Managing and Restoring Pollinator Habitat in Interior Pacific Northwest Grasslands and Riparian Areas

Lessons Learned from Eastern Oregon

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Cover Photograph

Western bumble bee foraging on lupine at the USFS Starkey Experimental Forest and Range. Photo courtesy of S. Mitchell

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I. Executive Summary

The purpose of this report is to provide an overview of pollinator research in interior Pacific Northwest (PNW) grasslands and riparian areas conducted by Oregon State University, The Nature Conservancy, and the US Forest Service. These organizations have been working together over the last two decades to better understand pollinators in eastern Oregon grasslands and riparian areas, including the best ways to conserve them by managing and restoring the habitats they depend upon. This report provides background information on the systems studied, the pollinators that inhabit the region, and the key findings and management implications of the studies. Research projects addressed a variety of topics, ranging from describing pollinator and blooming plant communities in time and space, to investigating how ungulate grazing, fire, and non-native annual grass invasions influence pollinators. The research described in this report primarily focused on native bees, but also includes work on moths and butterflies. The production of this technical report was partially funded by the Oregon Watershed Enhancement Board (OWEB) as part of their targeted Telling the Restoration Story grant offering. This funding helps grantees evaluate existing data from watershed restoration projects and produce outreach materials that describe the outcomes. Since 2001, OWEB has invested almost $4 million in the Zumwalt Prairie region, including acquisitions, restoration projects, invasive weed removal, and monitoring grants. The pollinator research presented in this report is associated with habitat improvements that have been made possible through OWEB funds. The summaries below provide broad overviews of the major sections of the report.

Interior PNW Grasslands, Riparian Areas, and Their Pollinators

Both grassland and riparian areas have been drastically altered since the beginning of European settlement in the 1800s. For example, PNW bunchgrass prairie, which once covered about 3.2 million ha, has been reduced by 99%. One of the largest remnants of PNW bunchgrass prairie occurs at The Nature Conservancy’s Zumwalt Prairie Preserve, which is one of the three main study locations described in this report.

Bunchgrasses also occur in drier portions of the interior PNW, often in combination with sagebrush. While these grasslands have also largely been converted to croplands with European settlement, The Nature Conservancy manages a large, relatively intact system at the Boardman Conservation Area, which is also a focus of this report.

Like bunchgrass prairie, meadows associated with riparian areas, which form a transition between aquatic and upland habitats, are among the most altered habitats in western North America. Many have been heavily impacted by past land uses including river and stream flow alterations, livestock grazing, channelization, and conversion to agriculture and built environments. The habitat loss and alteration of grasslands and riparian areas have led to reduced biodiversity and ecosystem functions, including those associated with pollinating insects. Riparian areas at Meadow Creek in the Unites States Forest Service Starkey Experimental Forest and Range (Starkey) is the third location of studies described in this report.

Some of the major groups of invertebrate pollinators found in interior PNW grasslands and riparian areas include bees, wasps, flies, beetles, butterflies and moths. The effectiveness of pollinator groups varies according to the system, the plant species present, the season, and the attributes of the pollinating groups themselves. In general, the effectiveness of pollinators is influenced by the amount of pollen they transport, the fidelity they display for foraging on the same plant species, and the frequency with which they visit flowers. Bees are often considered the most efficient pollinators, but wasps, flies, and beetles also play key roles in pollination. Moths are also important pollinators, especially for nocturnally blooming plants. Butterflies, although frequent flower visitors and popular amongst the general public, are generally considered to be the least effective pollinators. All insect pollinators depend on adequate food and nesting habitat, and their varied life histories require managers to consider habitat needs at all stages of development (egg, larvae, pupae, and adults).

Regional Pollinator and Blooming Plant Diversity

Studies at the three locations showed that pollinator and blooming plants of interior Pacific Northwest grasslands and meadows are very diverse, with 364 bee species, 55 butterfly species, 255 moth species, and 220 blooming forbs and shrub species documented overall. Native bee and blooming plant communities in riparian areas are particularly diverse, with the highest number of species detected and the greatest proportion of unique species of the three grassland types investigated. Species of conservation concern included pollinators (e.g., the western bumble bee) and plants (e.g., the threatened Spalding’s catchfly). Some insect groups that may include important pollinators, such as moths, are particularly species-rich.

Several management implications arise from this work. Protecting interior PNW grasslands and meadows is a high priority for pollinator conservation given the high levels of biodiversity associated with them. The western bumble bee’s occurrence at the Zumwalt Prairie Preserve and at Starkey illustrates the importance of large tracts of intact pollinator habitat for conserving species of concern in Oregon. The work also shows that surveying pollinator communities provides fundamental information needed to develop pollinator management and conservation plans. Even fairly limited surveys (e.g., one year of moth survey data at the Zumwalt Prairie) can yield large amounts of useful information. Effective pollinator management plans will take into account the different pollinator species that occur within the areas of interest and the specific habitat types encompassed within the area. However, all studies rely on taxonomic expertise, which is limited but imperative for pollinator research. The projects also showed that research and conservation efforts aimed at pollinators should be expanded beyond native bees and butterflies, with groups such as beetles, flies, and moths of particularly high priority given their diversity and potential importance as pollinators of many native plant species. Finally, given their great diversity, understanding life histories of pollinator species will be key to conserving them. However, given the enormous variation in life histories, maintaining a diversity of habitat conditions and plant species may be the best strategy for preserving pollinator communities given insufficient knowledge of many pollinator life histories.

Variability in Time and Space in Pollinator and Flowering Plant Communities

Grasslands and riparian meadows of the interior Pacific Northwest are not homogenous. A wide range of temperatures, precipitation, and elevations results in a patchwork of habitats that not only vary spatially, but also through the growing season. However, the influence of this variability in interior PNW grasslands had not been well-studied until the work described in this report was initiated. Key findings were that bee and blooming plant communities differed in the major grassland types studied, with distinctive communities associated with each. Even within a grassland type, different habitats are associated with different bee and blooming plant communities. For example, Isolated quaking aspen stands at The Nature Conservancy's Zumwalt Prairie Preserve were associated with different native bee and blooming plant communities relative to grassland sites. Species composition also changed strongly through the growing season, with distinct early, mid, and late season communities. Seasonal peaks in bee and blooming plant richness and diversity depend on weather and elevation. Inter-annual variation in flowering phenology and bee emergence and activity can be substantial and appears to be influenced by spring precipitation and spring/summer temperatures. Blooming plant richness and abundance drop precipitously at the end of the growing season when bee communities tend to be dominated by several common species of generalist sweat bees.

Management implications associated with these findings touch on a broad range of topics, including the timing of management actions, the design of monitoring programs, the conservation of sensitive habitats embedded in these larger grassland types, and the direction for future research. For example, the earlier portion of the growing season supports the highest diversity of blooming plants and bee species, including several specialists, so reducing negative impacts on plants and bees in these periods is a higher priority than later in the season. In addition, given inter-annual weather variation, long-term pollinator monitoring should not necessarily occur on the same calendar date each year, but timed to occur at similar points in bee phenology. The results also show that conserving sensitive habitat within grasslands, such as aspen stands, benefits native bees. Finally, given the sensitivity of both blooming plant and bee communities to climatic conditions, further research is needed to understand how predicted changes in climate over the next several decades may affect native bee abundance and diversity and the consequences of phenological mismatches from both the plant and the pollinator perspective.

Relationships between Plants and Pollinators

All pollinators depend on plants at some point in their life cycle. Bees are one of the few groups in which both adults and larvae rely on flowers for all of their food. Understanding native bee foraging preferences is key to guiding conservation and restoration strategies aimed at enhancing their habitat. However, identifying flower species that are best at providing pollen for a variety of bee species can be challenging. A common approach to identifying key plants for bees is to observe or collect individuals foraging on flowers, with recent advances in molecular ecology providing additional tools to better understand plant-pollinator relationships. Over 15 years, research described in this report has resulted in over 4,000 observations of bees belonging to more than 220 bee species visiting over 150 plant species.

The results of this work have shown that certain forb and shrub species are used by many native bee species and are good candidates to serve as "floral work horses" in restoration projects. In addition, some forb and shrub species are preferred by native bee species (i.e., visited at a higher rate than expected given their availability in the environment) and essentially serve as "bee ice cream." Other bee species rely on a narrow set of plants, and conversely, some rare plant species rely on a very narrow group of pollinators. In addition, new techniques, like DNA metabarcoding of pollen, provide a more complete understanding of bee foraging behavior.

Management implications arising from this work are that effective restoration that aims to support the most bees will target plants used commonly by bees or preferred by bees. The value of restoration plantings to native bees can also be Increased by including plants with a diversity in bloom morphologies. In addition, including some of the species on which western bumble bee was observed foraging may aid in the conservation of this species of concern. Similarly, plant species that pollinator specialists rely on should be protected or enhanced through restoration efforts. The research also suggests that bee species that provide pollination services to rare plants should be monitored regularly and habitat managed to support healthy populations of those pollinator species. For example, because Spalding's catchfly may be pollinated by just a few species of pollinators (one of which is a bee species of concern), the risk of pollination failure is higher. Thus, the continued maintenance of robust populations of these insect pollinators is a high priority for the conservation of this threatened plant species. Finally, more research is needed to document pollinator networks to better understand their temporal and spatial stability and the consequences of various management actions.

Ungulate Grazing

Productive rangelands rely on high quality forage, which include not only grasses, but also a diversity of forbs. Insect pollinators contribute to rangeland health because they pollinate many of the forbs that form important components of livestock diets. Rangelands in the interior PNW benefit pollinators as well, by providing large tracts of undeveloped land that often support floral resources for native pollinators and provide nesting habitat, including bunchgrass tussocks, bare ground, plant stems, and other structures. However, livestock and native ungulates, like deer and elk, can consume flowers, a vital source of nectar and pollen for these insects. If grazing or browsing occurs at high levels or on plant species preferred by pollinators, grazing can decrease pollinator abundance and diversity. This can be more of a concern in bunchgrass systems, such as those in the PNW, compared to rangelands dominated by rhizomatous grasses, like those occurring in the Midwest, where grasslands evolved in the presence of large herds of bison.

The studies of ungulates and pollinators in grasslands and riparian meadows of the interior PNW produced a number of key findings. Results consistently showed that herbivory by livestock and native ungulates, such as deer and elk, can decrease floral resources available for pollinators, with effects partially depending on the dietary preferences of the ungulate species. Ungulate activity can also affect nesting habitat, enhancing it for some pollinators and degrading it for others. However, the recent spread of the invasive annual grass, ventenata, may modify grazing effects on nesting habitat in negative ways. The research also shows that certain pollinators, such as bumble bees and butterflies, and certain habitats, such as riparian meadows, may be more sensitive to livestock grazing than other pollinator taxa and grassland habitats. The research also sheds light on the benefits of using utilization in studies designed to quantify grazing intensity (rather than stocking rate) to better understand livestock effects on pollinators and their habitat. Finally, a recent study showed the potential benefits of timing grazing to occur after peak bloom (i.e., phenologically targeted grazing) for flower availability and native bee conservation.

One management implication arising from this work is that decreasing stocking rates and keeping utilization <40% may benefit rangeland pollinator species. In addition, using approaches that increase habitat heterogeneity (i.e., result in small patches of different types of habitats) may be the best approach to conserving native pollinator habitat. Examples include high-density short-duration approaches, rest and rotation systems, or having some areas that are not grazed by livestock. Phenologically-targeted grazing (i.e., commencing grazing after peak bloom) may reduce negative effects on bee communities in areas that include high quality bee habitat. This approach may be particularly useful if managers are able to use alternative locations (e.g., old fields, more intensively managed pasture) until after peak bloom. Further, managing grassland and riparian areas for healthy pollinator habitat should take into account not only impacts of cattle, but also native ungulates like deer and elk. Finally, the work suggests that bumble bees and butterflies, especially species of conservation concern, should be monitored carefully in rangelands.

Fire

While fires can be destructive, they can also be a useful tool for maintaining diverse grassland systems. Wildfire is ubiquitous across the US, with both the severity and prevalence increasing as the climate changes. However, fire can also be a beneficial management tool in many grasslands, helping to limit woody species encroachment, reduce fuels, and potentially decrease non-native species, like invasive annual grasses. Pollinators are predicted to be sensitive to fire, both through direct and indirect effects and responses are expected to vary with the time since fire. Fire can cause direct mortality to pollinators, with the most vulnerable individuals being those with limited flight ability and those occurring on the soil surface or associated with vegetation. However, while certain pollinators, such as butterfly and moth larvae, may be likely to experience mortality, many pollinators are expected to be primarily influenced by fire’s short-term and long-term effects on vegetation and nesting habitat.

Multiple studies described in this report examined fire effects on pollinators and their habitat. Short-term responses to a 2015 wildfire at The Nature Conservancy’s Boardman Conservation Area included changes in blooming plant composition, with forb abundance increasing in burned sites, and certain forb species flourishing in burned areas. Bee species richness and diversity were higher in burned areas, and some bee species (primarily large, generalist species) were associated with burned areas. Responses in bee communities may have been driven by a combination of factors including increased forb abundance, changes in forb community composition, and by more bare ground and nesting resources (e.g., charred wood). Burned areas also showed decreased cover of two common invasive annual grasses – cheatgrass and medusahead. However, biological soil crust cover also decreased, making these areas potentially more vulnerable to cheatgrass invasion in the future. Long-term studies on prescribed burning at The Nature Conservancy’s Zumwalt Prairie Preserve also showed that burning resulted in changes in forb community composition, with some species of fire-adapted forbs associated with burned areas. More species of bees occurred in burned sites two years after prescribed burns. Together, these results indicate that prescribed burning can have both short- and longer-term beneficial effects on bees by increasing select floral resources and creating more nesting habitat. Although fires may be helpful in reducing some invasive annual grasses in the short-term, longer-term effects of fire on invasive grasses are less clear and may depend on the severity and season of burning, as well as the specific species involved.

Management implications from this research suggest that prescribed burning may be a useful tool to increase forb species that benefit some pollinator species and to enhance nesting habitat for native bees that nest in ground or charred wood. In addition, while fire may result in short-term decreases in some invasive annual grasses (e.g., cheatgrass, medusahead), there is little evidence that fire reduces other annual grasses in the long-term (e.g., ventenata). Thus, negative effects of annual grasses like ventenata on pollinator habitat should not be expected to improve with prescribed burning. The results of these studies also indicate that effects of fire on biological soil crust may be a key management consideration for pollinator conservation, if loss of soil crusts increases future annual grass invasion potential. Long-term monitoring after fires is necessary to investigate the effects of losses of biological soil crusts and associated annual grass invasions.

