwheat	ERIUMB

Based on these metrics, we developed a scorecard to identify the plants that serve a central role in providing resources to bee communities (i.e., “pollinator-friendly” plants) (Dixon 2009; Menz et al. 2011). Additionally, we report all plant species visited by the western bumble bee (*B. occidentalis*) to identify plants that could be used within seed mixes specifically designed for this SCC. The methods developed for this project can be applied toward improving seed mixes for pollinator restoration in other regions of the National Forest System to accomplish a nationwide strategy for pollinator conservation on public lands.

METHODS

Site Selection

Naturally occurring populations of focal plant species were located across the HLCNF to observe bee visitation to these plant species under multiple environmental conditions. The HLCNF was chosen as the location of this study because it spans more than 7,500 km^2 in west-central Montana and contains multiple environments common to the Intermountain West, including conifer-grassland systems dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), Douglas-fir (P*seudotsuga menziesii*), and whitebark pine (*Pinus albicaulis*), sagebrush (*Artemisia* spp.) steppe, montane grasslands, and riparian corridors. Disturbance from fire, grazing, logging, and other human activities frequently affects habitats and shapes landscape patterns. As a result, natural environmental variability exists across the landscape and provides the opportunity to evaluate the pollinator friendliness of focal plant species within a naturally complex ecosystem. Additionally, the revised forest management plan for the HLCNF includes a goal of collecting data about bees and improving the best available information on species’ diversity and their ecological requirements.

Sites were established based on the presence and high abundance of focal plant species. The center of each site was recorded using a GPS device (Oregon 700, Garmin Ltd., Olathe, KS). Site boundaries were defined by pacing a distance from the center of the plot to a point where focal plant species decreased in species richness and abundance (major axis). Perpendicular to the major axis, a distance was paced to a point where the floral community decreased in species richness and floral abundance (minor axis). Distances were measured with a meter tape and the rectangular site area was calculated by multiplying the major axis by the minor axis. The median site area was 706 m^2 and ranged from 21 to 9,500 m^2. To reduce the likelihood of sampling bees that could forage between sites, sites were separated by at least 400 m (Gibson et al. 2011). Site selection methods resulted in 63 total sites distributed across the HLCNF (fig. 5).

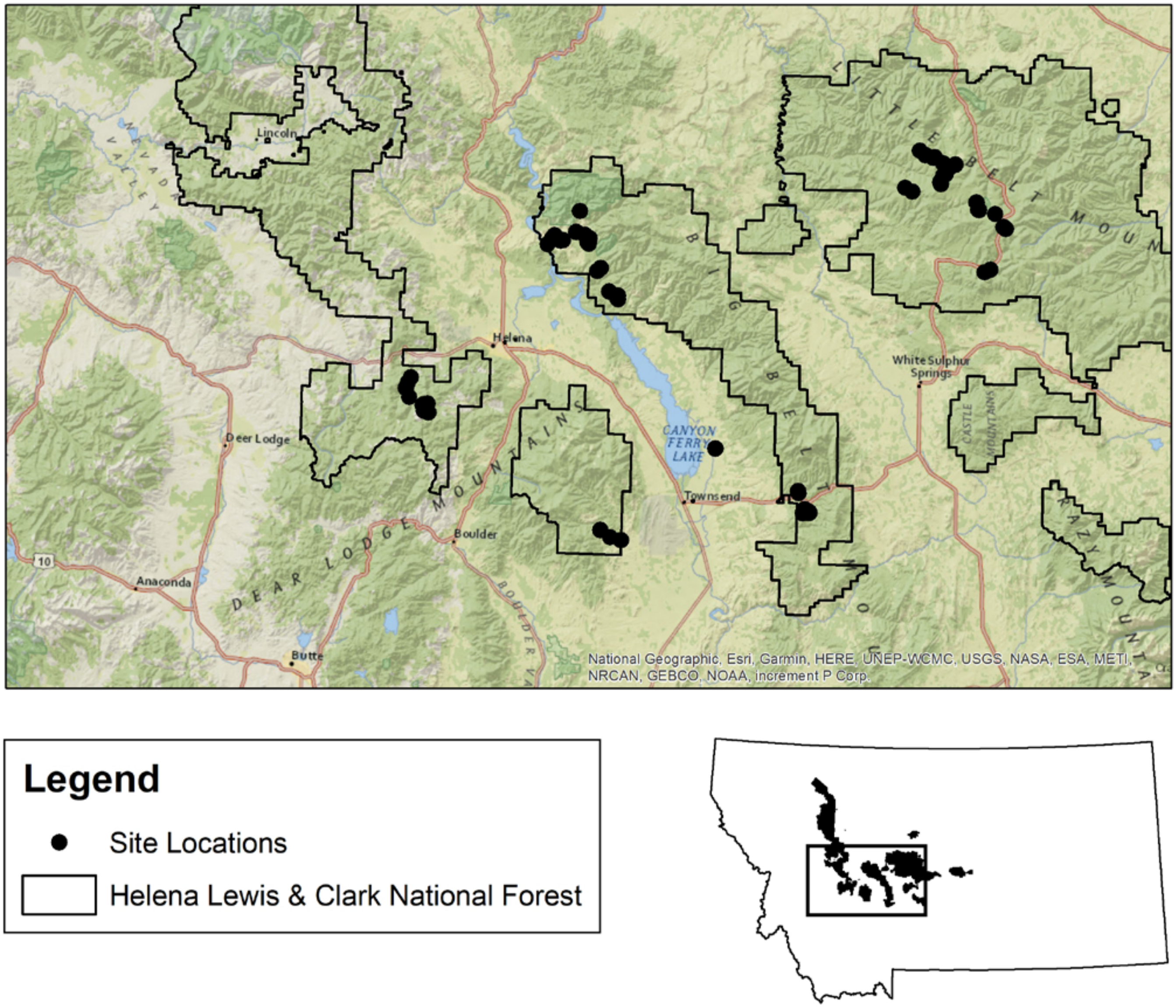

Figure 5—Study sites (black circles) in the Helena-Lewis and Clark National Forest (black line) in west-central Montana to sample bee visitation to focal plants across a range of environmental conditions.

Plant-Bee Interactions

To evaluate the species abundance, richness, and community composition of bees visiting focal plant species, bee visitation was observed to all focal plant species occurring at each site multiple times throughout the growing season. Plant-bee interactions were observed equally at sites throughout the growing season in 2018 and 2019. Timed observations (observation periods) of plant-bee interactions were typically conducted for 30 minutes at sites by randomly walking within site boundaries and collecting (using hand nets) any bee that came into contact with the reproductive parts of open flowers. The frequency of observation periods at each site varied depending on the phenology of the focal plant species and site accessibility but were sampled between 4 and 17 times at each site. Cumulatively, observation periods for each growing season spanned about 100 days, beginning in early May after snowmelt when plant species began blooming and ending in August when plants senesced and produced seed. Because shrubs (e.g., *Cornus sericea*) are large, distributed at low densities, and have large floral displays, they were observed one individual at a time. Individual shrubs were observed for 5-minute intervals before observing a different plant. For each shrub species, observations were repeated on up to 6 different plants per day (30 total minutes of observation per day). All bee observations took place during peak bee activity (1000 through 1700 hours).

Specimens captured in the field were identified in the laboratory to the lowest taxonomic level possible (typically to species or morphospecies) using published keys and with the help of expert taxonomists. Bee species were identified by Will Glenny (Montana State University), Elizabeth Reese (Montana State University), Dr. Casey Delphia (Montana State University), Skyler Burrows (Utah State University), and Dr. Terry Griswold (ARS, Logan, UT). Bee identifications were determined to the lowest possible taxonomic level using published works and a reference collection of authoritatively identified bee species from the study region (Reese et al. 2018). When published works were not available, we designated specimens to morphospecies based on morphological characteristics. Male morphospecies were labeled with an "M" and females were labeled with an "F," then paired with a unique number to distinguish species.

Floral Community

Focal plant species were identified at each site and counted to account for the effects of floral abundance on bee visitation patterns to plants. Floral abundance was estimated for each focal plant species by counting the number of open inflorescences in one-half of the plot and multiplying the count by two. Floral density was calculated by dividing the floral abundance of each species by the area of the plot. *Penstemon albertinus* and *Penstemon attenuatus* could not be reliably distinguished and were grouped into the same focal species (PENATT/PENALB).

Analytical Methods

Visitation Rate

During each observation period, we collected bees visiting flowers. At the end of each observation period, we counted the number of bees that visited each plant species. This sum provided the raw visitation for each plant species. However, the raw visitation can be biased depending on the floral abundance and the total amount of time spent observing each plant species. Therefore, we standardized the raw value of bee visitation by the floral abundance per plant and duration of observation (visits/flower/minute, [VFM]). The standardized visitation rate was averaged for each focal plant species across all observation periods during the growing season, and standard errors were calculated. Focal plant species within the top 25th percentile of observed visitation rates were considered the most attractive plants. Focal plant species within the bottom 25th percentile of visitation rates were considered the least attractive plants for bees.

Visitation Richness

Visitation richness was calculated as the total number of bee species that visited each focal plant species across all observation periods. However, the number of bee species visiting plants potentially reflects sampling effort instead of pollinator preferences because more bee species are likely to be caught from plants with higher total observation time. Therefore, we standardized the raw value of species richness for each focal plant by randomly subsampling the number of bee species that visits a focal plant, and plotting this response as a function of the number of samples (i.e., rarefaction). This technique allowed us to estimate the expected number of bee species visiting a focal plant given a similar sized, random sample. Focal plant species within the top 25th percentile of rarefied species richness were considered the most attractive plants, while focal plant species within the bottom 25th percentile of rarefied species richness were considered the least attractive plants for bees.

Specialists

Plants that provide resources for rare and specialist bees may be important to support bee species that are sensitive to habitat loss. We constructed bee-plant interaction networks to visualize the visitation patterns of bees to focal plant species across all sites. Specialist bees were defined as bee species that were only observed to visit a single focal plant species during the study. The total number of specialist bees observed visiting each focal plant species was compared among plant species.

Spatial and Temporal Availability of Floral Resources

The ability of plants to provide bees with foraging resources depends on the duration and time period when flowers are open and receptive to bee visitation, and the frequency with which plants occur across the landscape. Focal plants were classified into early, middle, or late season bloomers depending on the median day bees were observed visiting plants. Focal plants visited by bees within the first third of the sampling period between May and August were categorized as "early," second third as "middle," and final third as "late" season blooming plants. The mean bloom duration of each focal plant was calculated at each site by subtracting the first Julian day a plant was observed in bloom from the last Julian day a plant was observed in bloom, and calculating the average bloom duration across all sites. Additionally, focal plants that are broadly distributed provide resources for bees across large areas. Focal plants that occurred at the greatest number of sites should provide resources to bees across many habitat types.

Score Cards

Within seasonal groups (early, middle, and late), focal plant species were ranked according to the standardized visitation rate, standardized visitation richness (rarefied number of bee species), the number of specialist species visiting each focal plant species, the duration of the visitation period, and frequency of occurrence across all sites. These rankings were summed to create a composite score of pollinator friendliness. Focal plants with high composite scores were considered more pollinator friendly than plant species with low scores.

Western Bumble Bee

Plants that support the western bumble bee could serve as valuable resources for this SCC. We collected specimens of the western bumble bee from any plant species (focal or not) to document important plants that could be incorporated into seed mixes designed for conservation and restoration of this SCC.

Statistical Software

All analyses were performed using the statistical software “R” (R Core Team 2020). Plant-bee visitation networks were performed using the “bipartite” package (Dormann et al. 2008), and rarefaction and species accumulation curves were performed using the “vegan” package (Oksanen et al. 2007).

RESULTS

Sampling efforts across both growing seasons culminated in around 400 hours of observations and 3,415 bee specimens. We collected 246 bee species (Appendix) that were observed visiting focal plant species (216 identified to species, 30 to morphospecies). All specimens are deposited in the Montana State University Pollinator Health Center Collection located in the Burkle Community Ecology Lab at Montana State University in Bozeman, Montana.