Restoration

Grassland and riparian areas are a common focus of restoration projects in the interior Pacific Northwest, partially because of their history of conversion and disturbance, but also because of their importance in supporting high levels of biodiversity and as habitat for many sensitive species. Although vertebrate species are often the focus of grassland and riparian restoration efforts, many natural resource managers are also interested in how these restoration efforts influence pollinator habitat. The studies described in this report examined a variety of aspects of restoration in both grassland and riparian systems, including passive vs. active approaches, and effects of plant species used in restoration projects. In grasslands, studies at TNC's two grassland locations showed that the context and history of the grassland influenced their response to restoration. The Nature Conservancy's Boardman Conservation Area is a low elevation, drier grassland, surrounded by irrigated agriculture. In that system, active and passive restoration did not result in the abundant flowering resources or distinct bee communities that were associated with high quality sites. In the Zumwalt Prairie, studies of passively restored seeded old fields showed that they had fewer flowering forbs and less bare ground compared to native prairie habitats and many of the flowers that were absent or at low densities in old fields are species that are frequently visited or preferred by native bees in the region. However, bee communities did not differ between old field and native sites, potentially because large tracts of intact prairie adjacent to formerly cultivated grasslands compensated for decreased floral resources associated with those sites.

At riparian areas at the USFS Starkey Experimental Forest and Range, a study examined the degree to which shrub species that are commonly planted in riparian restoration projects supported native bees. Results showed that, in spring, the majority of flower-visiting bees foraged on shrubs – particularly willows, a commonly planted riparian shrub. This was true despite the fact that blooming forbs were more species-rich and abundant at riparian sites in spring. In addition, the composition of bees visiting shrubs differed from those visiting forbs. Wax currant and willow had the most diverse group of bees visiting in early spring and black hawthorn and mallow ninebark had the most diverse bee visitors later in the season. The results also showed that some bee species strongly preferred particular shrub species.

Management implications arising from this research are that passive restoration of interior PNW grasslands may not be sufficient to restore flowering plant and pollinator communities, especially in those surrounded by highly modified landscapes. Active restoration should include not only planting native bunchgrasses (that provide nesting habitat for bumble bees) but also flowering forbs. Pollinator-focused restoration should also aim to provide season-long floral resources that include plant species with different flower shapes. Finally, while controlling non-native annual grasses alone is insufficient for restoring bee habitat, it can help improve nesting habitat for ground nesting bees by increasing bare ground. For riparian areas, research shows that planting shrubs may not only improve stream health by shading and stabilizing banks but may also provide forage to a diverse group of pollinators. The work also illustrates the importance of considering phenology in pollinator-plant relationships when designing projects whose goal is to restore structure and function of degraded systems. Finally, given the significant effect that many large herbivores exert in interior PNW systems, especially in riparian areas, planting wax currant and black hawthorn may be especially useful because they provide forage for diverse native bees and are relatively resistant to ungulate herbivory. Planting bee-friendly shrubs in interior PNW riparian areas is an effective strategy to accomplish multiple restoration goals, including pollinator habitat enhancement, and to leverage limited restoration funding.

Non-Native Annual Grass Invasions

Non-native annual grass invasions are an increasing problem in PNW grasslands and riparian meadows. Although non-native annual grasses, such as cheatgrass, have been a problem in western grasslands for many decades, the rapid spread of other types of annual grasses in previously uninvaded systems is concerning. For example, the Zumwalt Prairie has experienced a dramatic increase in the prevalence of ventenata (*Ventenata dubia*). Studies examining the effect of ventenata invasions at the Zumwalt Prairie clearly show that the invasion negatively affects native bee habitat by decreasing forb cover and species richness. Ventenata litter also reduced the availability of bare soil, which decreases nesting habitat for soil-nesting bees. Research at the Zumwalt Prairie shows that native bee communities in invaded sites are negatively affected by ventenata, showing decreases in species richness. This research highlights the importance of developing management strategies to decrease the spread of non-native annual grasses to safeguard pollinator habitat. Limiting actions that may disturb biological soil crusts, where they remain intact, may be key to preventing annual grasses from expanding their distribution. In addition, further research into measures that effectively control non-native invasive annual grasses is a top priority. These measures may include new herbicides, developing new burning and grazing strategies that effectively control or limit invasions, or combinations of actions.

Future Research

Numerous areas of further research are outlined. One of the most important is to expand studies of pollinator responses to restoration and management to include more taxa. Most studies have focused on native bees, an understandable focus given their importance in pollination and contribution to diversity. However, with the exception of some work on butterflies and moths, most pollinating taxa have not been studied in grasslands or riparian areas of the interior PNW.

A recurring theme of the projects described in this report is the inter-relatedness of disturbance, management actions, and restoration, all in the larger context of a changing climate. Changing climate not only results in changes in the players in the community (i.e., which species persist in given locations and at what levels), but also the relationships between them and quickly changing abiotic variables impacted by climate change (e.g., soil moisture).

II. Introduction

A. Grasslands and Riparian Areas – Habitats of Concern in the Interior PNW

The interior Pacific Northwest (PNW), a region that includes northeastern Oregon, eastern Washington, northern Idaho, and western Montana (Figure 1), is not only home to some of the most productive dryland and irrigated cropland in the nation, but also hosts diverse non-cultivated landscapes, including conifer and mixed-conifer forests, shrub-steppe, grasslands, and streams with their associated riparian areas. Grasslands and riparian areas – the two habitat types that are the focus of this report – have been drastically altered since the beginning of European settlement in the 1800s.

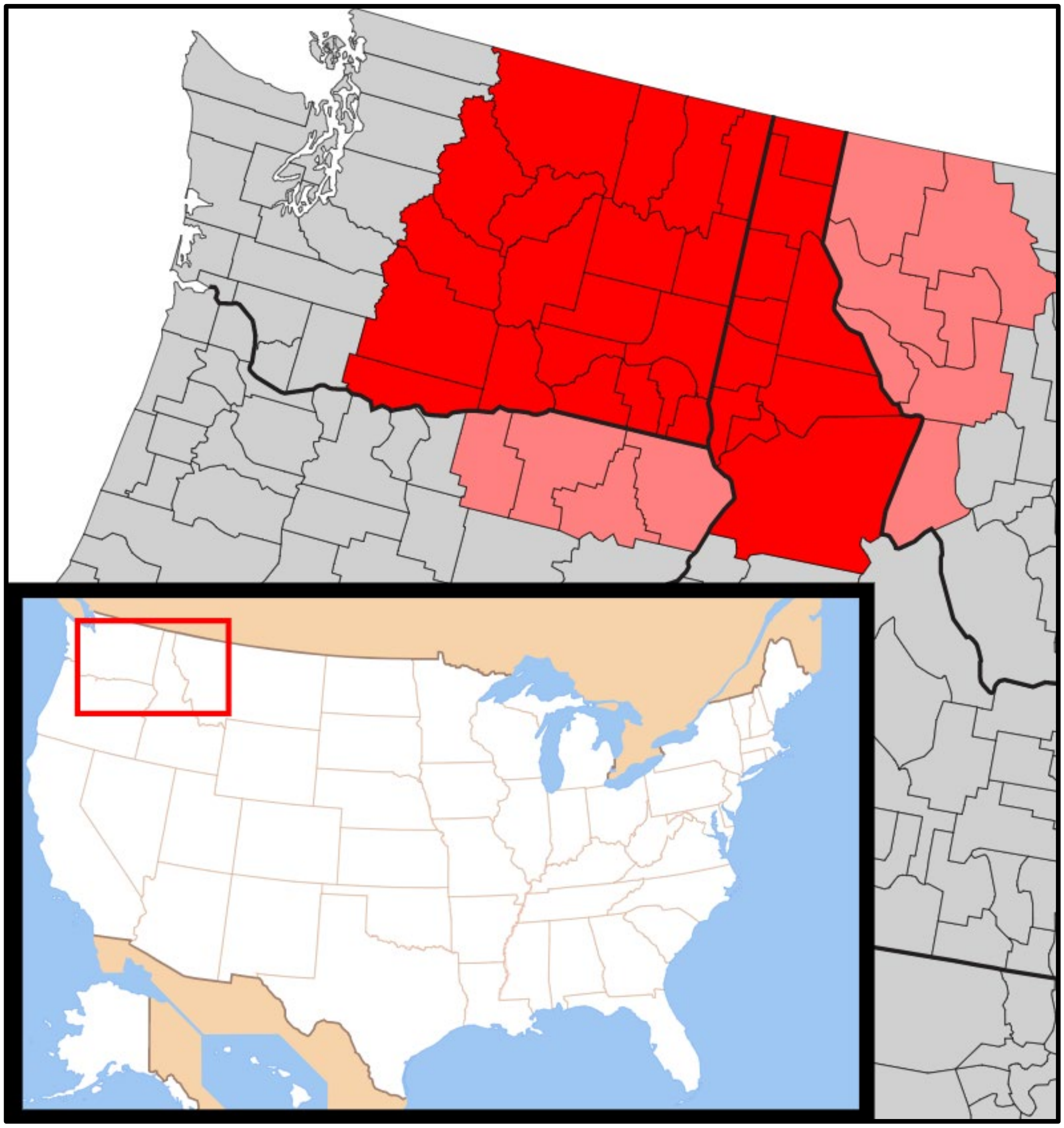


Figure 1. Map of the interior Pacific Northwest (dark red shading indicates the most narrow definition of the region and pink indicates additional areas included in more broad definitions). Map by Howpper (own work, CC BY-SA 4.0, https://commons.wikimedia.org/w/index.php?curid=54882591)

Although a variety of grassland types occur in the region (Burcsu et al. 2014), the PNW bunchgrass prairie was historically one of the most common and once covered about 3.2 million ha (Tisdale 1982). However, since European settlement, PNW bunchgrass prairie has been reduced to about 1% of its historical range (Sampson and Knopf 1994; Noss et al. 1995; Black et al. 1998 a,b; Johnson and Swanson 2005), with the largest intact remnant being the Zumwalt Prairie in northeastern Oregon (Bartuszevige et al. 2012). Bunchgrasses are also common in drier portions of the interior PNW, often in combination with sagebrush in shrub-steppe ecosystems (Burcsu et al. 2014; Figure 2). Much of the deep-soil shrub-steppe in the PNW was also converted to croplands with European settlement. However, some large areas in the region escaped cultivation, often because of their utility as sites for military training and weapon development and storage, including the Navy Bombing Range, the Umatilla Weapons Depot, and the Hanford Nuclear Site (Adams 2021; Tilt et al. 2022). Although these sites represent some of the best existing shrub-steppe habitat in the world, many have been heavily invaded by non-native annual grasses, including cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusae*), and North Africa grass (*Ventenata dubia*) (Jones et al. 2018, 2020; Applestein and Germino 2022).

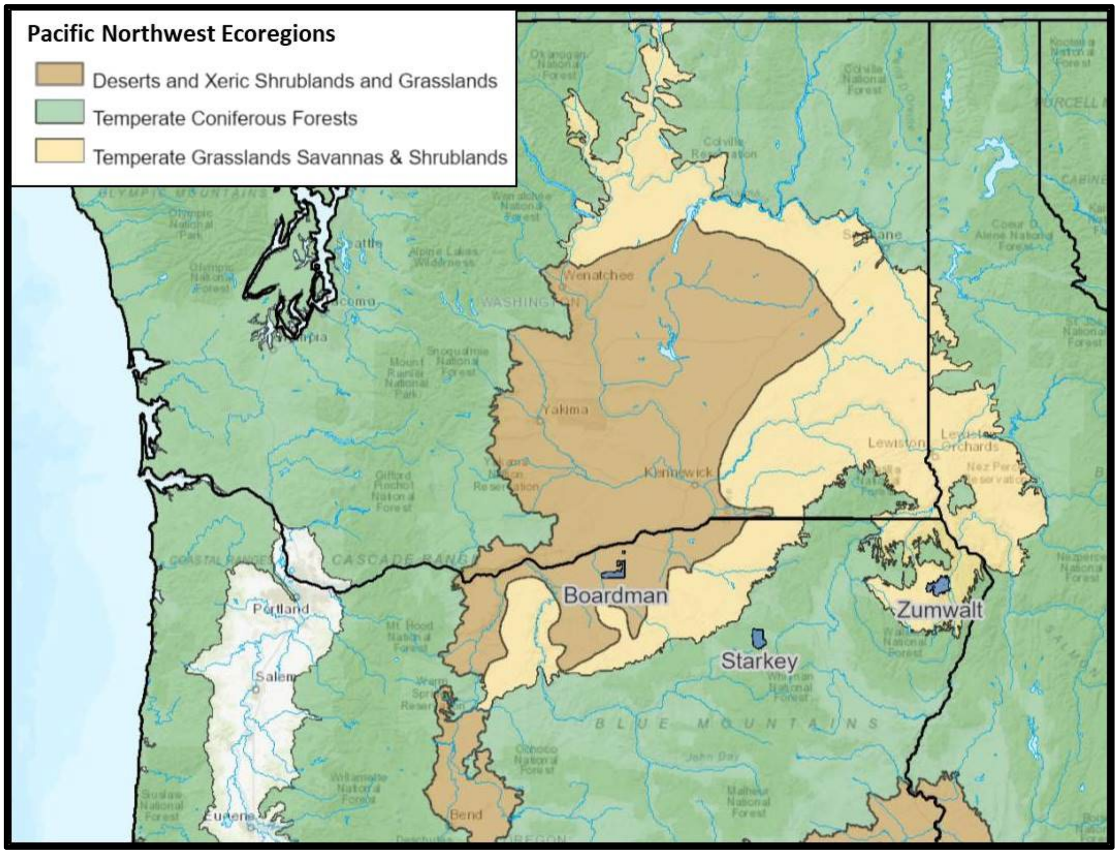


Figure 2. Ecoregions of the Pacific Northwest, following Olson et al. (2001), with the three main location in which studies described in this report (Boardman, Starkey, and the Zumwalt). Temperate grasslands shown in this map correspond to Pacific Northwest Bunchgrass prairie.

Riparian areas, which form a transition between aquatic and upland habitats, are among the most altered habitats in western North America (DeBano et al. 2003a; NRC 2002; Naiman et al. 2005). Riparian systems have been heavily impacted by past land uses including river and stream flow alterations, livestock grazing, channelization, and conversion to agriculture and built environments (Svejcar 1997; DeBano et al. 2003a; Rood et al. 2020), including those in the PNW (Theobald et al. 2010; Figure 3). In the interior Columbia River Basin, almost 50% of watersheds exhibit significant departures from historical plant communities (Macfarlane et al. 2017).