Bee Visitation Metrics

Standardized Visitation Rate

Focal plant species that are visited by the greatest numbers of bees provide important floral resources to the bee community. Visitation rates were variable depending on the focal plant. Across all sites, the top 25th percentile of plant species for visitation rates included *Arctostaphylos uva-ursi*, S*ymphoricarpos albus*, *Berberis repens*, *Rosa woodsii*, and *Gaillardia aristata*, whereas the bottom 25th percentile of plants for visitation rate included *Penstemon procerus*, *Lupinus sericeus*, *Antennaria rosea*, *Eriogonum umbellatum*, and *Achillea millefolium* (fig. 6).

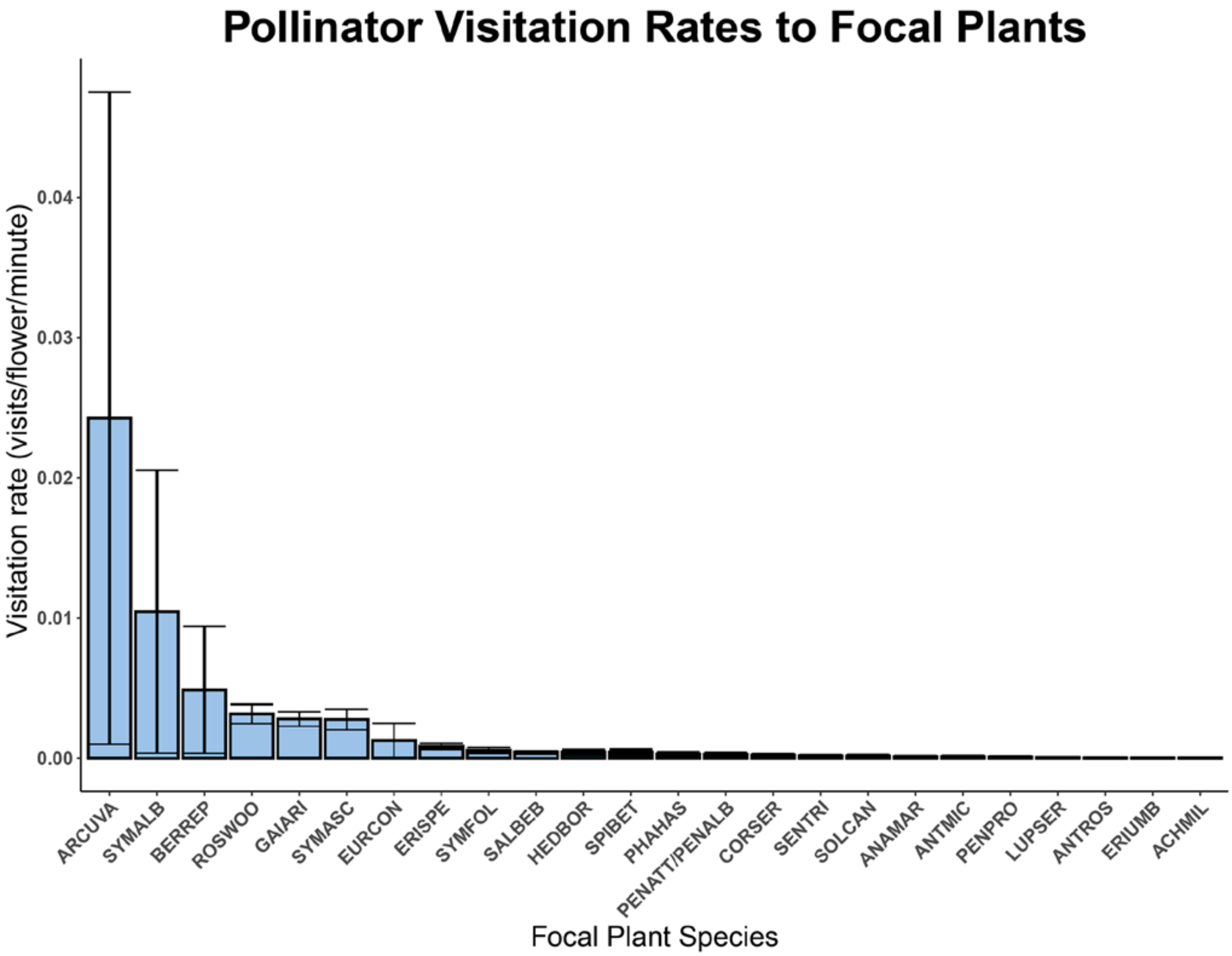

Figure 6—The standardized visitation rate (y-axis) of bees to each focal plant species (x-axis). Focal plants are arranged in descending order according to the number of bee specimens per flower per minute of observation collected from each plant species. Error bars are SE +/- 1. Focal plants are reported using the six-letter abbreviation in table 1.

Visitation Richness

Focal plant species that attract the most bee species provide foraging resources for a diverse bee community. Across all sites, the top 25th percentile of plants for visitation richness included *Rosa woodsii*, *Cornus sericea*, *Erigeron speciosus*, *Salix bebbiana*, and *Phacelia hastata*, whereas the bottom 25th percentile of plants for visitation richness included *Eurybia conspicua*, *Senecio triangularis*, *Antennaria microphylla*, and *Antennaria rosea* (fig. 7). The top 25th percentile of plants for rarefied visitation richness included *Rosa woodsii*, *Eurybia conspicua*, *Achillea millefolium*, *Arctostaphylos uva-ursi*, and *Erigeron speciosus*, whereas the bottom 25th percentile of plants for rarefied visitation richness included *Salix bebbiana*, *Berberis repens*, *Symphyotrichum foliaceum*, *Penstemon procerus*, and *Senecio triangularis*, and *Antennaria microphylla* (fig. 8).

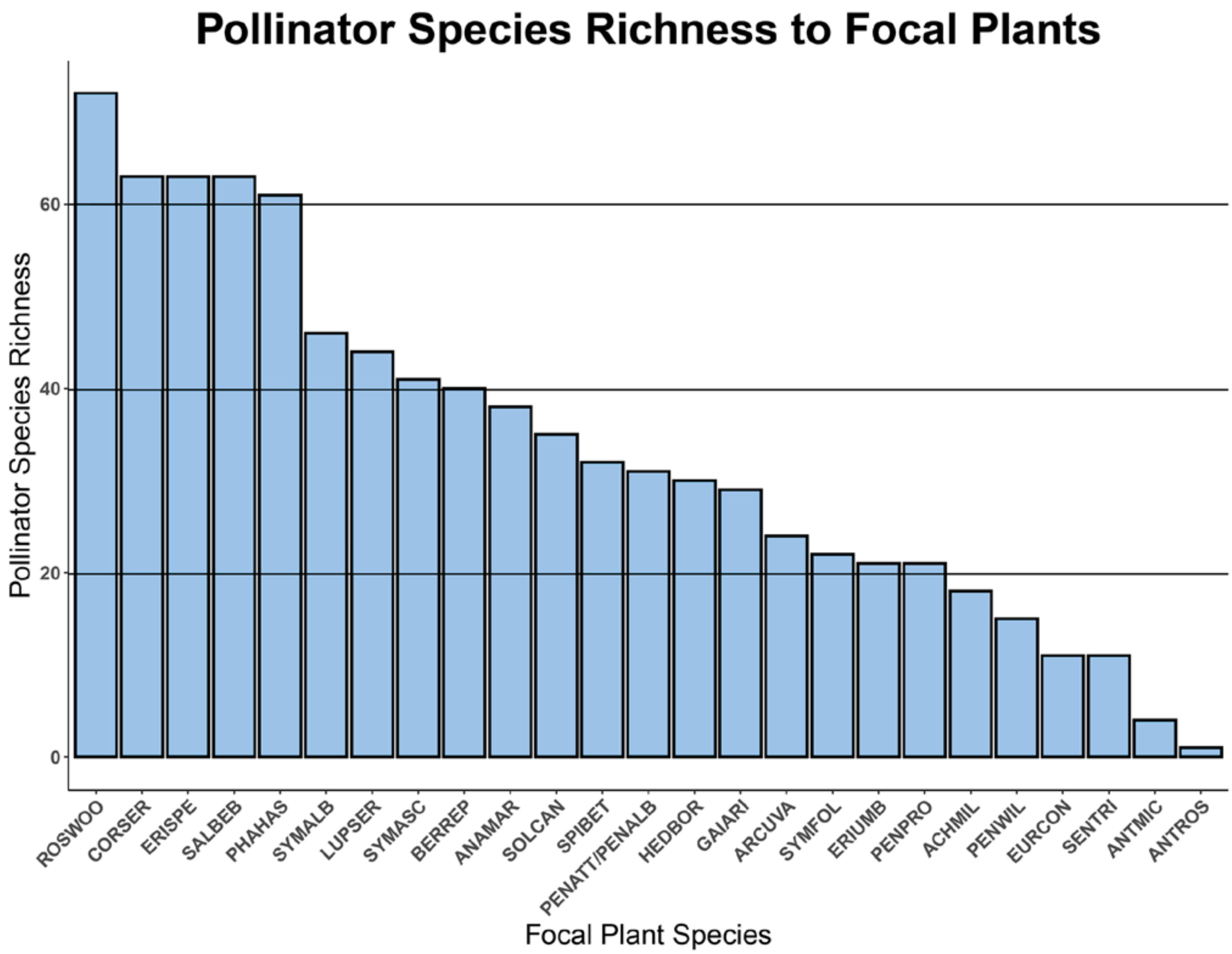

Figure 7—Bee species richness (y-axis) visiting each focal plant species (x-axis). Focal plants are arranged in descending order according to the raw number of bee species observed visiting each plant species. Focal plants are reported using the six-letter abbreviation in table 1.

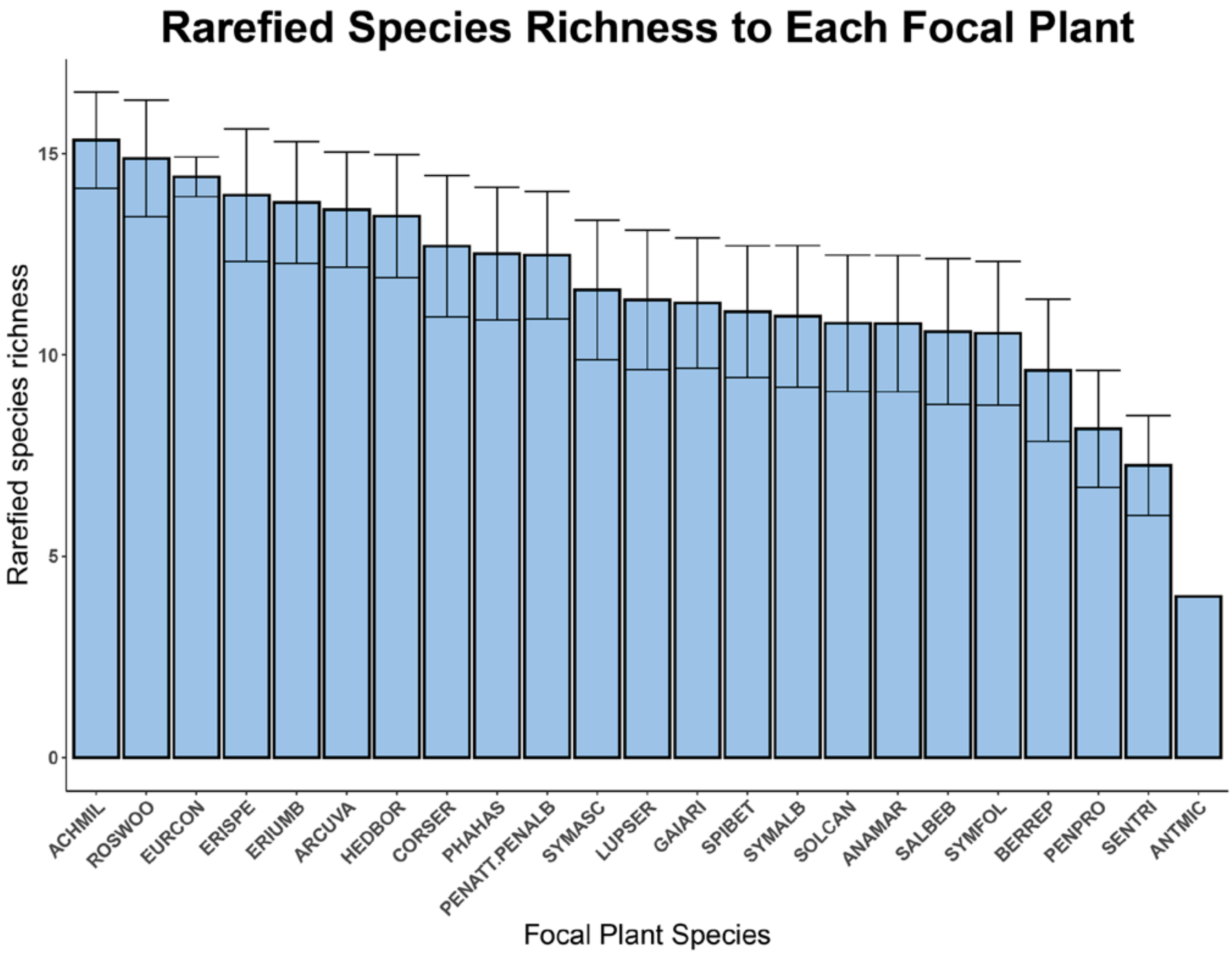

Figure 8—Rarefied bee species richness (y-axis) for each focal plant species (x-axis). Focal plants are arranged in descending order according to the number of bee species expected to visit each focal plant species given a random, similar sample size. Error bars are SE +/- 1. Focal plants are reported using the six-letter abbreviation in table 1. Rarefaction was based on the focal plant species with the smallest sample size (ANTMIC) and therefore lacks error bars.

Specialist Bees

Specialist bees form strong associations with only a few plant species. These host plants are occasionally the only source of floral resources for specialist bees. We identified 71 bee species that were observed to visit only a single focal plant species (fig. 9). *Salix bebbiana* was visited by 12 unique bee species, followed by *Phacelia hastata* (n = 9) and *Symphyotrichum ascendens* (n = 7) (table 7).

Spatial and Temporal Availability of Floral Resources

Focal plants that occurred across the most sites (top 25th percentile) included *Achillea millefolium*, *Erigeron speciosus*, *Lupinus sericeus*, *Gaillardia aristata*, and *Symphyotrichum foliaceum*, whereas plant species that occurred in the fewest number of sites (bottom 25th percentile) included *Antennaria microphylla*, *Eurybia conspicua*, *Hedysarum boreale*, *Solidago canadensis*, and *Antennaria rosea* (fig. 10).

Based on the period during the growing season when bees were observed visiting flowers, we classified 6 plant species as early bloomers (fig. 11, cyan top rows), 8 plant species as mid-season bloomers (fig. 11, magenta, middle rows), and 11 plant species as late bloomers (fig. 11, brown, bottom rows). Early blooming plants were receptive to pollinators from early to mid-May, middle bloomers from late May through mid-June, and late bloomers from mid-June through August (fig. 11). *Salix bebbiana*, *Arctostaphylos uva-ursi*, *Berberis repens*, and *Cornus sericeus* were the earliest plants visited by bees, whereas *Eurybia conspicua*, *Symphyotrichum ascendens*, *Symphyotrichum foliaceum*, and *Solidago canadensis* were some of the last to be visited. Mid-season plant species included *Rosa woodsii* and *Phacelia hastata*, which, as described above, were also visited by the most bee species. Plants within the top 25th percentile for the longest bloom duration included *Eurybia conspicua*, *Salix bebbiana*, *Senecio triangularis*, *Lupinus sericeus*, and *Penstemon* spp., whereas, plant species in the bottom 25th percentile of bloom duration included *Penstemon procerus*, *Symphyotrichum ascendens*, *Symphyotrichum foliaceum*, *Erigeron speciosus*, and *Cornus sericeus* (fig. 12).

“Pollinator-Friendliness” Score Cards

Focal plants within each seasonal group were ranked for each bee visitation and flowering phenology metric, which were summed to create a composite score of “pollinator friendliness.” Within early season plants, *Salix bebbiana* and *Arctostaphylos uva-ursi* received the highest composite rank score (table 8). Within middle-season plants, *Rosa woodsii*, *Lupinus sericeus*, and *Symphoricarpos albus* received the highest composite rank score (table 8). For late season plants, *Gaillardia aristata*, *Erigeron speciosus*, and *Symphyotrichum ascendens* received the highest composite rank score (table 8).

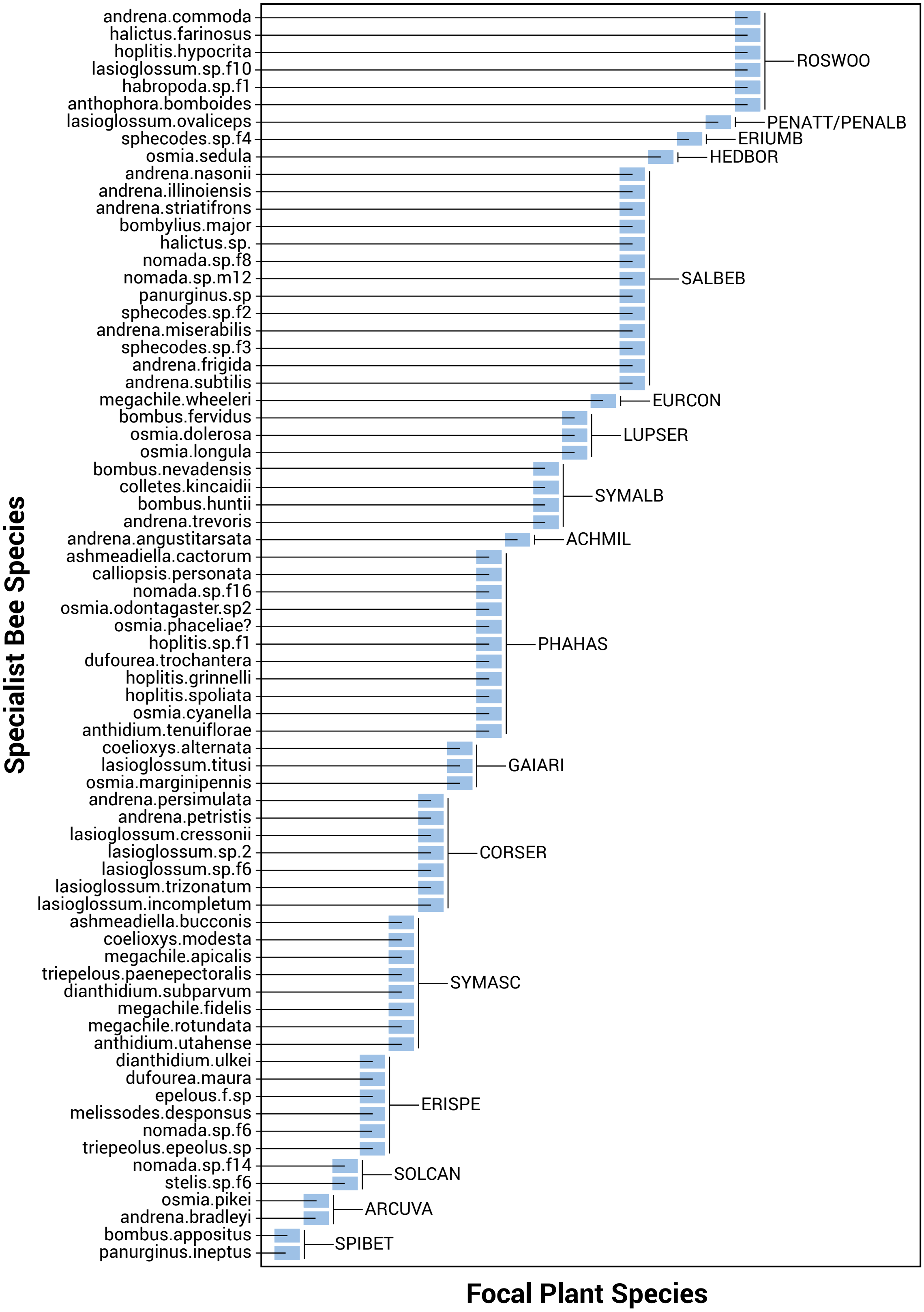

Figure 9—Matrix representation of bee-flower interactions between focal-plant species and specialist bees (rows). Specialist bees were defined as a bee species that only visited one of the focal plant species. Blue boxes represent an observed interaction between a specialist bee species and a focal plant species. Focal species with more blue boxes are visited by more specialist bee species. Focal plants are reported using the six-letter abbreviation in table 1.

Table 7—The total number of specialist bee species that visit each focal plant species. The number of specialists corresponds to the number of blue boxes from the bee-plant interaction matrix (fig. 9).

Forb and shrub species	Common name	Number of specialists
Salix bebbiana	Bebb's willow	12
Phacelia hastata	Silverleaf scorpion weed	9
Symphyotrichum ascendens	Showy aster	7
Cornus sericea	Red osier dogwood	7
Erigeron speciosus	Showy fleabane	6
Lupinus sericeus	Silky lupine	5
Symphoricarpos albus	Snowberry	4
Rosa woodsii	Wood's rose	4
Spiraea betulifolia	Birchleaf spiraea	3
Gaillardia aristata	Blanket flower	3
Solidago canadensis	Canada goldenrod	2
Arctostaphylos uva-ursi	Kinnikinnick	2
Achillea millefolium	Yarrow	2
Symphyotrichum foliaceum	Smooth aster	1
Penstemon attenuatus/albertinus	Penstemon species	1
Hedysarum boreale	Boreal sweetvetch	1
Eriogonum umbellatum	Sulphur buckwheat	1
Berberis repens	Oregon grape	1