Habitat loss and alteration of grasslands and riparian areas have led to reduced biodiversity and ecosystem functions that have generated intense conservation attention (Rood et al. 2020). Riparian areas, in particular, are the focus of restoration and rehabilitation efforts while conservation of remaining grasslands is frequently approached through management of livestock grazing.

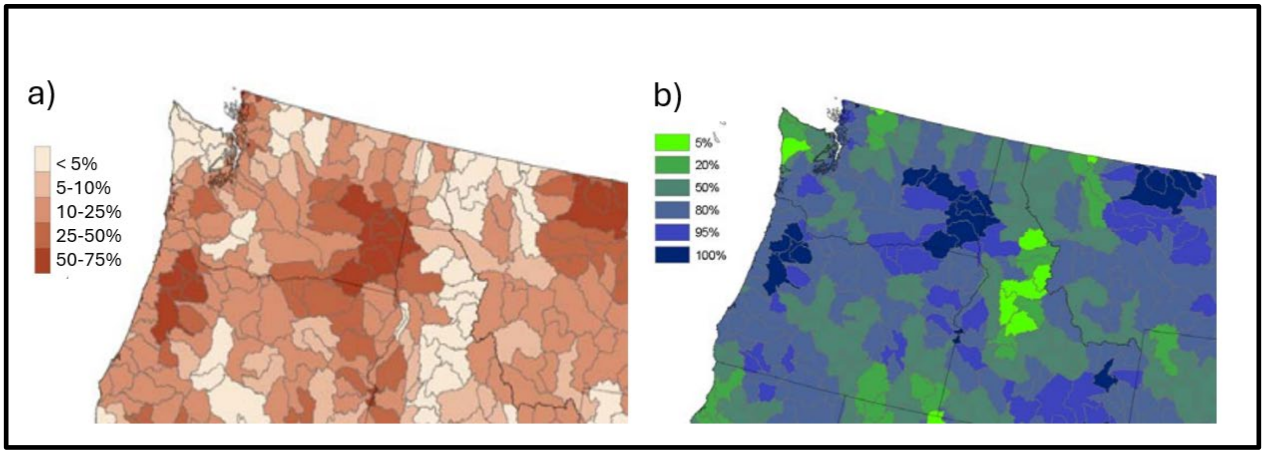


Figure 3. Estimated loss and degradation of riparian areas as modeled by Theobald et al. (2010), with a) the estimated percentage of riparian areas modified by development, roads, or agriculture and b) watersheds with the least and most modified potent potential riparian zones. Modified from Figures 8 and 9 of Theobald et al. (2010).

B. History of Use

All habitats in the PNW region, including grasslands and riparian areas, were regularly used by Native American Tribes as sources of foods and medicines. Although Native Americans set fires periodically to maintain plant communities conducive to their hunting and gathering practices, extensive alterations of natural environments were not widespread or commonplace in this region prior to European settlement (Baker 2002).

Grasslands

Within the PNW bunchgrass prairie, the most productive grasslands, classified as Palouse Prairie, have been converted almost entirely to crop production (Lichthardt and Moseley 1997; Looney and Eigenbrode 2012). The deep silty soil of this region is known world-wide for high yields of dryland wheat. The remaining grassland, which could not sustain cultivation, is found on steep canyon slopes and on the high plateau of the Zumwalt Prairie in northeastern Oregon. These grasslands have been used for livestock grazing – first by horses of the Nez Perce Tribe in the 1700s, then by sheep in the late 1800s and early 1900s, and then by cattle, which continues to be the primary land use today. Some areas of the Zumwalt Prairie were cultivated for a short time during the homesteading era as part of securing Homestead Act claims, but nearly all of these cultivated fields were gradually abandoned by the late 20th century (Bartuszevige et al. 2012).

Riparian Areas

Since water is a scarce and highly managed resource in the semi-arid regions of the western US, riparian areas have been extensively utilized and altered, experiencing a disproportionately high level of multiple disturbances (NRC 1992; Theobald et al. 2010). The extirpation of beavers in the PNW by the late 1800s had drastic effects on hydrology (Wohl 2021), followed by dams and water diversions, road building, mining, timber harvesting, and channelization (Kauffman 1988). Livestock grazing has had extensive and sustained effects on riparian ecosystems, including the replacement of native vegetation with non-native grasses to provide forage for livestock (Fleischner 1994). Owing to their importance, the threats to riparian areas have been well-documented (Belsky et al. 1999; Poff et al. 2011) and the imperative for restoration is widely recognized (Kauffman et al. 1997; Rood et al. 2020).

C. Current Land Ownership and Users

Grasslands

Nearly all of the remaining PNW bunchgrass prairie (Figure 4), located in Wallowa County, Oregon, is privately owned and managed for livestock grazing, wildlife habitat, and recreational/aesthetic use. The management of these lands has direct effects on those involved in the ranching industry, hunters and fishermen, and local tourism. Management of the grasslands is intertwined with forest management and fish and game management. Collaborative resource management groups in


Figure 4. Sampling blooming plants on the Zumwalt Prairie (Photo credit L. Ketchum)

the region include members of private industry (e.g., ranching and timber), federal land managers (e.g., USDA Forest Service), tribal land managers (e.g., Umatilla and Nez Perce fisheries), state fish and game managers (e.g., Oregon Department of Fish and Wildlife) and county vegetation management.

Riparian Areas

Riparian areas of the interior PNW region present a complicated ownership and management situation (Figure 5). Streams pass through multiple habitats under all types of ownership (federal, state, private) and carry the effects of management downstream. Timber harvesting and livestock grazing on both public and private lands are subject to numerous regulations intended to limit direct and downstream effects on water quality and habitat for endangered salmonid species (Adams 2007; Fleischner 2010), with management made more challenging because of the numerous stakeholder groups with interests that are potentially influenced by riparian area management (Charnley et al. 2018).

Figure 5. Meadow Creek, flowing through the USDA Forest Service Starkey Experimental Forest and Range. Photo: M. Rowland.

D. Ecosystem Services Provided

Over the last quarter of the 20th century, the management of natural resources gradually began to incorporate the knowledge that natural landscapes have many values beyond extraction of raw materials. These values, referred to as ecosystem services (Costanza et al. 1997), continue to gain traction in management frameworks as more is understood about how ecosystems function and how they are affected by human influences. Societal values are also reflected in this broadening management framework.

Grasslands

Grasslands in the interior PNW region that remain in an uncultivated state are valuable sources of forage for livestock and ungulate wildlife. Livestock production and hunting are the primary economically-driven uses of these lands. Grasslands also harbor a high diversity of species, including plants, invertebrates, birds, small mammals, and top predators such as wolves and cougars. The rich assembly of species that depend on grasslands for some or all of their habitat needs is an important value acknowledged by many land managers. Ecosystem services provided by grasslands include carbon sequestration, nutrient cycling, erosion control, regulation of water flow and pollination (Havstad et al. 2007; Bengtsson et al. 2019; Zhao et al. 2020). Grasslands also have a potent presence in human cultural history and aesthetic appreciation, although these values have proven difficult to quantify (Pellaton et al. 2022; Wang et al. 2024).

Riparian Areas

Riparian areas in the interior PNW region range from those associated with small headwater streams in mountain habitats to narrow corridors winding through desert vegetation to extensive riparian zones surrounding one of the largest rivers on the continent (the Columbia River). Similar to grasslands, ecosystem services provided by riparian areas and their associated streams and rivers are diverse. They are used as water sources for municipalities, agricultural irrigation, and livestock and provide myriad recreational opportunities, including fishing and boating. Their condition also affects aquatic species of concern in the PNW, such as salmonids (DeBano et al. 2016b). also provide cultural services with significant aesthetic and symbolic value (Riis et al. 2020) including supporting biodiversity. Because they occur at the interface of streams and uplands (e.g., forests), riparian areas support high levels of biodiversity and unique groups of species (DeBano et al. 2003a; Rood et al. 2020). Although riparian areas occupy only 2% or less of land area, they provide critical habitat for plants and wildlife (Svejcar 1997; NRC 2002; Naiman et al. 2005). Other ecosystem services associated with riparian areas include carbon sequestration, nutrient cycling, erosion control, regulation of water flow, dispersal of seeds and propagules, evaporative cooling, fire regulation, and pollination (Riis et al. 2020).

Work in other regions suggests that grasslands and riparian areas host diverse pollinator communities, and thus contribute to the overall diversity of these habitats (Williams 2011). This biodiversity also provides pollination services to many of the plants that occur in these habitats, which in turn also contribute to the overall biodiversity of the region. Further, these plants provide food for grazing livestock and are often adjacent to agricultural land, where spillover pollination services may benefit agricultural production. There is a growing realization of the importance of documenting pollinator diversity in PNW grassland and riparian areas and understanding how management actions affect them (PHTF 2015; DeBano et al. 2016a; Wojcik et al. 2018). This report focuses on reporting lessons learned from these efforts.

E. Pollinators

Types of Pollinators

Although the reproduction of many plants involves some type of pollination, some species rely on wind or even water as agents to transfer pollen from the male part of the plant (anther) to the female part (stigma). However, many plants depend on animals to aid in pollination. In fact, some are completely dependent on animal pollinators. Animal pollinators are a diverse group that includes both vertebrates (e.g., birds, bats) and invertebrates. For most animal-pollinated plants, insects perform the bulk of pollination services, and important pollinating groups include bees, wasps, moths, butterflies, flies, and beetles (Rader et al. 2016, 2020; Hanberry et al. 2021).

Several factors influence the relative importance of each group as pollinators, including the amount of pollen transferred to a stigma per visit, the frequency of visits, and plant fidelity (i.e., the probability the insect will visit the same plant faithfully) (Larson et al. 2018). Bees are considered to be the most efficient and common pollinators, but flies, wasps, beetles, moths, and butterflies can also play significant roles in pollination (Larson et al. 2018; Rader et al. 2016, 2020), especially in certain systems or times of the year, when some of these groups may be more common than bees (Rohde and Pilliod 2021). For example, one study, conducted in southeastern Oregon in sagebrush steppe found that the abundance of bees peaked earlier in the season (mid-July), while the abundance of flies peaked in mid-season (late July), and the abundance of butterflies and moths peaked later in the season (late August) (Rohde and Pilliod 2021). Each flower-visiting group is described briefly in the following sections.

Bees

Bees are members of the insect order Hymenoptera, and are familiar to most people, especially the non-native European honey bee (*Apis mellifera*). However, there are more than 20,000 described species of bees globally (Zattara and Aizen 2021), ~3,500 in North America (Travers et al. 2011), and over 600 species estimated to occur in Oregon alone (Best et al. 2021). Bees are typically the most efficient of all insect pollinators, partly because they are often the most frequent flower visitors, but also because they typically carry much larger amounts of pollen than other groups (Larson et al. 2018; Hanberry et al. 2021). However, some work has shown that bees are more likely to carry mixed pollen loads compared to other taxa (Larson et al. 2018), which decrease their efficacy as pollinators. Regardless, because of their ubiquitous presence and general importance as pollinators, native bees were the focus of most of the research described in this report (Figure 6).

Figure 6. A mining bee foraging on willow (*Salix* sp.) at the USFS Starkey Experimental Forest and Range. Photo: S. Mitchell.

One difference between bees and most other pollinating insects is that bees are central-place foragers, meaning that females will consistently return to the nest after each foraging bout (Ulyshen et al. 2023). For social bees, workers will return to the colony with the pollen and nectar collected in a foraging bout, and for solitary bees, females will return to the individual nest she is currently provisioning. In contrast, females of most other pollinating insect taxa lay eggs and do not return to the same site again. One consequence of this difference is that adult bees are more likely to be restricted to particular locations throughout their lifespan while adults of other taxa may roam more freely. In addition, body size, regardless of the group, also affects the range of adult insect pollinators. Smaller bodied insects generally travel shorter distances. Thus, for bees, small-bodied species may be more susceptible to negative effects of disturbance because of the combination of being central-place foragers and having small foraging distances (Ulyshen et al. 2023).

Wasps

Wasps are another hymenopteran group that contains many species that are significant pollinators (Brock et al. 2021). Although the definition of wasps varies, even among scientists, here it is used to refer to Hymenoptera that are not bees, ants, sawflies, or horntails – which leaves species in the suborder Apocrita, whose members have constricted "waists" (Hoffman et al. 2024). Although closely related, wasps differ from bees because almost all wasps are carnivores at some point in their lives – typically in the immature stage. Wasps often have a bad reputation because of just a few species that tend to be a nuisance (e.g., yellow jackets, paper wasps). However, most of the more than 100,000 species estimated to occur globally are highly beneficial to humans (Aguiar et al. 2013; Brock et al. 2021). These include minute parasitoid wasps, which often control agricultural pests by laying eggs of their offspring in the body of their host.

Most adult wasps visit flowers to feed on nectar to fuel their daily activities, with research so far suggesting that most are generalists with regard to nectar foraging (Mello et al. 2011). In the process, wasps may come in contact with pollen, which they may carry to other plants. Larson et al. (2018) found that although wasps were not as common flower visitors as bees, they were still frequent visitors. In addition, a large proportion of flowering-visiting wasps carried pollen – a proportion as high as bees. But wasps were more likely to have mixed pollen loads (i.e., loads with pollen from multiple plant species) compared to bees (Larson et al. 2018). Larson et al. (2018) also found wasp families varied in the amount of pollen they transported, with vespid wasps (Vespidae) most likely to carry pollen and braconids (Braconidae) and spider wasps (Pompilidae) least likely. The importance of vespid wasps in pollination is consistent with other research (Brock et al. 2021). For example, one study showed that vespid wasps in the genus *Polistes* could completely replace the pollination services of bumble bees in greenhouses (Hallet et al. 2017). Another group of vespid wasps that are considered effective generalist pollinators are pollen wasps (subfamily Masarinae) (Gess and Gess 2010). Because pollen wasps provision their larvae with pollen instead of insect prey, they have been suggested to be as effective pollinators as bees in some systems (Gess and Gess 2004).

Other wasp families that have been found to play a role in pollination include thread-waisted wasps (Sphecidae) that pollinate milkweed (*Asclepias* spp.) (Theiss et al. 2007), and spider wasps in South Africa (Shuttleworth and Johnson 2012). In addition, figs and many orchids are exclusively pollinated by specialized wasps (Pereira 2024). Travers et al. (2011) estimate that over 200 species of cuckoo wasps (Chrysididae) in North America visit flowers (Figure 7). Unfortunately, little is known about wasp biodiversity in the interior PNW, although a recent study conducted in Oregon white oak (*Quercus garryana*) in the Columbia Basin showed wasp communities are extremely diverse and abundant (Hoffman et al. In Review).


Photo: S. Mitchell

Figure 7. A cuckoo wasp (Chrysididae) visiting varileaf phacelia (*Phacelia heterophylla*).

Flies

Flies, which comprise the order Diptera, are a diverse group of insects, with over 160,000 described species (Ssymank et al. 2008). Although more than 86 families of flies have been documented visiting flowers (Inouye et al. 2015), the families of flies most often identified as potential pollinators are hover flies (Syrphidae; Figure 8), bee flies (Bombyliidae), and house flies and their relatives (superfamily Muscoidea) (Orford et al. 2015; Ulyshen et al. 2023). The two common families of hover flies and bee flies are comprised of more than 1,700 species (Travers et al. 2011). While flower-visiting flies are typically foraging for nectar, some species have been observed eating pollen (Inouye et al. 2015). Larson et al. (2018) found that although flies were generally not as common flower visitors as bees, they were still frequent visitors. In fact, flies may be more frequent visitors to flowers at certain times or in particular places and thus may provide more pollinating services than bees in those situations. For example, Kearns and Inouye (1994) found that flies are the most important pollinators of *Linum lewisii* (a common flower in many PNW systems) at high elevations. Within the course of the day, flies are often active when bees and butterflies are not, either because temperatures are too warm or too cool for these other taxa (Inouye et al. 2015). In addition, flies may reach peak abundance within the course of the season when other taxa are declining or have not yet reached their peak (Rohde and Pilliod 2021).

Larson et al. (2018) found that different types of flies varied with respect to how much pollen they carried. Hover flies (Syrphidae) were the most common flower visitors in their study, and were most likely to carry pollen loads, while dung flies (Anthomyiidae), robber flies (Asilidae), and bee flies (Bombyliidae) were least likely to have any pollen. Interestingly, blow flies (Calliphoridae) and dance flies (Empididae) were most likely to have pure pollen loads (i.e., just one species).

Figure 8. The black-margined flower fly (*Syrphus opinator*) visiting a flower. Photo: S. Mitchell.

Beetles

Beetles, which comprise the order Coleoptera, are the most diverse group of insects, with more than 300,000 described species globally (McKenna et al. 2019) and an estimated additional 1.2 million undescribed species (Stork et al. 2015). Beetles are often overlooked as potential pollinators, but the adults of many species visit flowers, primarily to feed on pollen or plant tissue rather than nectar. In the process, they often end up with pollen covering their bodies (Figure 9). Beetles have high flower visitation rates compared to many other groups of pollinators (Rader et al. 2020) and Larson et al. (2018) showed that beetles were more likely to carry pollen of the same flower species compared to all other pollinator groups including bees, which enhances their pollination efficiency. This may be partially due to the fact that flower-visiting beetles typically spend long periods of time on flowers and tend to visit the same species of flowers (Larson et al. 2018).

Several of the 190 families of beetles have been suggested to be effective pollinators, including over 2,000 species in the following families: flower longhorned beetles (Cerambycidae: Lepturinae), soft-winged flower beetles (Melyridae), shining flower beetles (Phalacridae), flower beetles (Anthicidae: Antrhicini), soldier beetles (Cantharidae), clerid beetles (Cleridae), ladybug beetles (Coccinellidae), leaf beetles (Chrysomelidae), sap beetles (Nitulidae), and flower chafers (Scarabiidae: Cetonini) (Travers et al. 2011; McKenna et al. 2019; Rader et al. 2020; Ulyshen et al. 2023). Given the immense diversity of the group, much more research is needed to understand the role beetles play in pollination in grassland systems (Larson et al. 2018).

Figure 9. Pollen is easily visible on the bodies of this mating couple of flower longhorn beetles (*Anastrangalia laetifica*). Photo: H. Hoffman.

Butterflies and Moths

Lepidoptera is an insect order that includes butterflies and moths and has ~180,000 described species world-wide (Hamm and Wittmann 2009). Both butterflies and moths are common flower-visiting insects in grasslands, with butterflies particularly well-known because they are usually active during the day and are often showy and charismatic. Although most moths are primarily nocturnal, others are active during the day, such as many common hawkmoths (Family Sphingidae). Butterflies can be distinguished from moths by the knobs at the end of their antennae (Figure 10). Moths have no knobs at the end of their antennae, which are either straight or very hairy. While there are many species of butterflies (~ 17,500 species globally), moths are even more specious (with over 160,000 species globally) (Hahn and Brühl 2016; Van Zandt et al. 2020; Bladon et al. 2023). In contrast to bee larvae, caterpillars feed primarily on non-reproductive plant tissue, and caterpillars of some species (like the monarch pictured in Figure 10) are narrow specialists.

Although butterflies and moths are very frequent flower visitors, they visit flowers to feed on nectar and so are less likely to come in close contact with pollen. In fact, Larson et al. (2018) showed that diurnal Lepidoptera were the least likely flower-visiting insects to be carrying pollen, indicating their limited role in pollination in that Midwestern grassland system (Larson et al. 2018).

Figure 10. A monarch butterfly (*Danaus plexippus*) visiting milkweed (*Asclepias* sp.) (left, photo: R. Sutherland) and a white-lined sphinx moth (*Hyles lineata*) (right, photo: S. Mitchell).

In contrast to butterflies, much less is known about moth communities in most systems, including grasslands of the interior PNW. However, moths are known to be highly effective pollinators for some plants, especially those that bloom in evening hours (Ulyshen et al. 2023). Described cases of moth pollination often involve very specialized, co-evolved systems (e.g., orchids) (Travers et al. 2011; Hahn and Brühl 2016; Larson et al. 2018). For example, several species of hawkmoths are key pollinators of the threatened Great Plains white-fringed orchid (*Platanathera praeclara*) (Travers et al. 2011; Fox et al. 2013). However, little is currently known about how many moth species contribute to pollination (Hahn and Brühl 2016; Van Zandt et al.

2020; Bladon et al. 2023), although several families with nectar-feeding adults are most likely to contain species that aid in plant pollination, including hawkmoths (Sphingidae), owlet moths (Nocutiidae), erebid moths (Erebidae), geometrid moths (Geometridae), crambid snout moths (Crambidae), and yucca moths and related species (Prodoxidae) (Van Zandt et al. 2020).

What Pollinators Need

One of the most basic needs of pollinators is food (Figure 11). Most common pollinating insects undergo complete metamorphosis, with four stages of development (egg, larva, pupa, and adult). All pollinating insects depend on flowers for at least one stage of their lifecycle, although which stage varies by group. As outlined in the preceding section, for bees, both adult and larval bees feed on nectar and pollen. In contrast, wasps differ from their hymenopteran cousins in that while most adults feed on nectar, their larvae typically rely on animal tissue. Not surprisingly, given their diversity, beetles' food needs are variable. While many adult beetles feed on pollen, and some on nectar, larval diets vary widely depending on the species, ranging from vegetarian to carnivorous. The vast majority of moths and butterflies are herbivores. Lepidopteran adults have siphoning mouthparts to drink nectar from flowers, while larvae (i.e., caterpillars) typically feed on a variety of plant tissue.

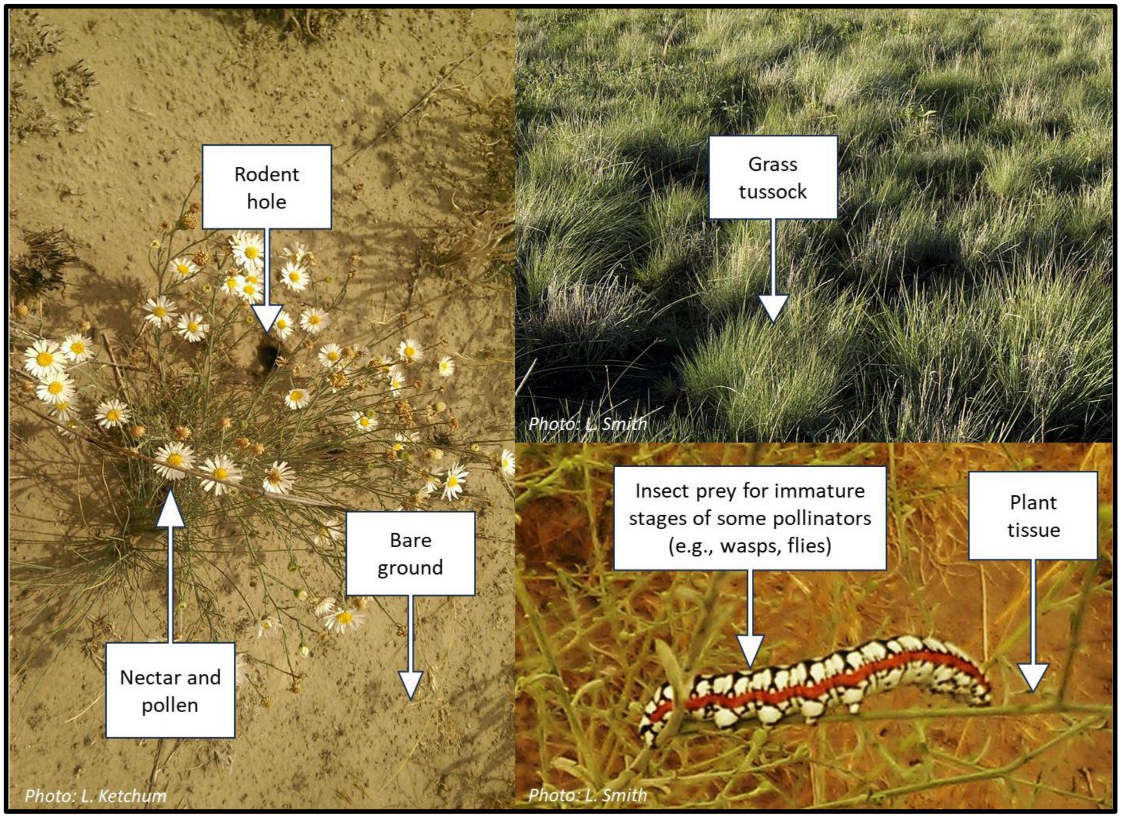


Figure 11. Insect pollinators have a variety of needs, including food (which can include plant and animal material), nesting sites (e.g., abandoned rodent holes, the base of grass tussocks), and overwintering habitat.

Another important need of pollinators is nesting habitat (Figure 11). Some pollinators lay eggs and then let their developing young fend for themselves. A good example of this strategy is shown by moths and butterflies, who lay eggs in habitat with abundant food (plant material) for the caterpillars that emerge from eggs (Figure 11) (Travers et al. 2011; Hanberry et al. 2021). However, many other pollinators, such as bees and wasps, make nests for their offspring and supply them with food – either in one big package when the egg is laid (e.g., solitary bees and wasps) – a strategy called mass provisioning – or continually through their larval development (e.g., social bees and wasps) – a strategy called progressive provisioning (Danforth et al. 2019). For pollinators that make nests, grasslands provide a diversity of nesting habitats. Bare ground between bunchgrasses, for example, provides nesting habitat for the more than 80% of all solitary bees that nest in soil (Harmon-Threatt 2020). Ground-nesting species vary in their preferences for soil characteristics, including texture, compaction, stability, bare ground, and litter and organic layer (Cane 1991; Potts and Willmer 1997, 1998; Harmon-Threatt 2020). Social bees, like bumble bees, often build nests in the base of bunchgrasses, or in abandoned rodent holes (Figure 11). Still other bees and wasps nest in stems, wood cavities, and other nooks and crannies. Many hover flies (and flower-visiting beetles) use dead wood for nesting (Ulyshen et al. 2023).

In addition to food and nesting, pollinators need habitat conducive to finding mates, sheltering from inclement weather, and overwintering. Little is known about preferred sites for overwintering for most pollinator species (Hanberry et al. 2021), but these sites may be very different from foraging or nesting sites for species that overwinter as adults (Williams et al. 2019). Some species also require mating sites, such as landmarks used by some bees and butterflies to locate mates (Gonzalez et al. 2013; Danforth et al. 2019).

The differences in life histories in insect pollinator groups influence their management and conservation. Although some pollinators, such as bees and butterflies, rely almost exclusively on plants for food, for most other insect pollinator groups, while adults feed on nectar and/or pollen, their immature stages require a wide range of foods, ranging from the non-flowering portion of plants (e.g., stems, leaves), to dead wood, to insects, to fungi (Ulyshen et al. 2023). This means that many pollinators require multiple habitat features that support both immature and adult stages of the lifecycle, which can make managing and conserving habitat for these species more challenging.

F. Current Management Challenges and Opportunities

Globally, pollinators face threats on multiple fronts, and many groups of pollinators are declining (Dicks et al. 2021; Zattara and Aizen 2021; Osterman et al. 2021; Janousek et al. 2023). Some of the most significant threats to pollinators are habitat loss due to conversion of habitat to agriculture and built environments, climate change, invasive species, agrochemical exposure, and habitat degradation due to human land activities and disturbances (Dicks et al. 2021; Aizen et al. 2022). In the US, the need to address threats impacting pollinators has become more well recognized in the last two decades and, in 2014, President Barack Obama issued a Presidential Memorandum to create a federal strategy to promote the health of honey bees and other pollinators. The Memorandum established a national Pollinator Health Task Force and spurred research and conservation efforts by a wide range of federal agencies.

All of the factors implicated in global pollinator declines also play roles in interior PNW grasslands and riparian areas, but certain factors are more relevant than others to the region. One widespread use of grasslands and riparian areas in the interior PNW is livestock grazing, so a high priority is to 1) understand how livestock grazing affects pollinators and 2) identify opportunities to minimize any negative effects of grazing on pollinators. This information can aid producers in developing pollinator-friendly grazing strategies. Understanding the effect of native ungulates on pollinators is also a research priority to inform management of deer and elk populations. In addition, as wildfire becomes more common and severe, its effect on pollinator habitat is expected to increase. However, fire can also be a management tool, and the potential use of prescribed burning to enhance pollinator habitat is a promising area that needs further research in inland PNW systems. The continued and, in some places, accelerated invasion of non-native grasses (e.g., *Ventenata dubia* in the Zumwalt Prairie) poses a major threat to grassland diversity and function, including for pollinators. In addition, drier, warmer summers and altered precipitation patterns continue, and these climatic changes interact with fire, ungulate herbivory, and invasive weed invasions in complex ways that likely impact pollinators. Finally, although many of the grasslands of the region have already been converted to agriculture and other purposes, some areas are no longer cultivated, so opportunities exist to investigate the best ways to restore grasslands. Similarly, riparian areas are often the focus of restoration because of salmonid issues, and studies can investigate how to restore streams and riparian areas in ways that also benefit pollinators, leading to win-win solutions.