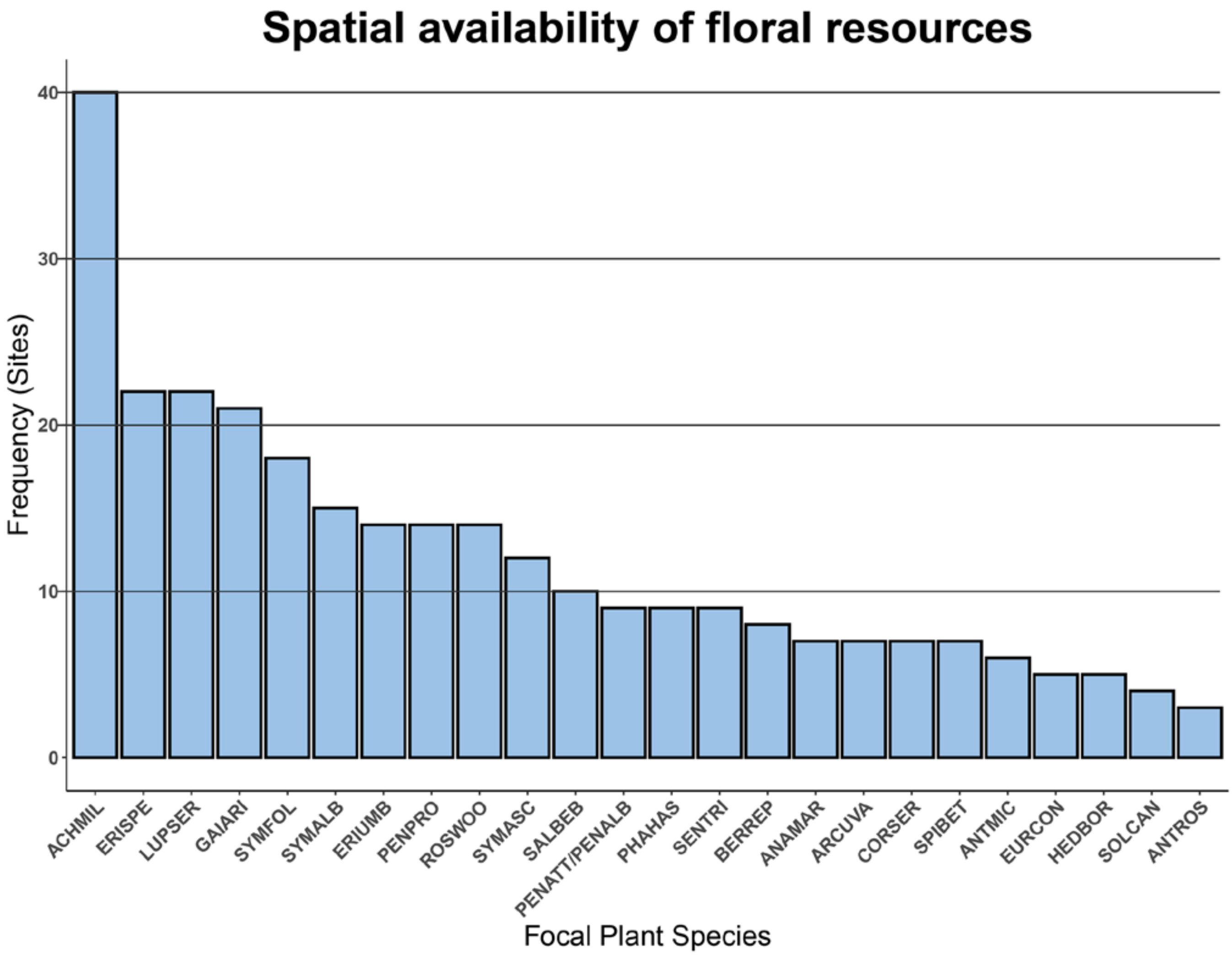

Figure 10—Frequency of occurrence (y-axis) for each focal plant species (x-axis) at sites across the study area. Focal plants that occur more frequently are thought to provide foraging resources for bees across space because flowers are common in different habitat contexts. Focal plants are arranged in descending order for frequency of occurrence across the study sites. Focal plants are reported using the six-letter abbreviation in table 1.

Early

Common Name	Scientific Name	Plant Type	Flower Color	April	May	June	July	August	September
Bebb's Willow	*Salix bebbiana*	shrub	white						
Oregon Grape	*Berberis repens*	shrub	yellow						
Kinnikinnick Berry	*Arctostaphylos uva-ursi*	shrub	pink/ white						
Red Osier Dogwood	*Cornus sericea*	shrub	white						
Littleleaf Pussytoes	*Antennaria microphylla*	forb	white						
Rosy Pussytoes	*Antennaria rosea*	forb	pink/ white						

Middle

Common Name	Scientific Name	Plant Type	Flower Color	April	May	June	July	August	September
Silky Lupine	*Lupinus sericeus*	forb	purple						
Wood's Rose	*Rosa woodsii*	shrub	pink						
Taper-Leaved Penstemon	*Penstemon attenuatus*	forb	blue/ purple						
Alberta Beardtongue	*Penstemon albertinus*	forb	blue/ purple						
Yarrow	*Achillea millefolium*	forb	white						
Boreal sweet-vetch	*Hedysarum boreale*	forb	purple						
Sulphur Buckwheat	*Eriogonum umbellatum*	forb	yellow						

Late

Common Name	Scientific Name	Plant Type	Flower Color	April	May	June	July	August	September
Blanketflower	*Gaillardia aristata*	forb	yellow/red						
Snowberry	*Symphoricarpos albus*	shrub	white						
Birchleaf Spiraea	*Spiraea betulifolia*	forb	white						
Littleflower Penstemon	*Penstemon procerus*	forb	purple						
Showy Fleabane	*Erigeron speciosus*	forb	purple						
Arrowleaf groundsel	*Senecio triangularis*	forb	yellow						
Pearly Everlasting	*Anaphalis margaritaceae*	forb	white						
Showy Aster	*Eurybia conspicua*	forb	purple						
Western Aster	*Symphyotrichum ascendens*	forb	purple						
Smooth Aster	*Symphyotrichum foliaceum*	forb	purple						
Canada Goldenrod	*Solidago canadensis*	forb	yellow						

Figure 11—Focal plant species arranged in sequential order according to the first day of observed bee visitation to flowers and the duration of the bloom time across the growing season. Colored bars correspond to the bee visitation period of each plant in early, middle, and late periods of the growing season. Plant type and flower color are also listed.

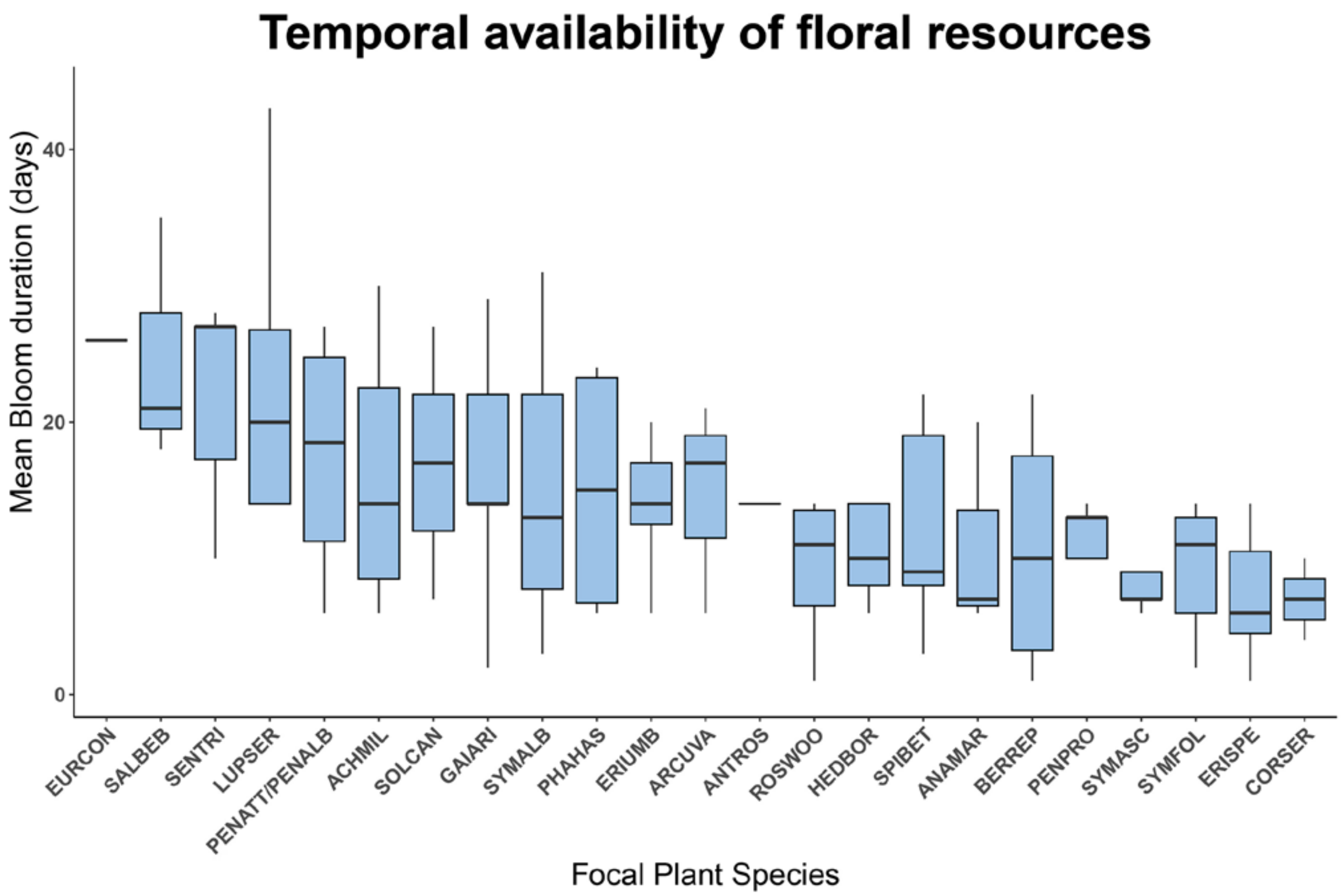

Figure 12—Mean bloom duration (y-axis) of focal plant species (x-axis) at each site, ordered from longest to shortest. Bloom duration was used as a metric for how long flowers can provide resources for bees during the growing season. Focal plants are reported using the six-letter abbreviation in table 1.

Table 8—Scoring cards for early, middle, and late season focal plant species based on the species richness, abundance, uniqueness of visiting bee communities, and bloom duration. Scores are the rank of each plant for each metric relative to plants within the same seasonal group, with the highest rank being awarded to the plants with the greatest value in a category. Plants with the highest total score are considered the most pollinator friendly within their seasonal group. These cards can be used to select and tailor pollinator-friendly mixes (e.g., by habitat). Plants should be selected from each season to ensure floral resources are provided across seasons.

Forb and shrub species	Season	Visitation rate	Bee richness	Specialists	Temporal availability	Spatial availability	Total score
Salix bebbiana	Early	4	4	6	6	6	26
Arcostaphylos uva-ursi	Early	6	6	4	5	4	25
Berberis repens	Early	5	3	3	3	5	19
Cornus sericea	Early	3	5	5	2	3	18
Antennaria rosea	Early	1	1	2	4	1	9
Antennaria microphylla	Early	2	2	2	1	2	9

Forb and shrub species	Season	Visitation rate	Bee richness	Specialists	Temporal availability	Spatial availability	Total score
Rosa woodsii	Middle	8	9	7	3	5	32
Lupinus sericeus	Middle	3	3	8	9	8	31
Symphoricarpos albus	Middle	9	1	7	6	7	30
Achillea millefolium	Middle	1	8	4	7	9	29
Phacelia hastata	Middle	5	6	9	5	3	28
Penstemon spp.	Middle	4	5	3	8	4	22
Hedysarum boreale	Middle	7	7	3	2	1	20
Erogonum umbellatum	Middle	2	4	3	4	6	19
Spiraea betulifolia	Middle	6	2	5	1	2	16

Forb and shrub species	Season	Visitation rate	Bee richness	Specialists	Temporal availability	Spatial availability	Total score
Gaillardia aristata	Late	9	5	7	6	8	35
Erigeron speciosus	Late	6	8	8	1	9	32
Symphyotrichum ascendens	Late	8	6	9	3	5	31
Eurybia conspicua	Late	7	9	4	9	2	31
Solidago canadensis	Late	3	7	6	7	1	24
Symphyotrichum foliaceum	Late	5	3	5	2	7	22
Senecio triangularis	Late	4	1	4	8	4	21
Anaphalis margaritacea	Late	2	4	4	5	3	18
Penstemon procerus	Late	1	2	4	4	6	17

The Western Bumble Bee

The western bumble bee is an SCC on multiple units in the National Forest System. Preferred plants of the western bumble bee could be incorporated into seed mixes to advance restoration efforts for this species in decline. We observed the western bumble bee visiting seven native plant species that are not commercially available to Region 1 (i.e., nonfocal plant species), one invasive plant species, and four focal plant species, including *Spiraea betulifolia*, *Solidago canadensis*, *Symphoricarpos albus*, and *Lupinus sericeus* (fig. 13; table 9)

Designing Pollinator-Friendly Seed Mixes

The overall best mix of pollinator-friendly plants that span the growing season is shown in figure 14. The combination of these plants were visited by 198 of the 246 (80 percent) bee species, which supports a considerable amount of the observed bee community.