G. About this Report

This report focuses on pollinator research conducted in three locations (Figure 2):

a. The Nature Conservancy's Zumwalt Prairie Preserve
b. The Nature Conservancy's Boardman Grassland Preserve
c. The US Forest Service Starkey Experimental Forest and Range

These three locations represent some of the extensive variability in interior PNW grasslands and riparian areas, and many of the patterns and relationships described in this report will apply to other areas in the interior PNW. For example, general patterns in pollinator and blooming plant phenology are expected to be consistent, but species composition and exact timing will vary from place to place. Much of the research aims to understand mechanistic drivers of response of pollinators to stressors, management, and restoration, and should be transferable to other grassland and riparian areas in the interior PNW.

Readers can browse the Table of Contents to identify areas of interest. Each section includes boxes highlighting key findings of the research and management implications. Highlights of the information presented in this report are available in an interactive Story Map (Pollinators of Oregon Grasslands and Riparian Meadows) and three short factsheets provide overviews of the main ideas presented in this technical report for a general audience:

- Getting to Know Pollinators in Pacific Northwest Rangelands
- Pollinator-Friendly Livestock Management in the Interior Pacific Northwest
- Habitat Enhancement for Pollinators in the Interior Pacific Northwest

III. Objectives of Report

The overall goal of this technical report is to communicate key findings of studies conducted in three locations in eastern Oregon over the last 15 years and to use those findings to provide insights about managing and restoring grassland and riparian habitats in the interior PNW for the benefit of pollinators – primarily native bees and butterflies. The specific objectives of the report are to:

1. Describe the diversity of pollinators and flowering plants documented in these studies, and their spatial and temporal variability
2. Review the state of our knowledge of plant-pollinator relationships in these systems
3. Provide an overview of how management (e.g., ungulate grazing, fire, non-native invasive annual grasses) affects native pollinators and the flowers they rely on
4. Present results regarding the response of pollinator and flowering plant communities to restoration of grasslands and riparian areas

This report summarizes relevant research results and their management implications related to each objective, then provides an overview of the broader implications of the research, identifies knowledge gaps, and future areas of research.

IV. Overview of Pollinator Research

A. Description of Systems

The research described in this report was conducted at three locations in eastern Oregon (Figure 2): The Nature Conservancy's Zumwalt Prairie Preserve, The United States Forest Service Starkey Experimental Forest and Range, and The Nature Conservancy's Boardman Grassland Preserve. These habitats encompass a wide variety of grassland and riparian habitats that occur in the interior PNW, ranging from higher elevation grasslands and riparian meadows to lower elevation, semi-arid grassland/shrub-steppe.

The Nature Conservancy's Zumwalt Prairie Preserve

Located in Wallowa County in northeastern Oregon (45˚34′ N, 116˚ 58′ W), the 13,269 ha Zumwalt Prairie Preserve (Zumwalt) is owned and managed by The Nature Conservancy (TNC) (Figure 12). The larger Zumwalt Prairie (~65,000 ha) is considered to be the largest relatively intact remnant of Pacific Northwest Bunchgrass Prairie (Bartuszevige et al. 2012), a grassland type that once covered approximately ~8 million ha in the PNW and portions of western Canada (Tisdale, 1982). The preserve is characterized by relatively high elevations (1,060 -1,680 m), an annual mean temperature of 6.7 °C (with an average annual minimum of 0.5 °C and an average maximum of 13.0 °C), and 43.0 cm precipitation, primarily occurring as snow in winter (30-year average; US Climate Data 2020, Joseph, OR). The preserve is dominated by bunchgrass grassland habitat on rolling hills, but also includes a variety of other habitat types, including conifer forest, riparian areas, canyon grasslands, and isolated aspen stands (Gonzalez et al. 2013).

Figure 12. Zumwalt Prairie Preserve in spring. Photo: R. McEwan.

Soils on the Zumwalt are primarily Xerolls, formed on basalt bedrock with more recent depositions of loess and colluvium (Bartuszevige et al. 2012; Schmalz et al. 2013). Historically, the Zumwalt was dominated by native grass species including Idaho fescue (*Festuca idahoensis*), Sandberg bluegrass (*Poa secunda*), prairie Junegrass (*Koeleria macrantha*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) (Kennedy et al. 2009). However, the non-native annual grass, Ventenata (*Ventenata dubia*), has steadily invaded over the last 15 years, increasing by 30% (as measured by foliar cover) between 2008 and 2018 (Ridder et al. 2021), becoming the fourth most dominant grass (by foliar cover value) in some areas of the Zumwalt

(Endress et al. 2020). The forb community is diverse, with over 350 species documented on the preserve, comprising about 65% of vascular plant diversity (The Nature Conservancy 2017).

Indigenous people, including the Nez Perce, grazed horses (*Equus calballus*) and cattle (*Bos tauras*) on the Zumwalt in the late 1700s (Bartuszevige et al. 2012; Endress et al. 2020). In the late 1800s, settlers grazed larger herds of cattle and horses, as well as sheep, on the Zumwalt and cultivation of some deeper-soiled areas began during this period as part of Homesteading Act requirements. Most year-round homesteads were abandoned by the 1940s as it proved too difficult to maintain winter residency. In the 1950s, hundreds of push-up dams were installed on headwater streams to create stock ponds, which affected distribution and stocking rates of livestock and wildlife. By the 1980s, most areas that had been cultivated were seeded with perennial pasture grasses – areas known as “old fields.” TNC acquired ~11,000 ha of the Preserve in 2000, and then added another ~2400 ha with an additional purchase in 2006. The preserve has been managed for livestock grazing at low to moderate stocking rates, with a lease system that secures grass for local ranchers. TNC also manages for several conservation targets, including the ESA-listed threatened plant Spalding’s catchfly (*Silene spaldingii*), riparian habitat and quaking aspen stands and allows limited hunting of cow and bull elk and turkey.

The USFS Starkey Experimental Forest and Range

Located in Union County in northeastern Oregon (45˚12' N, 118˚ 3' W), the United States Forest Service (USFS) Starkey Experimental Forest and Range (Starkey) encompasses 10,125 ha, and was established in 1989 to research elk, mule deer and livestock responses to intensive management of forests and rangelands at a landscape scale (Rowland et al. 1997). The pollinator studies described here occurred in a 2,217-ha portion of the Meadow Creek drainage (Figure 13); the riparian study area comprises 157 ha (7.1%), with uplands occupying the remainder. Elevations range from 1,120 m along Meadow Creek to 1,500 m in the uplands. Average annual mean temperature is 9.7 °C (with an average annual minimum of 3.1° C and an average maximum of 16.3°C), and 44.2 cm precipitation (30-year average; US Climate Data 2020, La Grande, OR). Meadow Creek is used extensively by two wild ungulate species - mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) - spring through fall, with densities comparable to those in adjacent herd ranges (2.8-3.6 per km^2 (deer), 5.6-6.8 per km^2 (elk)). Cattle historically grazed in the Meadow Creek drainage, but were excluded from some areas in 1990 (Case and Kauffman 1997) and from all of Meadow Creek in Starkey from 2012-2017. Cattle grazing was reintroduced along Meadow Creek in 2017 using a deferred rotation grazing system as part of a long-term experiment (Mitchell et al. 2023).

Figure 13. Riparian area along Meadow Creek at Starkey Experimental Forest and Range. Photo: M. Rowland.

Dominant riparian shrubs in the Meadow Creek riparian areas include willow (*Salix* spp.), black hawthorn (*Crataegus douglasii*), thinleaf alder (*Alnus incana*), black cottonwood (*Populus balsamifera*, and common snowberry (*Symphoricarpos albus*). Scattered ponderosa pine (*Pinus* *ponderosa*), Douglas fir (*Pseudotsuga menziesii*), and western larch (*Larix occidentalis*) also occur in the riparian corridor. Herbaceous vegetation includes a variety of forbs, as well as sedges (*Carex* spp.), rushes (*Juncus* spp.), common spikerush (*Eleocharis palustris*), creeping bentgrass (*Agrostis stolonifera*), and fowl mannagrass (*Glyceria striata*). Upland habitat consists of mixed coniferous forest with Douglas-fir and grand fir (*Abies grandis*), along with lodgepole (*P. contorta*) and ponderosa pine. Over 600 plant species have been described at Starkey, including over 450 flowering forbs and shrubs (USFS, unpublished data).

The Nature Conservancy's Boardman Grassland Preserve

The Nature Conservancy's Boardman Conservation Area (BCA) is located in Morrow County, Oregon (45° 38' N, -119° 51' W), and is surrounded on three sides by pivot-irrigated agricultural fields (Figure 14). The 9,163 ha preserve is characterized by relatively low elevations (1,060 - 1,680 m), high temperatures (average annual mean of 12.2 °C, minimum of 5.6 °C, and maximum of 18.8 °C), and 21.7 cm of precipitation (30-year average; US Climate Data 2020, Boardman, OR). Soils across the BCA range from deep silty loess-derived soil to sandy fluvial deposits and eolian dunes. Vegetation is typical of shrub-steppe, characterized by big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and antelope bitterbrush (*Purshia tridentata*) as common shrubs interspersed with bluebunch wheatgrass, Sandberg's bluegrass and needle-and-thread grass (*Hesperostipa comata*). Over 190 plant species have been documented to occur at the BCA, with ~165 species of forbs (The Nature Conservancy 2016). The focus of conservation efforts at BCA is the low-elevation shrub-steppe habitat, with Washington ground squirrel (*Urocitellus washingtoni*), loggerhead shrike (*Lanius ludovicianus*), ferruginous hawk (*Buteo regalis*) and sagebrush sparrow (*Artemisiospiza nevadensis*) as specific conservation targets. Significant restoration efforts have been made to reestablish native vegetation in places that had become dominated by annual invasive grasses and other non-native weeds (Cahill 2016).

Figure 14. The Nature Conservancy's Boardman Grassland Preserve. Photo: R. McEwan.

B. Types and Timeline of Studies

Figure 15. Native bee researcher, Chiho Kimoto, at the Zumwalt Prairie, as she conducted the first study using blue vane traps in a grassland habitat. Photo: S. DeBano.

The work described in this report began on The Nature Conservancy's Zumwalt Prairie Preserve in 2007 (Table 1; Appendix A) with a study that was not only the first to systematically document bee communities in a PNW grassland, but also the first to use a new technique for sampling native bees in grasslands – the blue vane trap (Figure 15). Since that seminal study, over 15 studies have been conducted in eastern Oregon grasslands and riparian areas on native bees and other pollinators and at all three of the locations described above (Table 1). Studies have ranged from basic descriptions of pollinator community diversity and documentation of sensitive species, to examinations of pollinators associated with rare plant species and rare habitats, to investigations of plant-pollinator relationships, to research on how various types of land management and restoration efforts affect pollinator communities and the resources they depend upon.

As the research effort expanded, additional bee sampling methods were employed (Figure 16). Many of the studies described in this report used pan traps to sample bees. Both pan traps and vane traps are passive sampling methods that are useful for characterizing bee communities. However, one limitation of passive sampling is that the methods do not produce information on plant-insect relationships. One way to obtain this information is through hand-netting or observing bees and other insects on flowers (Figure 16).

Figure 16. Methods used to study native bees including A) blue vane traps, B) pan traps, and C) hand-netting.

Table 1. Studies included in this report, organized by location. Note: Publications that included multiple locations are listed under each location.

The Nature Conservancy's Zumwalt Prairie Preserve		
Year(s) Study Conducted	**Study Name - Description**	**Relevant Publications**
2007	Moth Diversity of the Zumwalt Prairie – described moth diversity associated with a riparian canyonland at the Zumwalt Prairie Preserve	Schmalz et al. unpublished data
2007-2008	Western Bumble Bee - first record of substantial population of western bumble bee (*Bombus occidentalis*) in the Pacific Northwest since its decline	Rao et al. 2011
2007-2008	Native Bee Communities of the Zumwalt Prairie – described flowering plant and native bee communities and their temporal and spatial variability; first study to use vane traps to sample native bees in grasslands	Kimoto et al., 2012a
2007-2008	Effect of Grazing Intensity on Native Bees – examined how grazing intensity influences flowering plant and native bee communities	Kimoto et al. 2012b
2007-2008	Effect of Grazing Intensity on Butterflies - examined how grazing intensity influences butterfly communities; butterflies were sampled and identified by Dana Ross, Lepidoptera expert	DeBano et al., In Prep.
2010	Bee Communities of Zumwalt Aspen Stands – compared floral and bee communities of aspen stands with adjacent grasslands	Gonzalez et al. 2013
2010	Pollinator Visitation of Spalding's Catchfly – identified pollinators visiting this threatened plant species	Tubbesing et al. 2014
2015	Factors Influencing Grassland Bee Communities – identified environmental variables influencing floral and native bee communities in three different types of interior PNW grasslands	Smith DiCarlo et al. In Prep.
2008, 2010, 2016, 2018	Effect of Prescribed Fire, Grazing, and Annual Grass Invasions on Forb Communities – used a long-term dataset of forb communities that provide nectar and pollen to bees to examine how fire, grazing, and a ventenata invasion affected those forb communities.	Watson et al. 2021
2018	Phenologically-Targeted Grazing Effects on Native Bees – examined how grazing that occurs after peak bloom periods affects floral and native bee communities	Mitchell et al. 2023

The Nature Conservancy’s Zumwalt Prairie Preserve (continued)		
Year(s) Study Conducted	**Study Name - Description**	**Relevant Publications**
2018	Metabarcoding Pollen to Understand Plant-Pollinator Interactions – compared pollinator networks generated from visual observations with networks generated using metabarcoding data from pollen collected from foraging bees	Arstingstall et al. 2021
2018-2019	Effect of Passive Restoration on Floral Availability in Formerly Cultivated Fields – compared forb communities in fields cultivated decades ago with intact native prairie	Watson 2020
2018-2019	Effect of *Ventenata dubia* invasion on Native Bee Communities – compared native bee community responses to varying levels of ventenata invasion	DeBano et al. In Prep.
2018-2019	Effect of Passive Restoration on Bee Communities in Formerly Cultivated Fields – compared bee communities in fields cultivated decades ago with intact native prairie	DeBano et al. In Prep.
2018-2019	Fire and Livestock Grazing Influences on Native Bees and Their Floral Resources – compared fire, livestock grazing, and their interaction on native bee communities	DeBano et al. In Prep.
The Nature Conservancy’s Boardman Grassland Preserve		
2014-2016	Effect of Wildfire on Native Bee and Flowering Plant Communities - described effects of wildfire on grassland flowering plant and native bee communities using a “before-after-control-impact” (BACI) design	Smith DiCarlo et al. 2019
2014-2016	Grassland Restoration Effects on Bee and Flowering Plant Communities – described flowering plant and native bee communities and the environmental variables influencing them, and how those communities responded to grassland restoration	Smith DiCarlo et al. 2020
2015	Factors Influencing Grassland Bee Communities – identified environmental variables influencing floral and native bee communities in three different types of interior PNW grasslands	Smith DiCarlo In Prep.
USDA Forest Service Starkey Experimental Forest and Range		
2014	Dietary Overlap of Mammalian Herbivores and Native Bees – documented which flowers bees use in riparian areas and conducted literature review to determine which of those plants are preferred or avoided by native and domestic ungulates	DeBano et al. 2016a

2014-2015	Plant-Bee Associations in Riparian Areas – examined the use of forbs by native bees in riparian areas at Starkey, identifying those most commonly used and those preferred by bees; also examined how native status, flower color, and flower morphology affected the types of bees visiting flowers	Roof et al. 2018
2017-2018	Metabarcoding Pollen to Understand Plant-Pollinator Interactions – compared pollinator networks generated from visual observations with networks generated using metabarcoding data from pollen collected from foraging bees; investigated the use of sequence reads as a proxy for relative abundance of pollen in a mixed pollen load, the consequences of selecting different sequence count removal thresholds, and how sequence artefacts may confound conclusions about bee foraging behavior	Arstingstall et al. 2021, 2023
2018	Importance of Early Season Shrubs for Native Bees – Examined the native bees use of forbs and shrubs throughout the season – shrubs a win-win for fish and bees	Mitchell et al. 2022
2018	Phenologically-Targeted Grazing Effects on Native Bees – examined effect of grazing that occurs after peak bloom periods on native bee communities	Mitchell et al. 2023
2014-2016	Effect of Native Ungulate Herbivory on Native Bees – investigated how exposure to deer and elk in riparian meadows affected native bee and flowering communities	Wojcik et al 2018; DeBano et al. In Review
2017-2019	Effects of Livestock and Native Ungulates on Native Bees – examined how native ungulates and cattle individually and in combination, affect native bee and blooming plant communities.	Glenny et al. In Prep.
2018-2019	Riparian vs. Upland Native Bee Communities – Compares native bee abundance, species richness, and community composition at riparian sites in Meadow Creek with upland forest types.	DeBano et al. In Prep.

V. Lessons Learned

A. Overview of Pollinators, Plants, and Their Relationships

1. Regional Pollinator and Plant Diversity

When the research described in this report was initiated in 2007 (Table 1), very little was known about interior PNW pollinators, with no systematic studies having been conducted in eastern Oregon grasslands and riparian meadows. This knowledge gap represented a significant obstacle to developing conservation and management plans for pollinators. Thus, the first step in developing effective strategies for native pollinator management and conservation was determining which pollinators occur in the region. Since that time, a variety of pollinators have been studied and described. While the greatest number of studies have been aimed at native bees (Figure 17), by far, other groups have also been studied, including butterflies and moths (Table 1). The studies described in Table 1 focused not only on documenting the pollinator communities themselves, but also on describing the blooming plant communities that occur in these locations. The geographic locations of the study ranged from high and low elevation bunchgrass prairie to riparian meadows.

Figure 17. The urban digger bee (*Anthophora urbana*). Photo: S. Mitchell.

Key Findings

The numerous studies described in this report further our knowledge of some of the key pollinator groups in grasslands and riparian meadows in the PNW and provided much needed information about the presence of pollinator species of conservation concern. In addition, the body of research has provided a solid understanding of the plant communities in these regions.

The first descriptions of native bee and blooming plant communities came from work at The Nature Conservancy's Zumwalt Prairie Preserve (Kimoto et al. 2012a). The Zumwalt Prairie was also the focus of additional work on butterflies and moths (Table 1). Later projects expanded the geographic scope of native bee and blooming plant studies to include The Nature Conservancy's Boardman Conservation Area and the USFS Starkey Experimental Forest and Range.

Diverse Pollinator Communities

The first work at the Zumwalt Prairie revealed an extremely diverse native bee community that was as species-rich as any bee community documented in other grasslands in the US at that time, including those in the Great Plains (Kimoto et al. 2012a). Through the years, over 210 bee species have been identified at The Nature Conservancy's Zumwalt Prairie Preserve (Appendix B). The three-year study at The Nature Conservancy's Boardman Conservation Area documented 85 species, and six-years of sampling at Meadow Creek riparian areas at the USFS Starkey Experimental Forest and Range resulted in 285 described species. Remarkably, just these three locations in eastern Oregon have documented over 364 bee species, which represent more than 50% of the 600 bee species estimated to occur in Oregon (Best et al. 2021). Although the three locations shared 39 bee species, many species were unique to each location (Figure 18), and others, while present at all three locations, were much more common in some compared to others (Figure 19). Thus, differences in species composition and relative abundance at the three locations show that even grasslands within the same region support distinct bee communities. See Appendix B for lists of species at each location. Notably, this work (as well as the butterfly and moth work described later in this report) could not have been completed without the help of taxonomic experts in the field.

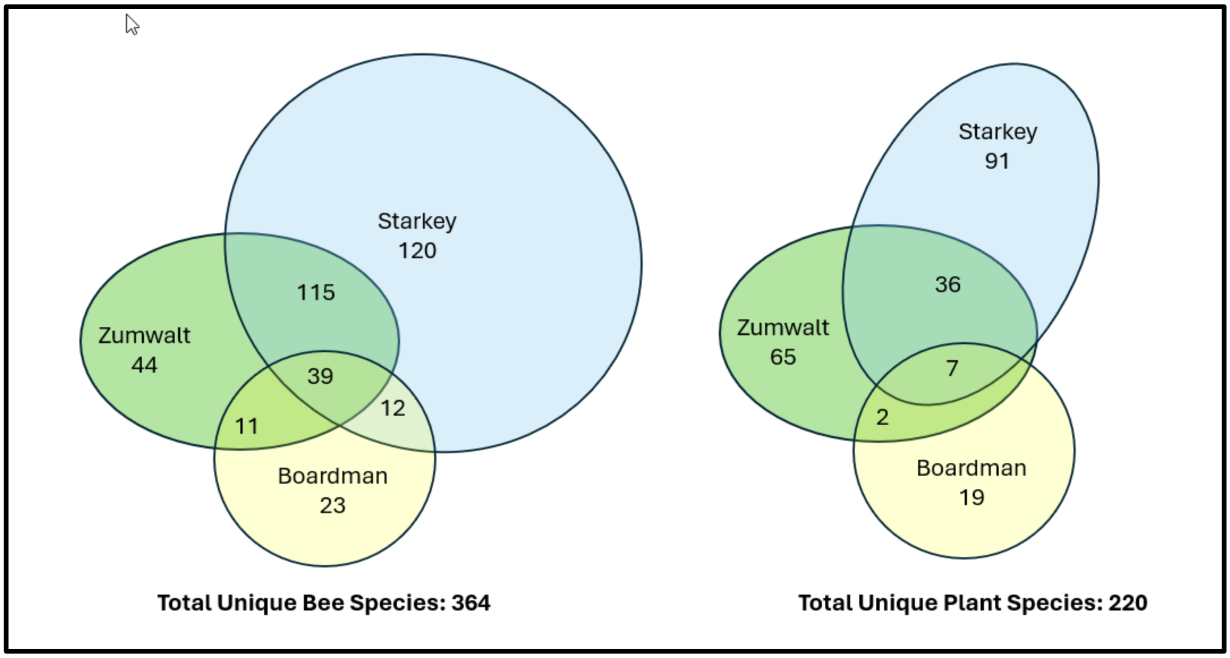


Figure 18. Venn diagram showing bee (collected with hand-netting and passive traps) and blooming plant species (documented on study transects) that are distinct and overlapping for the three study locations (The Nature Conservancy's Zumwalt Prairie Preserve, The Nature Conservancy's Boardman Conservation Area, and the USFS Starkey Experimental Forest and Range). See Appendices B and E for lists of species occurring at each location.

Figure 19. A foraging metallic sweat bee (*Agapostemon* sp.). Individuals of this genus were much more common in The Nature Conservancy's Boardman Conservation Area as compared to the other two locations. Photo: S. Mitchell.

Additional pollinator groups beyond native bees have been studied at The Nature Conservancy's Zumwalt Prairie Preserve. In 2008 and 2009, Dana Ross, a Lepidoptera expert, sampled butterflies at the 16 Zumwalt Food Web sites and documented 29 species of butterflies (Table 1). Since then, a total of 55 species have been identified by Ross and fellow lepidopterists Cliff Ferris and Paul Hammond (Appendix C; Figure 20). Although butterflies are less speciose compared to most other flower-visiting insect groups, the Zumwalt Prairie Preserve has over 30% of the estimated 171 naturally occurring species in Oregon (Warren 2005).

Figure 20. A blue butterfly (*Icaricia* sp.) visiting goldenrod (*Solidago* sp.). Photo: S. Mitchell.

In addition to bees and butterflies, moths have also been studied at The Nature Conservancy's Zumwalt Prairie Preserve. Although some moths are active during the day, such as many common hawkmoths (Family Sphingidae) (Figure 21), most moths are primarily nocturnal (Figure 22). Nocturnal moths were the focus of a study by Heidi Schmalz, Jason Dingeldein, and Dana Ross, which provided a first step towards understanding the role moths may play as pollinators in interior PNW grasslands. Schmalz and colleagues sampled moths from May to September 2017 using a black light trap, resulting in the description of 255 species of moths (Appendix D). Characterizing the moth community will allow future studies to investigate which species may play roles in pollination. Several families with nectar-feeding adults were identified (Appendix D), including hawkmoths (Sphingidae), owlet moths (Nocutiidae), erebid moths (Erebidae), geometrid moths (Geometridae), and crambid snout moths (Crambidae). These groups are most likely to contain species that aid in plant pollination (Van Zandt et al. 2020). The sheer diversity of moth species at the Zumwalt Prairie Preserve highlights the importance of continuing research on this group of insects to better understand not only their role in pollination of grassland and meadow species, but also how they are affected by management and disturbance (e.g., light pollution) (MacGregor et al. 2015; van Geffen et al. 2015; Owens et al. 2018).

Figure 21. A white-lined sphinx moth (*Hyles lineata*) sipping nectar from a flower. Photo: S. Mitchell.

Figure 22. A simple wave moth (*Scopula junctaria*) perching on vegetation. Photo: S. Mitchell.

Pollinator Species of Concern

A number of pollinator species in the interior PNW are of conservation concern (see Xerces Society's species profiles at: https://xerces.org/endangered-species/species-profiles). One such species is the western bumble bee, *Bombus occidentalis (*Figure 23). Historically, the western bumble bee was common throughout the PNW and beyond. However, in the late 1990s, the species experienced steep declines across much of its range (Figure 24). The suspected culprit was a pathogen *(Nosema bombi)* that may have been introduced to wild populations via commercial colonies produced in Europe and shipped to the US (Rao et al. 2011).

Figure 23. A female western bumble (*Bombus occidentalis*) foraging on lupine at the USFS Starkey Experimental Forest and Range**.** [Watch a video]() of this female western bumble bee forage on lupine at Starkey**.** Photo: S. Mitchell

The first pollinator study at The Nature Conservancy's Zumwalt Prairie Preserve (Kimoto et al. 2012a) was also the first study to find a robust population of western bumble bees documented in Oregon after this decline (Rao et al. 2011). Since then, the species has been regularly detected in eastern Oregon, including at Meadow Creek and elsewhere at Starkey. It does not occur at Boardman, where conditions are not conducive for high bumble bee diversity.

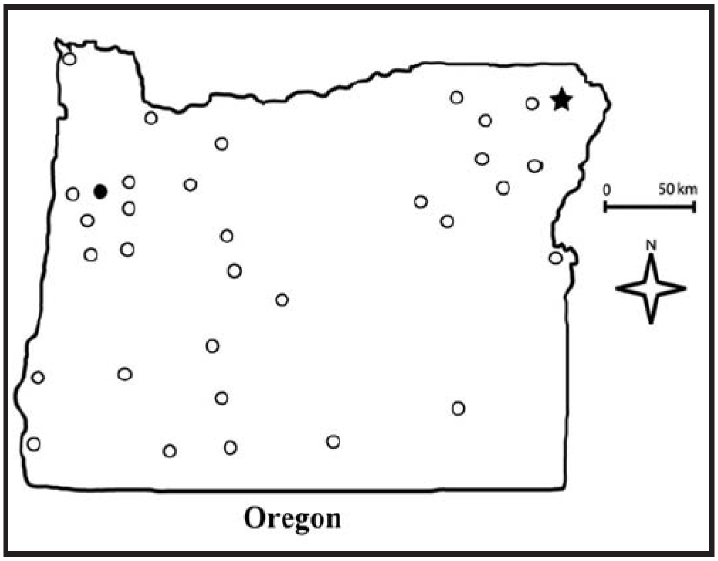


Figure 24. Historical range of the western bumble bee in Oregon (modified from Stephen 1957). The star indicates the location of The Nature Conservancy's Zumwalt Prairie Preserve, where the first robust population of western bumble bees was documented in Oregon after this decline.

In addition to the western bumble bee, interior PNW grasslands are home to other pollinator species of concern including the yellow bumble bee (*Bombus fervidus*), which, if current trends continue, may go extinct in the next 70-80 years (Hatfield et al. 2015). Two other bees listed as "at-risk" by the Xerces Society of Invertebrate Conservation, the small mason bee (*Hoplitis producta subgracilis)* and the long-horned bee (*Eucera frater lata*), occur at Starkey and the Zumwalt. Conserving, enhancing, and restoring habitat can help maintain and strengthen existing populations of these sensitive species, and potentially expand their distribution in the future.

Diverse Blooming Plant Communities

The Nature Conservancy had long engaged in plant surveys and research at the Zumwalt Prairie Preserve since they first acquired the land in 2001 (Taylor 2013). The work described in this report was focused specifically on understanding how the diverse plant community documented in past studies contributed to providing floral resources for pollinators. This was done by counting blooming stems of forbs and shrubs (Figure 25). Through the years, 110 blooming plant species have been identified in pollinator research plots at The Nature Conservancy's Zumwalt Prairie Preserve (Appendix B). The three-year study at The Nature Conservancy's Boardman Conservation Area documented just 28 blooming plant species, and the six-years of sampling at Meadow Creek riparian areas at the USFS Starkey Experimental Forest and Range resulted in documenting 134 blooming species. At all three locations, over 220 blooming forb and shrub species have been documented in pollinator plots (see Appendix E for lists of species at each location). Although the three locations shared 7 forb or shrub species, many other species were unique to each location (Figure 18), showing that even grasslands within the same region support distinct blooming forb and shrub communities. The flora of Nature Conservancy’s Zumwalt Prairie Preserve is also notable because it contains the largest population of Spalding’s catchfly (*Silene spaldingii*), which was listed as threatened in 2001 (Figure 26; Tubbesing et al. 2014).