DISCUSSION

Summary of the Primary Findings

Bees, and the pollination services they provide, are declining globally. To counteract trends in bee populations, federal land management agencies in the United States have been tasked with developing management strategies to conserve bee populations on multi-use public lands. However, restoration strategies for bee communities in wildlands remain poorly understood. Seed mixes are an effective strategy to supplement floral nectar and pollen resources across the landscape and improve bee species abundance and richness (Isaacs et al. 2009; Tuell et al. 2014; Williams et al. 2015). However, the plant species that compose seed mixes are rarely evaluated for their effectiveness at attracting and providing resources for bees. We conducted a study to compare bee community visitation and visitation periods among commercially available native plant species to design an optimal seed mix for bee restoration on national forests in western Montana. Based on the combination of bee community visitation and visitation period of each plant species, *Salix bebbiana*, *Arctostaphylos uva-ursi*, *Rosa woodsii*, *Lupinus sericeus*, *Symphoricarpos albus*, *Gaillardia aristata*, *Symphyotrichum foliaceum*, and *Erigeron speciosus* provide an optimal seed mix for bee restoration across the most common habitat types in western Montana. Furthermore, bee visitation patterns to nonfocal plant species were analyzed to inform future efforts advancing the availability of native plant materials for bee habitat revegetation and the conservation of endangered species.

Plant species with the highest bee visitation rates were predominately early or late season blooming plants. *Berberis repens*, *Arctostaphylos uva-ursi*, and *Salix bebbiana* are early season bloomers and were among the plants with the highest

Figure 13—The western bumble bee (*B. occidentalis*) was observed to visit these 11 native and 1 invasive plant species in this study (see table 9). These plant species could be important components in mixes focused on restoring habitat for this potentially endangered species. Public domain photos from Flickr and courtesy photos by Dr. Matt Lavin, Montana State University.

Table 9—Plant species visited by the western bumble bee (*Bombus occidentalis*). The scientific and common name for each plant species is listed. Plants in bold are also focal plant species.

Forb and shrub species	Common name
Spiraea betulifolia	**Birchleaf spirea**
Symphoricarpos albus	**Snowberry**
Frasera speciosa	Monument plant
Lupinus sericeus	**Silky lupine**
Carduus nutans	Musk thistle
Campanula rotundifolia	Purple harebell
Pedicularis groenlandica	Elephant head
Sedum lanceolatum	Stonecrop
Mimulus lewisii	Purple monkeyflower
Geranium richardsonii	Richardson's geranium
Solidago canadensis	**Canada goldenrod**
Solidago multiradiata	Rocky Mountain goldenrod

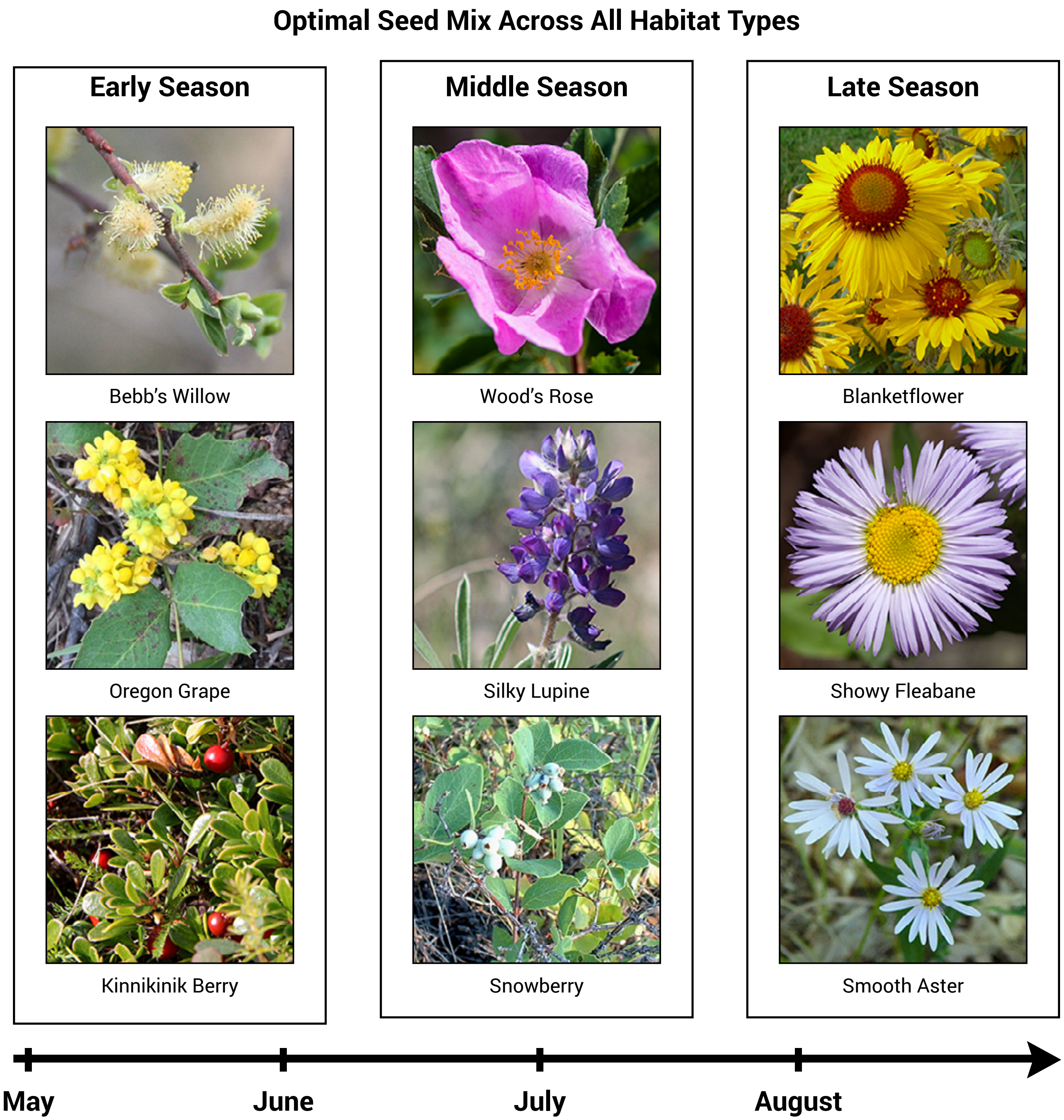

Figure 14—Based on the composite rating from the pollinator-friendly score card, these top scoring plant species are suggested for the early, middle, and late season, for most habitat types. Public domain photos from Flickr.

visitation rates. The beginning of the growing season can be a resource bottleneck for bees, when relatively few plants are flowering (Havens and Vitt 2016). Lack of resources early in the season can have important effects on bee populations later in the season. For example, bumble bee queens that are food-limited during nest initiation (beginning of the growing season) have reduced chances of survival and produced colonies with fewer larvae (Watrous et al. 2019; Woodard et al. 2015). Additionally, *Gaillardia aristata* and *Symphyotrichum ascendens* are late season bloomers and were among plants with the highest visitation rates. Late season represents another critical time during the growing season when many bee species collect floral resources before entering diapause for the winter. Interestingly, plants that bloomed during the middle of the growing season had relatively low visitation rates compared to early and late bloomers. The middle of the growing season is the peak of floral availability for pollinators, and it could be the case that co-occurring forb species increase competition for pollinator visitation. Restoration efforts that provide floral resources during critical periods when flowers are often scarce—especially early and late in the growing season—can fill these bottlenecks and may increase bee populations.

Riparian plants had high pollinator visitation richness and supported specialist bees despite being spatially restricted to water sources. *Salix bebbiana* and *Cornus sericea* had relatively high observed species richness, compared to plant species that were more common throughout the study area. Riparian habitats serve as the interface between terrestrial and aquatic habitats and support high levels of biodiversity in the northern Rocky Mountains (Baril et al. 2011). High densities of floral resources, structural vegetation, and microclimates that improve nesting success, and a high degree of connectivity with other habitat patches, underscore the potential importance of riparian zones for pollinators (Williams 2011). Restoration efforts focused within riparian habitats are likely to play a critical role for conserving bee communities.

Seed mixes could help restore whole pollinator communities by containing plants that support specialist bee species, which are the bees that are most vulnerable to habitat loss (Bommarco et al. 2010). Within this study, *Salix bebbiana* supported the most specialist bee species (n = 12), again suggesting that riparian habitats, early in the growing season, are concentrated areas of bee diversity. *Salix bebbiana* was visited primarily by bees within the family Andrenidae (commonly called mining bees), which is a speciose group of early season foraging species (Cane 2020; Nichols et al. 2019). Specialist *Andrena* species caught during this study included *Andrena angustitarsata*, *Andrena bradleyi*, *Andrena commoda*, *Andrena illinoiensis*, *Andrena miserabilis*, *Andrena nasonii*, *Andrena persimulata*, *Andrena petristis*, *Andrena striatifrons*, and *Andrena trevoris*. *Phacelia hastata* (n = 9) and *Symphyotrichum ascendens* (n = 7) were visited by the most specialist bee species among middle- and late-blooming plant species. These plant species were visited by bees belonging to several genera, including *Hoplitis* (Family: Megachilidae), *Osmia* (Family: Megachilidae), and *Nomada*

(Family: Apidae). Specialists in these genera include *Hoplitis grinelli*, *Osmia cyanella*, *Osmia dolerosa*, *Osmia marginipennis*, *Osmia longula*, and *Osmia pikei*. Specimens of *Nomada* could only be identified to morphospecies (Appendix). Seed mixes containing plants in different phenologic groups might be required to support specialist bee species that are active at different times during the growing season.

Plants that can tolerate a wide variety of environmental conditions and occur across a range of habitat types can comprise a broadly applicable seed mix for naturally complex ecosystems. *Achillea millefolium*, *Erigeron speciosus*, *Lupinus sericeus*, and *Gaillardia aristata* were the plants that occurred most frequently across the study system. These plants could represent a reliable source for floral resources regardless of the habitat type. Similarly, *Lupinus sericeus*, *Achillea millefolium*, and *Gaillardia aristata* had relatively long bloom durations, suggesting that these plants make resources available to bees by flowering for long periods during the growing season. Interestingly, *Achillea millefolium* was the most common plant species across all sites in this study, and one of the longest blooming plants, but had the lowest visitation rate among all plant species. This was consistent with another study from the Great Basin, which demonstrated that *Achillea millefolium* received the lowest visitation rate but was the most common plant of 17 plants evaluated in a seed mix (Cane and Love 2016). As a result, some plants that have a broad habitat distribution might be better suited as plants that can establish vegetation cover or outcompete invasive plant species, while providing minimal resources for pollinators.

Utilizing plants with the highest composite score from each seasonal group (table 8), we developed a seed mix that should support the majority of the bee community (80 percent of bee species; fig. 14). While the use of a single mix for all revegetation projects across a Forest might be desirable logistically, decreasing the site-to-site variability of plant communities might simplify landscapes and homogenize bee communities at a landscape scale. Land managers can use the pollinator-friendliness score cards to choose plants tailored to the specific needs of vegetation restoration at local scales, while providing floral resources for pollinators (table 8) and preserving the site-to-site variability of plant communities. Moreover, when possible, it is better to include as many species as possible in revegetation efforts, as adding plant species to the mix should add bee species that can be supported by the restored habitat. Lastly, the methods used here to design seed mixes for pollinators—identifying flowering plant species already available for restoration, and assessessing and ranking the relative value to pollinators in the field—can be used in other regions to identify pollinator-friendly restoration mixes.

Importantly, our study only evaluated the benefits of focal plants for bee communities following plant establishment but neglected other important aspects of focal plants for landscape revegetation including germination, dispersal ability, and the persistence of plants on the landscape. While annuals may be important to establish vegetation cover immediately following a disturbance, perennials could be important to establish vegetation cover and pollinator resources long-term. Additionally, seeds that are dispersed aerially may not be planted at the optimal seeding depths, which may influence rates of germination. Plants that can germinate and establish despite suboptimal seeding techniques may be important for providing foraging resources for pollinators across a landscape.