Figure 25. Sampling plants at The Nature Conservancy's Zumwalt Prairie. Photos: C. Kimoto

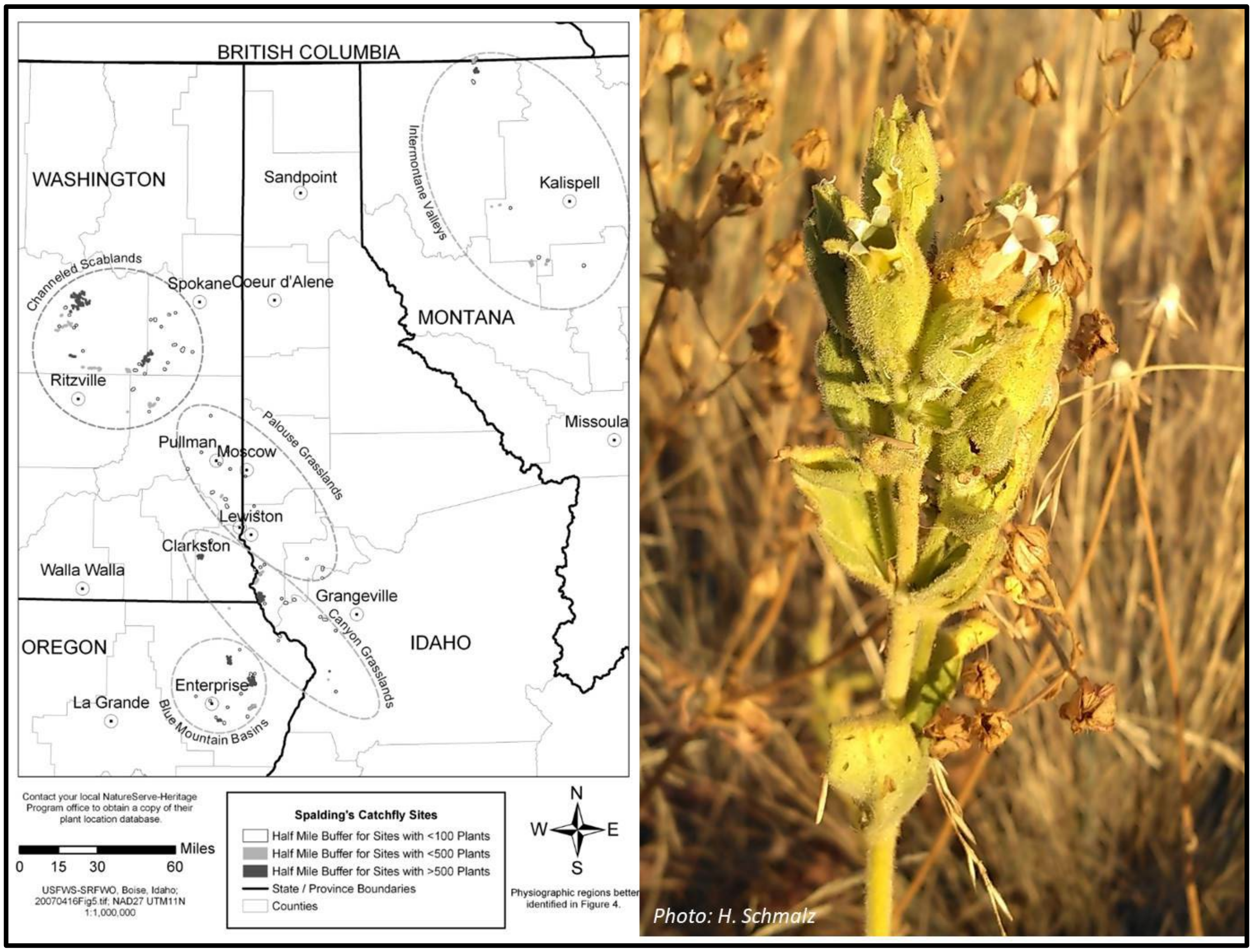


Figure 26. Distribution of Spalding's catchfly (*Silene spaldingii*) in the interior PNW and a plant in showing signs of herbivory.

Summary of Key Findings About Regional Pollinator and Plant Diversity

- Pollinator and blooming plant communities in interior Pacific Northwest grasslands and meadows are very diverse, and include species of conservation concern (e.g., the western bumble bee, the threatened Spalding's catchfly).
- Native bee and blooming plant communities in riparian areas are particularly diverse, with the highest number of species detected and the greatest proportion of unique species of the three grassland types investigated.
- Some insect groups that may include important pollinators, such as moths, are particularly species-rich and deserve more attention, both from a research and a conservation perspective.

Management Implications

The variety of studies conducted in eastern Oregon over the last two decades have led to the key management implications outlined below.

Management Implications

- Conserving existing species-rich pollinator communities is a top priority given the relatively high levels of biodiversity associated with these interior PNW grasslands compared to other systems.
- Conservation and restoration of riparian meadows may not only benefit many plants and vertebrates, but also ecologically significant invertebrates like native bees.
- Effective pollinator management plans will take into account the different pollinator species that occur within the areas of interest and the specific habitat types encompassed within the area.
- The western bumble bee's occurrence at the Zumwalt Prairie and Starkey illustrates the importance of large tracts of intact pollinator habitat for conserving species of concern in Oregon.
- Surveying pollinator communities provides fundamental information needed to develop pollinator management and conservation plans. Even fairly limited surveys (e.g., one year of moth survey data at the Zumwalt Prairie) can yield large amounts of useful information.
- Taxonomic expertise is key to understanding the diversity of invertebrate pollinator groups and is a limited but highly necessary skill.
- Research and conservation efforts aimed at pollinators should be expanded beyond native bees and butterflies, with groups such as moths and flies of particularly high priority given their diversity and potential importance as pollinators of many native plant species.
- Understanding the life histories of native pollinator species will be key to conserving them. However, given the enormous variation in life histories, maintaining a diversity of habitat conditions and plant species may be the best strategy for preserving pollinator communities given insufficient knowledge of many pollinator life histories.

2. Variability in Time and Space in Pollinator and Flowering Plant Communities

Grasslands and riparian meadows of the interior Pacific Northwest are not homogenous. A wide range of temperatures, precipitation, and elevations results in a patchwork of habitats that not only vary spatially, but also through the growing season. Monthly high and low temperatures and precipitation at the three locations differ (Figure 27), with The Nature Conservancy's Boardman Conservation Area being warmer and drier than the other two locations. These patterns in temperature and precipitation strongly influence vegetation, as evident in a regional map of "greenness" (i.e., the normalized difference vegetation index) (Figure 28). Not only does overall greenness vary spatially, but the timing of greenness differs.

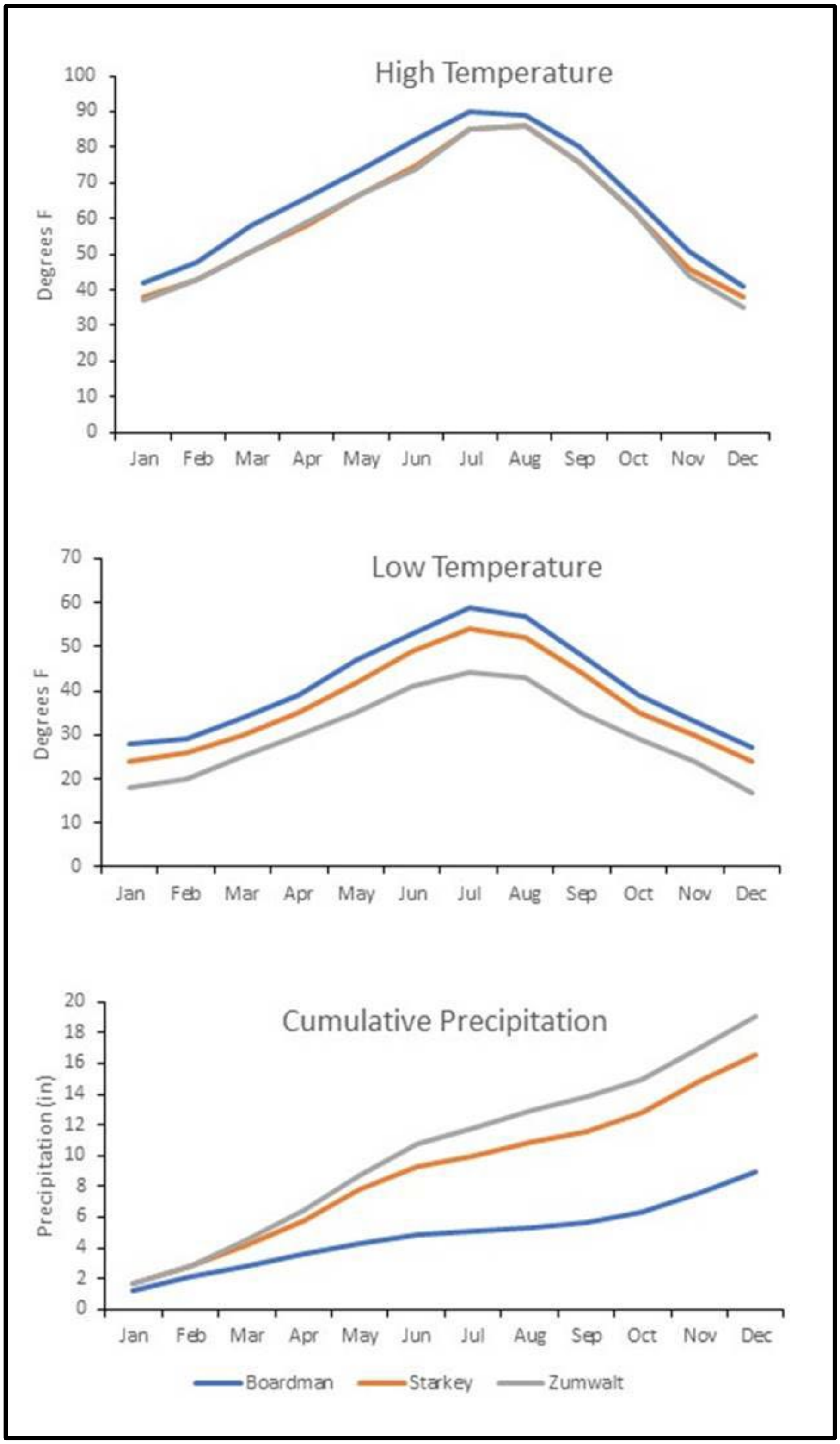


Figure 27. Mean high and low temperatures and cumulative precipitation at The Nature Conservancy's Boardman Conservation Area and Zumwalt Prairie Preserve, and the USFS Starkey Experimental Foerst and Range.

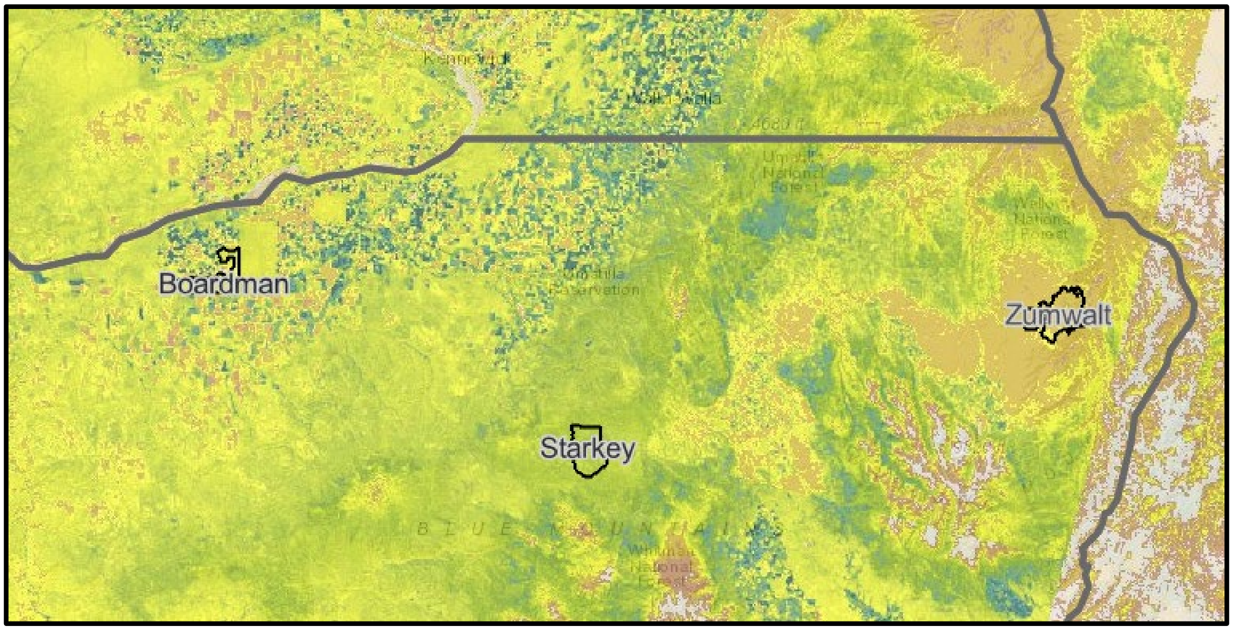


Figure 28. The three study locations described in this report located in a map displaying the normalized difference vegetation index (NDVI), a measure of "greenness" of the landscape. Greenness varies on a gradient from low (red-orange) to high (dark green). While this map shows overall greenness varying spatially, the timing of greenness also differs.

Key Findings

The studies described in this section all focused on one pollinator group – bees – because they were studied at all three locations. As outlined in the previous section, the diversity of native bee and bloomng plant communities at the three locations differed - an expected pattern given variation in elevation, temperature, and precipitation among the three locations (Table 2). Bee and blooming plant communities not only varied with respect to taxa richness, but also relative to community composition (Mitchell et al. 2023; DiCarlo Smith, In Prep), with each location dominated by different taxa (Table 2).