The Western Bumble Bee

The range and abundance of the western bumble bee has declined dramatically in recent decades, and this species is being considered for listing under the ESA (Graves et al. 2020). Information about the plant species visited by the western bumble bee is essential for managing and restoring their habitat. We observed the western bumble bee visiting 12 plant species, 4 of which were included in the original list of focal plant species: *Spiraea betulifolia*, *Symphoricarpos albus*, *Solidago canadensis*, and *Lupinus sericeus*. These four focal plant species are already commercially available in quantities large enough to incorporate into seed mixes to begin habitat rehabilitation for the western bumble bee. Furthermore, if nurseries can provide materials of other plant species preferred by the western bumble bee, then a specific seed mix could be designed to restore habitat for this potentially endangered species. In addition to habitat loss, western bumble bee population decline is correlated with the gut fungus *Nosema bombi* (Cameron et al. 2011; Cameron et al. 2016). Vegetation management that improves the availability of plants with medicinal value to bumble bees could benefit the western bumble bee. For instance, a diet of sunflower pollen reduced levels of the gut parasite *Crithidia bombi* in the common eastern bumble bee (*Bombus impatiens*) (Adler et al. 2020; Giacomini et al. 2018; Richardson et al. 2015). If native plants can be identified that are of medicinal value to bumble bees and can treat bee parasites, inclusion of such species in revegetation mixes might further improve bee restoration. The coordination of multiple federal agencies, and further research, are required to identify threats facing the western bumble bee and effective management strategies to reverse population trends (Graves et al. 2020).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Revegetation efforts that use native plants form the basis for the recovery of ecosystem function and services following disturbances. The restoration of bee communities has recently become a primary goal for federal land management agencies because bees are in decline but essential for the delivery of pollination services to crops enjoyed by humans and the maintenance of native vegetation communities. As a result, bees support ecosystem functions like pest control, soil and water quality, weed suppression, and aesthetics (Wratten et al. 2012), and thus are critical for maintaining healthy lands that face frequent disturbances from grazing, land use change, wildfire, mining, climate change, and recreation. Therefore, nurseries and seed stock programs that provide plant materials at commercial scales are critical in supplying land managers with resources to meet the growing demands from public lands. Optimizing the flow of plant materials from the Region 1 Native Plant Program to meet the demands of public lands, while benefiting bee communities, is the challenge that needs to be met to support healthy national forest lands (fig. 15).

Pollinator-friendly plant species have an outsized influence on providing foraging resources for the bee community. Native plant species are produced at commercial scale to meet the increasing demands of land managers for restoration materials. Among native plant species produced for restoration purposes, *Salix bebbiana*, *Arctostaphylos uva-ursi*, *Rosa woodsii*, *Symphoricarpos albus*, *Lupinus sericeus*, *Gaillardia aristata*, *Symphyotrichum ascendens*, and *Erigeron speciosus*, are eight plants that could be composed into a seed mix to potentially support a majority of the bee communities for the duration of the growing season. Different combinations of pollinator-friendly plants can be utilized within multiple habitat types found within Region 1 to provide a diversity of foraging

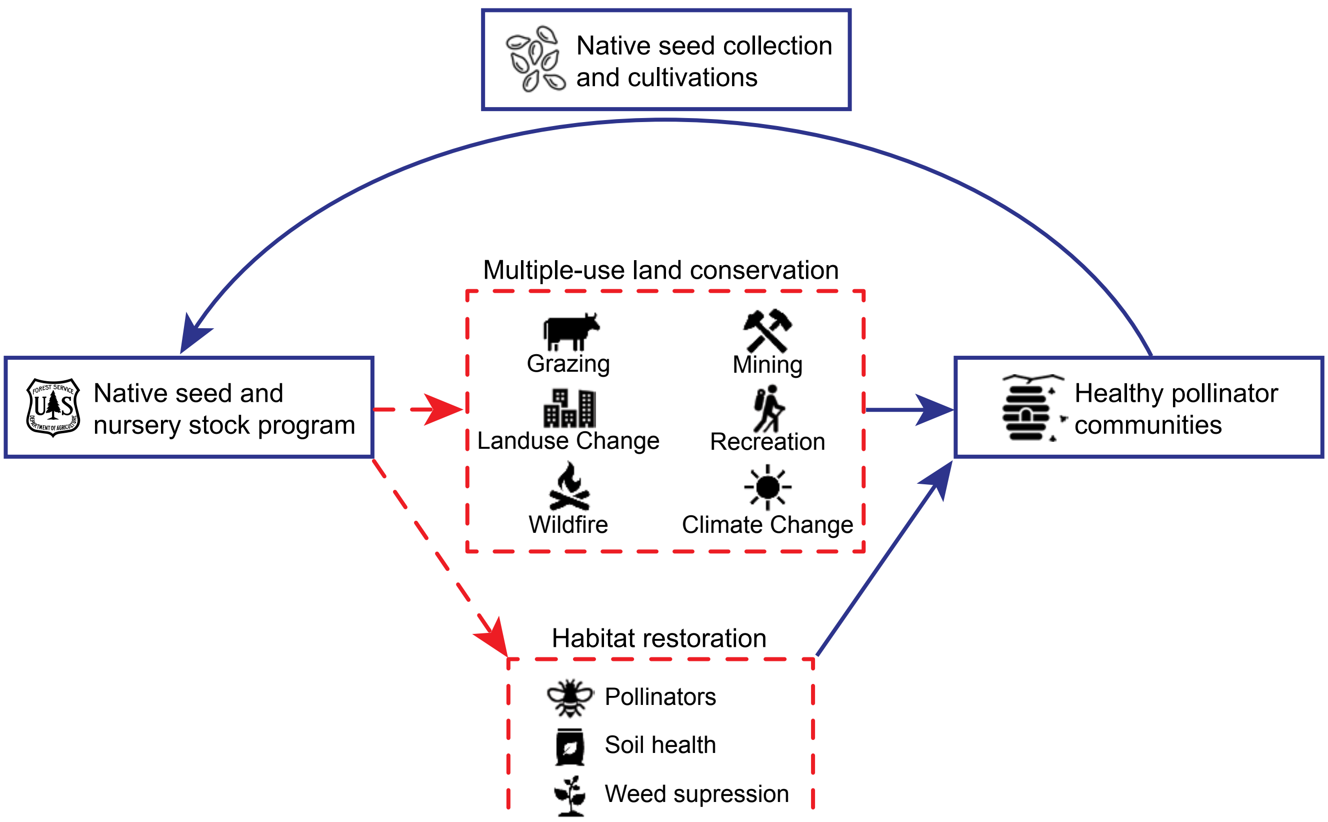

Figure 15—Flow chart outlining the supply and demand for pollinator-friendly plant materials that can be used to achieve multiple management goals on federally managed lands. Boxes are activities and programs that produce and consume native plant materials, while arrows indicate the directional movement of native plant materials. Blue lines produce native plant materials, while red lines consume plant resources. The native seed and nursery stock program provide native plant materials for the conservation of multiple use lands and restoration of pollinator habitat. Maintaining healthy ecosystems through seed mixes results in healthy pollinator communities that produce sources of locally adapted plant populations. These plant populations can be cultivated by native seed collection programs to provide more pollinator-friendly plant materials through the native seed and nursery stock program.

resources that are attractive to bee communities. Additionally, *Spiraea betualifolia*, *Lupinus sericeus*, *Solidago canadensis*, and *Symphoricarpos albus* were visited by the western bumble bee, suggesting these plants might be critical to support efforts aimed at protecting this rapidly declining species. Seed mixes that prioritize pollinator-friendly plants for habitat revegetation may improve pollinator habitat and ecosystem health to meet multiple management goals.

Seed Mixes in Region 1: An Evaluation of the Current Plant Materials and Opportunities to Improve Applications

Availability of Plant Materials for Future Restoration Projects

Future work could identify more pollinator-friendly plant species that can be cultivated in nursery programs and made available for bee restoration activities. Bees were observed visiting an additional 195 native plant species during this study, which could identify plants that are more effective for bee restoration than the focal plants evaluated. For instance, among plant species that occurred in over 20 sites, the 5 nonfocal plants with the highest visitation rates were *Geranium viscosissimum*, *Eurybia integrifolia*, *Geranium richardsonii*, *Fragaria virginiana*, and *Agoseris glauca*, suggesting the list of candidate focal plants could be improved to maximize the benefits to bees (fig. 16; table 10). Additionally, nursery programs could prioritize the availability of plant materials specifically from focal plant species that scored well in this study by developing field methods for seed production. Improving upon methods to cultivate pollinator-friendly plants and advance the availability of plant materials could help increase the ability of land managers to meet restoration goals for bees in the western United States. For instance, *Phacelia hastata* grows better in a 10-cm square pot than in a cone-shaped container, and aboveground biomass increases with fertilization rates up to 200 mg L^{-1} N (Bujak and Dougher 2017). Greater aboveground biomass could result in greater floral display, pollinator visitation, and seed production.

Considerations for Seeding Applications

It is important to consider practical strategies of seeding that will maximize the cost-effectiveness and cover of desired forbs in restoration settings, including the seeding rates and orientation of planting. Seeding at higher densities is important for forbs to outcompete and suppress invasive plant species (Carter and Blair 2012; Jaksetic et al. 2018). However, increasing seeding density has diminishing returns for restoration projects. While seeding at higher densities improves the cover of native forbs, the gains could be offset by the cost of native forb seeds (Wilkerson et al. 2014). For private lands in the Northern Rockies, the suggested seeding rate using seed mixes that contain annuals and short- and long-lived perennials is 500–600 seeds m^{-2} (Pokorny et al. 2020), while the suggested seeding rates using seed mixes containing annual and perennial grasses, forbs, and shrubs in prairies of northeastern Colorado have been suggested as high as 1,366

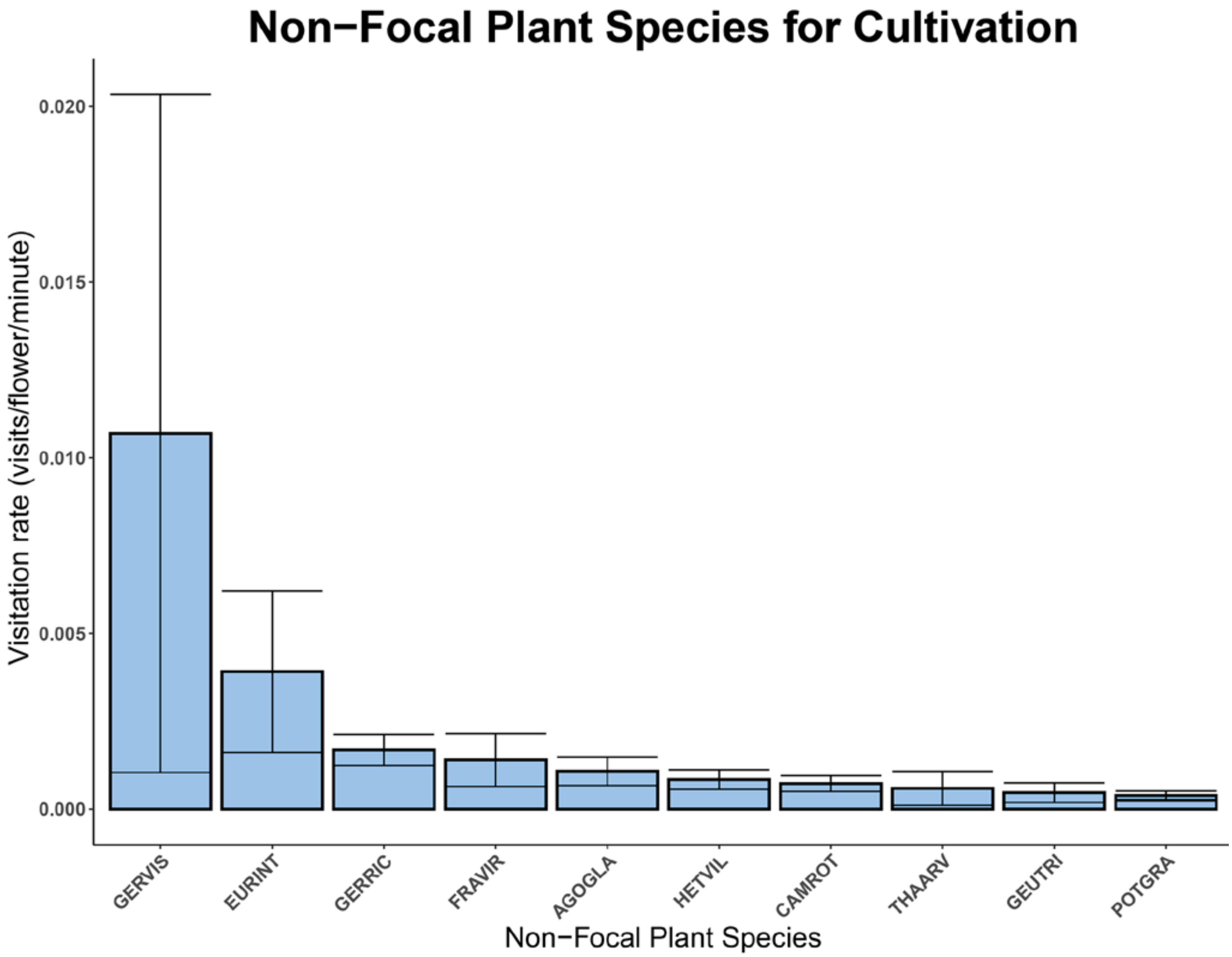

Figure 16—The standardized visitation rate per observation period (y-axis) of bees to nonfocal plant species (x-axis) that occurred at more than 20 sites. Plants are arranged in descending order according to the number of bee specimens per flower per minute collected from each plant species. Error bars are +/- 1 standard error. Focal plants are reported using the six-letter abbreviation in table 10.

Table 10—Nonfocal plant species that occurred in more than 20 sites with the greatest standardized visitation rates. Plants are arranged from highest to lowest standardized visitation rates. The scientific names, common names, and six-letter abbreviations are listed. These plants might direct future nursery efforts to make plant materials available for bee restoration.

Forb and shrub species	Common name	Six letter abbreviation
Geranium viscosissimum	Sticky geranium	GERVIS
Eurybia integrifolia	Thickstem aster	EURINT
Geranium richardsonii	Richard's geranium	GERRIC
Fragaria virginiana	Wild strawberry	FRAVIR
Agoseris glauca	Pale agoseris	AGOGLA
Heterotheca villosa	Hairy false goldenaster	HETVIL
Campanula rotundifolia	Purple harebell	CAMROT
Thlaspi arvense	Pennycress	THLARV
Geum triflorum	Prairie smoke	GEUTRI
Potentilla gracilis	Slender cinquefoil	POTGRA

live seeds m^{-2} (Barr et al. 2017). Additionally, planting native forbs in alternating rows reduced competition from seeded grasses, resulting in higher survival rates among native forbs when compared with seeding native forbs and grasses in the same rows (Pokorny et al. 2020). Understanding the seeding densities and orientation that maximize cover of native forbs and improve bee habitat, without unnecessarily increasing costs of restoration projects, will require additional research in wildland settings.

Restoration projects should weigh the costs and benefits of including grasses in seed mixes. Increasing the seed density of grasses reduced native forb cover and biomass following seeding in prairie grasslands (Dickson and Busby 2009) and in southern California chaparral following wildfire (Beyers 2004). This would likely have a negative effect on pollinators. It is also unclear if grasses have persistent effects on the ecosystem and potentially inhibit ecological integrity in the long term (Beyers 2004). For instance, grasses increase vegetation cover immediately following fire but suppress native forb cover (Barro and Conard 1991) and conifer seedling growth (Elliott and White 1987), which inhibits the establishment of old-growth plants. However, grasses quickly revegetate landscapes following wildfire to prevent soil erosion, prevent sediment runoff, provide forage for grazing ungulates, suppress invasive species, and regreen landscapes. With the frequency and severity of fires anticipated to increase into the future, grasses could play an important role to immediately offset threats to ecosystem integrity; however, mixes of both grasses and forbs should be considered. For example, seeding a mixture of native perennial flowering plants and grasses after fire increased perennial cover and inhibited cheatgrass invasion better than seeding a mix of nonnative perennial grasses (Urza et al. 2019). This suggests that mixes of forbs and grasses have restoration benefits beyond pollinators. Future research is needed to understand the restoration value of forb-grass mixtures.

Seed planting technologies and strategies might improve the effectiveness of seeding operations for bee communities on national forest land. Naturally complex landscapes typically have suboptimal growing conditions for plants. Chemical applications like soil surfactants (Madsen et al. 2012; Madsen et al. 2016), physical structures like snow fences (Fund et al. 2019), and habitat preparation like mulching and increasing planting surface area (Chambers 2000) help increase soil moisture and seedling survival. Additionally, clustering seeds into a single pellet (agglomerative seeding) can provide seedlings enough force to emerge from underneath soil crusts that harden in dry conditions (Madsen et al. 2012). Furthermore, large areas are usually reseeded using airplanes or seed drills, which likely do not dispense seeds at the appropriate seeding depth (Rawlins et al. 2009). Strategies to aid in bulk seed dispersal while improving seed germination and survival will be critical for effective applications of seed mixes.

Restoration Opportunities

Seed mixes can be designed to meet multiple management goals in addition to bee community restoration, including mine reclamation, revegetating grazed areas, soil health, and road decommissioning. Furthermore, seed mixes can be deployed strategically within linear landscape features (roads and powerline easements) to transform canopy openings into wildlife corridors and reconnect bee and plant populations.

Mine Reclamation

Phytoremediation uses plants to absorb mine contaminants from soils. In an example from Region 1, 100 years of mining disturbances in Butte, Montana, elevated concentrations of metals, metalloids, and acidity in soils to levels warranting designating the area as an EPA Superfund site (Trilling 2018). Pollinator-friendly plants with a tolerance for heavy metal-laden soils might be important for phytoremediation and bee community restoration. Snowberry, silverleaf scorpionweed, Wood’s rose, and yarrow are focal plants with known tolerances to acid and heavy metal contaminated soil in Montana (Trilling 2018). However, heavy metal accumulation in nectar can negatively affect bee fitness (Moroń et al. 2014; Xun et al. 2018). Future studies are needed to identify plants that can tolerate heavy metal-laden soils without accumulating contaminants in the nectar.

Forage for Wild and Domestic Animals

Plants form the basis of food webs and are critical foraging resources for animals other than bees. Forbs in particular contain micronutrients essential for animal nutrition. For instance, sage grouse (*Centrocerus urophasianus*) are almost entirely dependent on succulent forbs and arthropods during critical life stages, including pre-laying hens and post-fledging chicks (Dumroese et al. 2016). Vegetation improvements using native plants can improve wildlife conservation effectiveness in arid landscapes common throughout the Rocky Mountains (Dumroese et al. 2016). Additionally, seed mixes are commonly used to provide forage for grazing ungulates. However, diet overlap between ungulates and bees might exclude bees from grazing areas if ungulates remove flowers from a habitat (DeBano et al. 2016). Data from the Starkey Experimental Station in Eastern Oregon (Region 6) indicated that yarrow, showy fleabane, and penstemon were focal plants from this study that were documented in the diets of elk, mule deer, and cattle (DeBano et al. 2016). Conversely, plants that were visited by bees but rarely eaten by ungulates included gumweeds (*Grindelia* sp.), pale agoseris (*Agoseris glauca*), mountain tarweed (*Madia glomerata*), horsemint (*Agastache urticifolia*), common camas (*Camassia quamash*), Canadian burnet (*Sanguisorba canadensis*), Cusick's paintbrush (*Castilleja cusickii*), purple violet (*Viola adunca*), and Nuttall's violet (*Viola nuttalii*), suggesting that ungulates might be less likely to exclude bees from foraging resources if habitats are revegetated using these plant species (DeBano et al. 2016). Diet overlap studies should be replicated within Region 1 to develop seed mixes for heavily grazed habitats that benefit both cattle and bees.

Soil Health

Focal plants that grow, germinate, and reproduce quickly are critical for soil stability and productivity following disturbance. Willows and dogwoods can be cloned quickly from cuttings and planted in riparian areas for stream bank stabilization (Kopp et al. 2001). Legumes, like silky lupine, restore soil productivity by regenerating soil nitrogen that is lost following wildfires (Hendricks and Boring 1999; Newland and DeLuca 2000). Furthermore, plants within seed mixes can increase soil porosity, increase bare ground coverage, and reduce soil compaction, leading to more suitable nesting habitats for bees (Anderson and Harmon-Threatt 2016). Therefore, seed mixes might be tailored to include plants with stabilizing root structures and nitrogen-fixing plants in areas where soil erosion and health are priorities, especially as fire frequency and severity are predicted to increase into the future.

Road Decommissioning and Bee Population Connectivity

Seeding linear landscape features like roads and powerline easements can increase plant and bee population connectivity. Powerline easements and roads have high bee species diversity because they are marginal habitats with high light availability (Hopwood 2008; Jackson et al. 2014; Russell et al. 2005; Russell et al. 2018; Steinert et al. 2018; Steinert et al. 2020; Wagner et al. 2014; Wagner et al. 2019). Seed mixes used during the process of decommissioning roads (Grant et al. 2011), along roadways, or within powerline easements are likely to provide foraging resources in species-rich habitats. Additionally, linear landscape features with foraging resources arranged in a stepping-stone pattern can encourage the movement of bees between habitat fragments (Townsend and Levey 2005; Van Geert et al. 2010). Linear landscapes, like roads, offer a promising but understudied opportunity to use seed mixes to benefit pollinators.

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APPENDIX—List of Bee Species

The bee species listed below are those observed visiting focal plant species across the Helena-Lewis and Clark National Forest. Bee species were identified to the lowest taxonomic level (species or morphospecies) when reliable keys were available and with the help of expert taxonomists. Specimens that could not be identified to species were identified to morphospecies (assigned a number and the letter "F" for females and "M" for males). Species are listed alphabetically within bee families.

Andrenidae

Andrena (Andrena) frigida Smith, 1853

Andrena (Andrena) laminibucca Viereck and Cockerell, 1914

Andrena (Andrena) milwaukeensis Graenicher, 1903

Andrena (Andrena) saccata Viereck, 1904

Andrena (Andrena) thaspii Graenicher, 1903

Andrena (Andrena) topazana Cockerell, 1906

Andrena (Andrena) vicinoides Viereck, 1904

Andrena (Cnemidandrena) specularia Donovan, 1977

Andrena (Conandrena) bradleyi Viereck, 1907

Andrena (Euandrena) auricoma Smith, 1879

Andrena (Euandrena) nigrocaerulea Cockerell, 1897

Andrena (Geissandrena) trevoris Cockerell, 1897

Andrena (Gonandrena) persimulata Viereck, 1917

Andrena (Holandrena) cressonii Robertson, 1891

Andrena (Larandrena) miserabilis Cresson, 1872

Andrena (Melandrena) carlini Cockerell, 1901

Andrena (Melandrena) commoda Smith, 1879

Andrena (Melandrena) nivalis Smith, 1853

Andrena (Melandrena) pertristis Cockerell, 1905

Andrena (Melandrena) sola Viereck, 1917

Andrena (Melandrena) transnigra Viereck, 1904

Andrena (Melandrena) vicina Smith, 1853

Andrena (Micrandrena) illinoiensis Robertson, 1891

Andrena (Plastandrena) crataegi Robertson, 1893

Andrena (Plastandrena) prunorum Cockerell, 1896

Andrena (Scaphandrena) scurra Viereck, 1904

Andrena (Simandrena) angustitarsata Viereck, 1904

Andrena (Simandrena) nasonii Robertson, 1895

Andrena (Thysandrena) candida Smith, 1879

Andrena (Thysandrena) knuthiana Cockerell, 1901

Andrena (Thysandrena) medionitens Cockerell, 1902

Andrena (Thysandrena) vierecki Cockerell, 1904

Andrena (Trachandrena) amphibola (Viereck, 1904)

Andrena (Trachandrena) cupreotincta Cockerell, 1901

Andrena (Trachandrena) hippotes Robertson, 1895

Andrena (Trachandrena) miranda Smith, 1879

Andrena (Trachandrena) salicifloris Cockerell, 1897

Andrena (Trachandrena) sigmundi Cockerell, 1902

Andrena (Trachandrena) striatifrons Cockerell, 1897

Andrena (Tylandrena) subtilis Smith, 1879

Calliopsis (Nomadopsis) personata Cockerell, 1897

Panurginus atriceps (Cresson, 1878)

Panurginus ineptus Cockerell, 1922

Panurginus sp. F1

Apidae

Anthophora (Clisodon) terminalis Cresson, 1869

Anthophora (Lophanthophora) pacifica Cresson, 1878

Anthophora (Lophanthophora) ursina Cresson, 1869

Anthophora (Melea) bomboides Kirby, 1838

Apis mellifera Linnaeus, 1758

Bombus (Bombus) occidentalis Greene, 1858

Bombus (Cullumanobombus) rufocinctus Cresson, 1863

Bombus (Psithyrus) flavidus Eversmann, 1852

Bombus (Psithyrus) insularis (Smith, 1861)

Bombus (Pyrobombus) bifarius Cresson, 1878

Bombus (Pyrobombus) centralis Cresson, 1864

Bombus (Pyrobombus) flavifrons Cresson, 1863

Bombus (Pyrobombus) huntii Greene, 1860

Bombus (Pyrobombus) melanopygus Nylander, 1848

Bombus (Pyrobombus) mixtus Cresson, 1878

Bombus (Pyrobombus) sylvicola Kirby, 1837

Bombus (Subterraneobombus) appositus Cresson, 1878

Bombus (Thoracobombus) californicus Smith, 1854

Bombus (Thoracobombus) fervidus (Fabricius, 1798)

Ceratina (Zadontomerus) nanula Cockerell, 1897

Ceratina (Zadontomerus) neomexicana Cockerell, 1901

Epeolus sp.

Eucera (Synhalonia) edwardsii (Cresson, 1878)

Eucera (Synhalonia) frater (Cresson, 1878)

Habropoda sp. F1

Habropoda sp. M1

Habropoda sp. M2

Melecta (Melecta) pacifica subsp. *fulvida* Cresson, 1878

Melissodes (Eumelissodes) confusa Cresson, 1878

Melissodes (Eumelissodes) microstictus Cockerell, 1905

Melissodes (Heliomelissodes) desponsus Smith, 1854

Nomada edwardsii Cresson, 1878

Nomada sp. F1

Nomada sp. F2

Nomada sp. F3

Nomada sp. F4

Nomada sp. F5

Nomada sp. F6

Nomada sp. F7

Nomada sp. F8

Triepeolus/Epeolus sp. F1

Triepeolus paenepectoralis Viereck, 1905

Colletidae

Colletes consors subsp. *consors* Cresson, 1868

Colletes fulgidus Swenk, 1904

Colletes kincaidii Cockerell, 1898

Hylaeus (Cephalylaeus) basalis (Smith, 1853)

Hylaeus (Hylaeus) annulatus (Linnaeus, 1758)

Hylaeus (Hylaeus) leptocephalus (Morawitz, 1871)

Hylaeus (Hylaeus) mesillae (Cockerell, 1896)

Hylaeus (Hylaeus) rudbeckiae (Cockerell and Casad, 1895)

Hylaeus (Hylaeus) verticalis (Cresson, 1869)

Hylaeus (Paraprosopis) coloradensis (Cockerell, 1896)

Hylaeus (Paraprosopis) wootoni (Cockerell, 1896)

Hylaeus (Prosopis) episcopalis (Cockerell, 1896)

Hylaeus (Prosopis) modestus Say, 1837

Halictidae

Agapostemon (Agapostemon) texanus Cresson, 1872

Agapostemon (Agapostemon) virescens (Fabricius, 1775)

Dufourea holocyanea (Cockerell, 1925)

Dufourea maura (Cresson, 1878)

Dufourea trochantera Bohart, 1948

Halictus (Nealictus) farinosus Smith, 1853

Halictus (Odontalictus) ligatus Say, 1837

Halictus (Protohalictus) rubicundus (Christ, 1791)

Halictus (Seladonia) confusus Smith, 185

Halictus (Seladonia) tripartitus Cockerell, 1895

Lasioglossum (Dialictus) abundipunctum Gibbs, 2010

Lasioglossum (Dialictus) near *caducum* (Sandhouse, 1924)

Lasioglossum (Dialictus) near *nevadense* (Crawford, 1907)

Lasioglossum (Dialictus) albipenne (Robertson, 1890)

Lasioglossum (Dialictus) cressonii (Robertson, 1890)

Lasioglossum (Dialictus) ebmerellum Gibbs, 2010

Lasioglossum (Dialictus) ephialtum Gibbs, 2010

Lasioglossum (Dialictus) incompletum Gibbs, 2010

Lasioglossum (Dialictus) laevissimum (Smith, 1853)

Lasioglossum (Dialictus) lineatulum (Crawford, 1906)

Lasioglossum (Dialictus) marinense (Michener, 1936)

Lasioglossum (Dialictus) nigroviride (Graenicher, 1911)

Lasioglossum (Dialictus) obnubilum (Sandhouse, 1924)

Lasioglossum (Dialictus) pruinosum (Robertson, 1892)

Lasioglossum (Dialictus) ruidosense (Cockerell, 1897)

Lasioglossum (Dialictus) sedi (Sandhouse, 1924)

Lasioglossum (Dialictus) succinipenne (Ellis, 1913)

Lasioglossum (Dialictus) tenax (Sandhouse, 1924)

Lasioglossum (Evylaeus) sp. F1

Lasioglossum (Evylaeus) sp. F2

Lasioglossum (Evylaeus) sp. F3

Lasioglossum (Evylaeus) sp. F4

Lasioglossum (Evylaeus) sp. F5

Lasioglossum (Evylaeus) sp. F6

Lasioglossum (Evylaeus) sp. F7

Lasioglossum (Hemihalictus) inconditum Gibbs, 2010

Lasioglossum (Hemihalictus) ovaliceps (Cockerell, 1898)

Lasioglossum (Hemihalictus) sp. F1

Lasioglossum (Hemihalictus) sp. M1

Lasioglossum (Lasioglossum) anhypops McGinley, 1986

Lasioglossum (Lasioglossum) egregium Vachal, 1904

Lasioglossum (Lasioglossum) sisymbrii (Cockerell, 1895)

Lasioglossum (Lasioglossum) titusi (Crawford, 1902)

Lasioglossum (Lasioglossum) trizonatum (Cresson, 1874)

Sphecodes sp. F1

Sphecodes sp. F2

Sphecodes sp. F3

Sphecodes sp. F4

Sphecodes sp. M1

Sphecodes sp. M2

Megachilidae

Anthidium (Anthidium) mormonum Cresson, 1878

Anthidium (Anthidium) tenuiflorae Cockerell, 1907

Anthidium (Anthidium) utahense Swenk, 1914

Ashmeadiella (Ashmeadiella) bucconis (Say, 1837)

Ashmeadiella (Ashmeadiella) cactorum (Cockerell, 1897)

Ashmeadiella (Ashmeadiella) californica (Ashmead, 1897)

Ashmeadiella (Ashmeadiella) pronitens (Cockerell, 1906)

Coelioxys (Boreocoelioxys) banksi Crawford, 1914

Coelioxys (Boreocoelioxys) porterae Cockerell, 1900

Coelioxys (Coelioxys) sodalis Cresson, 1878

Coelioxys (Cyrtocoelioxys) modesta Smith, 1854

Coelioxys (Dasycoelioxys) occidentalis Holmberg, 1916

Coelioxys (Synocoelioxys) alternata Say, 1837

Coelioxys (Synocoelioxys) apacheorum Cockerell, 1900

Coelioxys (Xerocoelioxys) edita Cresson, 1872

Dianthidium (Dianthidium) subparvum Swenk, 1914

Dianthidium (Dianthidium) ulkei (Cresson, 1878)

Heriades (Neotrypetes) carinata Cresson, 1864

Heriades (Neotrypetes) cressoni Michener, 1938

Heriades (Neotrypetes) variolosa (Cresson, 1872)

Hoplitis (Alcidamea) albifrons subsp. *argentifrons* (Cresson, 1864)

Hoplitis (Alcidamea) fulgida subsp. *fulgida* (Cresson, 1864)

Hoplitis (Alcidamea) grinnelli (Cockerell, 1910)

Hoplitis (Alcidamea) hypocrita (Cockerell, 1906)

Hoplitis (Alcidamea) producta (Cresson, 1864)

Hoplitis (Alcidamea) spoliata (Provancher, 1888)

Hoplitis (Alcidamea) truncata (Cresson, 1878)

Hoplitis (Formicapis) robusta (Nylander, 1848)

Megachile (Chelostomoides) angelarum Cockerell, 1902

Megachile (Eutricharaea) apicalis Spinola, 1808

Megachile (Eutricharaea) rotundata (Fabricius, 1793)

Megachile (Megachile) lapponica Thomson, 1872

Megachile (Megachile) montivaga Cresson, 1878

Megachile (Megachile) relativa Cresson, 1878

Megachile (Megachiloides) wheeleri Mitchell, 1927

Megachile (Sayapis) fidelis Cresson, 1878

Megachile (Sayapis) pugnata Say, 1837

Megachile (Xanthosarus) frigida Smith, 1853

Megachile (Xanthosarus) gemula Cresson, 1878

Megachile (Xanthosarus) melanophaea Smith, 1853

Megachile (Xanthosarus) perihirta Cockerell, 1898

Osmia (Cephalosmia) californica Cresson, 1864

Osmia (Cephalosmia) marginipennis Cresson, 1878

Osmia (Cephalosmia) montana subsp. *montana* Cresson, 1864

Osmia (Cephalosmia) subaustralis Cockerell, 1900

Osmia (Melanosmia) aff.paradisica Sandhouse, 1924

Osmia (Melanosmia) albolateralis Cockerell, 1906

Osmia (Melanosmia) atrocyanea Cockerell, 1897

Osmia (Melanosmia) brevis Cresson, 1864

Osmia (Melanosmia) bruneri Cockerell, 1897

Osmia (Melanosmia) bucephala Cresson, 1864

Osmia (Helicosmia) coloradensis Cresson, 1878

Osmia (Melanosmia) cyanella Cockerell, 1897

Osmia (Melanosmia) densa Cresson, 1864

Osmia (Melanosmia) dolerosa Sandhouse, 1939

Osmia (Melanosmia) ednae Cockerell, 1907

Osmia (Melanosmia) grindeliae Cockerell, 1910

Osmia (Melanosmia) inermis (Zetterstedt, 1838)

Osmia (Melanosmia) juxta Cresson, 1864

Osmia (Melanosmia) kincaidii Cockerell, 1897

Osmia (Melanosmia) longula Cresson, 1864

Osmia (Melanosmia) nigrifrons Cresson, 1878

Osmia (Melanosmia) paradisica Sandhouse, 1924

Osmia (Melanosmia) pentstemonis Cockerell, 1906

Osmia (Melanosmia) phaceliae Cockerell, 1907

Osmia (Melanosmia) pikei Cockerell, 1907

Osmia (Melanosmia) pusilla Cresson, 1864

Osmia (Melanosmia) sedula Sandhouse, 1864

Osmia (Melanosmia) tersula Cockerell, 1912

Osmia (Melanosmia) trevoris Cockerell, 1897

Osmia (Melanosmia) tristella Cockerell, 1897

Osmia (Osmia) lignaria subsp. *propinqua* Cresson, 1864

Stelis (Stelis) montana Cresson, 1864

Stelis (Stelis) monticola Cresson, 1878

Stelis (Stelis) sp. F1

Stelis (Stelis) sp. F2

Stelis (Stelis) sp. M3

Stelis (Stelis) sp. M4

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