Temporal Variability

Not only do the overall native bee communities differ, but their phenology varies as well. In general, native bee richness peaks earlier in the season (May-July), but the particular month in which bee richness peaks depends not only on the location but also on the weather conditions of a given year (Kimoto 2012a; DeBano et al. 2016a; Mitchell et al. 2023). Patterns in native bee abundance vary seasonally as well, with peak abundance often occurring late in the season because of the prevalence of several species of primitively eusocial, generalist sweat bees such as *Halictus tripartitus*, *H. ligatus*, and *Lasioglossum incompletum* (Mitchell et al. 2023) (Figure 29). In contrast, with the exception of The Nature Conservancy's Boardman Conservation Area, blooming plant species richness, diversity, and abundance peak early in the season and decline monthly thereafter (Figure 30). In Boardman, blooming stem abundance, richness, and diversity peak late in the season, with large late-season flushes of blooms of two species: yellow rabbitbrush (*Chrysothamnus viscidiflorus*) and Douglas' knotweed (*Polygonum douglasii*) (Smith DiCarlo et al. 2020).

In addition to these changes in richness, diversity, and abundance, both native bee and plant communities change composition throughout the growing season (Kimoto et al. 2012a; DeBano et al. 2016a; Smith DiCarlo et al. 2020; Mitchell et al. 2023). Early season bees include many species of mining bees (*Andrena* spp.), long-horned bees (*Eucera* spp.), mason bees (*Osmia* spp.), cuckoo bees (*Nomada* spp.), and some bumble bee species (*Bombus* spp.) (Figure 31).

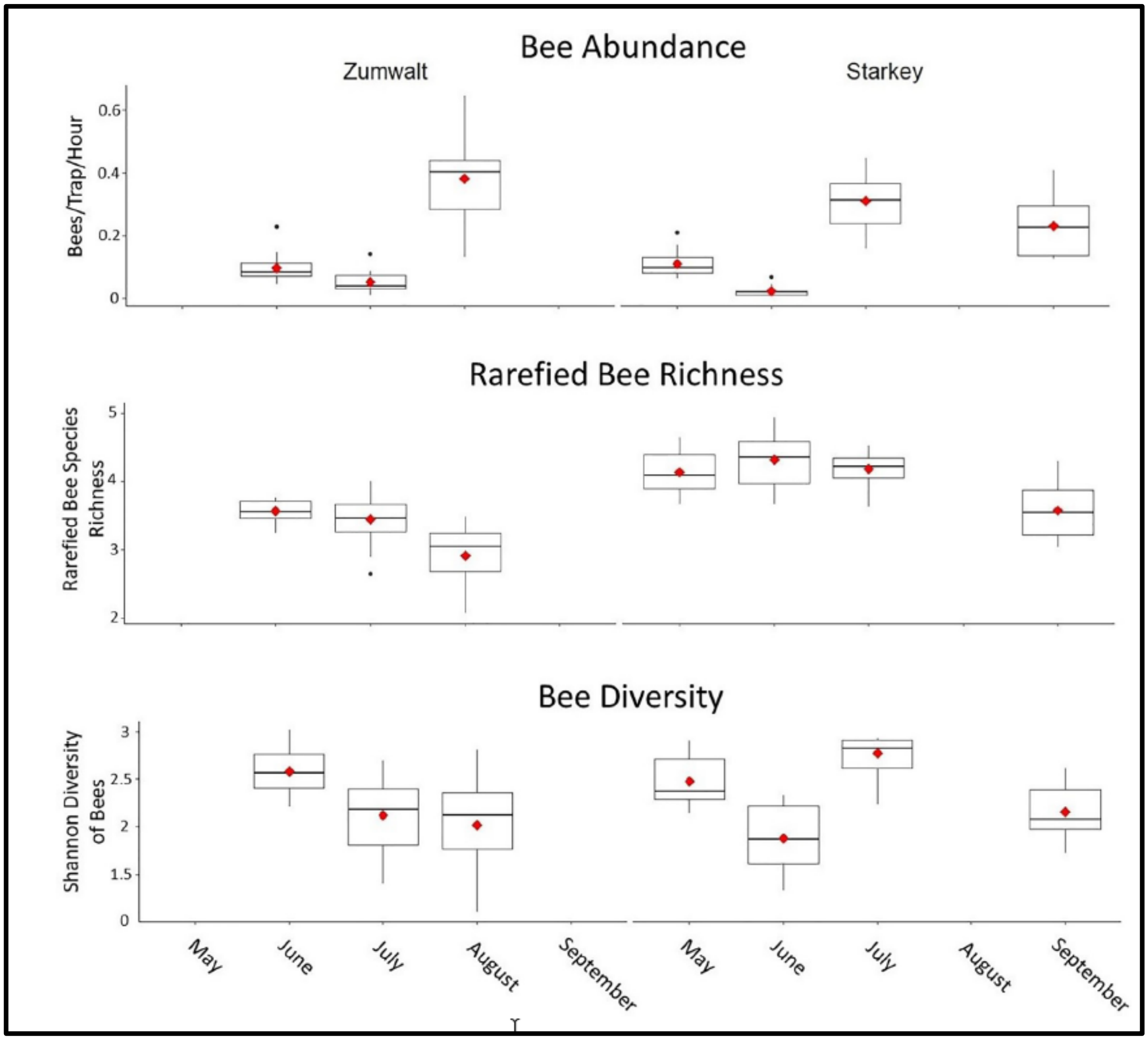


Figure 29. Patterns of native bee abundance, richness, and Shannon diversity at The Nature Conservancy's Zumwalt Prairie Preserve (left) and the USFS Starkey Experimental Forest and Range (right) in 2019. Adapted from Mitchell et al. (2023).

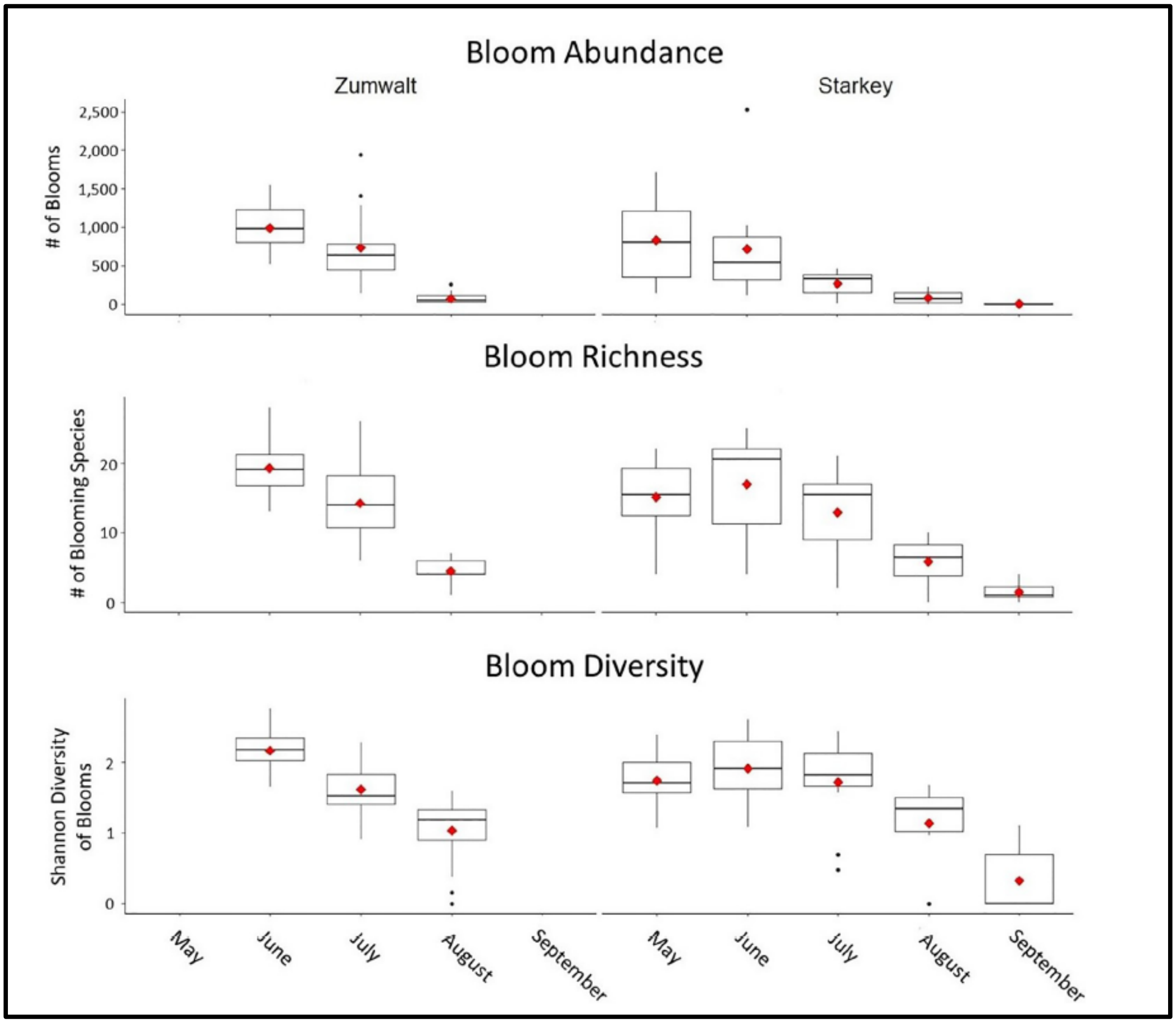


Figure 30. Patterns of blooming stem abundance, richness, and Shannon diversity at The Nature Conservancy's Zumwalt Prairie Preserve (left) and the USFS Starkey Experimental Forest and Range (right) in 2019. Adapted from Mitchell et al. (2023).

Table 2. Characteristics of the three study locations described in this report. Note: Data for bees and flowers for Starkey pertain only to the riparian areas of Starkey (not uplands).

Location	**TNC's Boardman Conservation Area**	**USFS Starkey Experimental Forest and Range**	**TNC's Zumwalt Prairie Preserve**
Elevation	120-295 m	1,120-1,500 m	1,060-1,680 m
Annual Precipitation	21.7 cm	44.2 cm	43.0 cm
Annual Snowfall	7.6 cm	28.0 cm	12.7 cm
Mean High Temp	18.8 °C	16.3 °C	13.0 °C
Mean Average Temp	12.2 °C	9.7 °C	6.7 °C
Mean Low Temp	5.6 °C	3.1 °C	0.5 °C
# Blooming Plant Species	28	134	110
Common Flowers	• Douglas' knotweed (*Polygonum douglasii*) • Yellow rabbitbrush (*Chrysothamnus viscidiflorus*) • Yellow star-thistle (*Centaurea solstitialis*)	• Common yarrow (*Achillea millefolium*) • Parsnipflower buckwheat (*Eriogonum heracleoides*) • Spring draba (*Draba verna*) • Slender cinquefoil (*Potentilla gracilis*) • Strict forget-me-not (*Myosotis stricta*)	• Twin arnica (*Arnica sororia*) • Thinleaved owl's clover (*Orthocarpus tenuifolius*) • Common yarrow (*Achillea millefolium*) • Lupines (*Lupinus*) • Prairie smoke (*Geum triflorum*) • Whitestem frasera (*Frasera albicaulis*) • Slender cinquefoil (*Potentilla gracilis*)

Location	**TNC's Boardman Conservation Area**	**USFS Starkey Experimental Forest and Range**	**TNC's Zumwalt Prairie Preserve**
Peak Bloom	July-September	May-July	June
Plant Notes of Interest	Two species of rabbitbrush bloom late in the season, providing nectar and pollen to a wide range of native pollinators	Oregon checkerbloom (*Sidalcea oregana*) is a common forb that supports a specialist bee species (*Diadasia nigrifrons*)	The Zumwalt Prairie is home to one of the largest populations of the threatened plant species, Spalding's catchfly (*Silene spaldingii*), which blooms relatively late in the summer.
# Bee Genera	23	36	34
# Bee Species	85	285	210
Most Common Bee Groups	• Metallic sweat bees (*Agapostemon*) (51%) • Sweat bees (*Lasioglossum*) (31%) • Long-horned bees (*Melissodes*) (10%)	• Sweat bees (*Lasioglossum* & *Halictus*) (65%) • Mason bees (*Osmia*) (9%) • Miner bees (*Andrena*) (7%) • Bumble bees (*Bombus*) (5%)	• Sweat bees (*Lasioglossum* & *Halictus)* (72%) • Bumble bees (*Bombus*) (7%) • Miner bees (*Andrena*) (6%) • Mason bees (*Osmia*) (7%) • Long-horned bees (*Melissodes*) (5%)
# Bumble Bee Species	4	15	16
Peak Bee Richness	June-July	May-July	June-July

Figure 31. A brown-belted bumble bee (*Bombus griseocollis*) foraging on Douglas' dustymaiden (*Chaenactis douglasii*) at The Nature Conservancy's Boardman Conservation Area. Photo: L. Smith DiCarlo.

Spatial Variation – Aspen Stands in Grasslands

In addition to seasonal variation, pollinator and blooming plant communities also vary spatially. As described in the preceding section, native bee and blooming plant communities differ among locations. However, even within a location, bee and plant communities can differ at smaller scales given the variable topography, soil conditions, and past land uses that combine to create a heterogenous landscape within grasslands. This is well illustrated at the Zumwalt Prairie, where isolated stands of woody species, like quaking aspen (*Populus tremuloides*) (Figure 32) can be found on north- and east-facing slopes of prairie hills.

Figure 32. An isolated quaking aspen stand on The Nature Conservancy's Zumwalt Prairie Preserve. Photo: N. Gonzalez.

Quaking aspen has experienced losses of 60-90% in the western US since European settlement (Lachowski et al. 1996). Like elsewhere, aspen on the Zumwalt Prairie have been impacted by multiple factors (Taylor and Rossman 2013; Figure 33), including browsing by native ungulates and livestock, which prevents aspen regeneration. Many species are closely associated with aspen stands and their decline threatens this biodiversity. Thus, to conserve the unique habitat that aspen stands provide, TNC has fenced many aspen stands to exclude ungulates (Taylor and Rossman 2013). Although plants, birds, and mammals had been studied, the value of quaking aspen stands as habitat for pollinators had not been examined until a project conducted by Gonzalez and colleagues. Their study at The Nature Conservancy's Zumwalt Prairie Preserve was the first to examine pollinators associated with aspen, and they found numerous differences between aspen and grassland habitat (summarized in Table 3). For example, bumble bees were more abundant in aspen stands compared to adjacent grassland habitat, which had more sweat bees and digger bees (Gonzalez et al. 2013). Aspen stands also had more blooming species and a distinct floral community, especially late in the season. Interestingly, Gonazlez et al (2013) also found that the types of male bumble bees that used aspen stands vs. grasslands varied. Male bumble bees that engage in territorial behavior were more common in grasslands relative to aspen stands. Males of these territorial species have larger eyes than females. ostensibly so they can see male competitors and incoming females better (Figure 34). In contrast, “normal-eyed” males were more common in aspen stands; these males find females by scent-marking structures, such as tree stumps, which are more common in aspen stands.

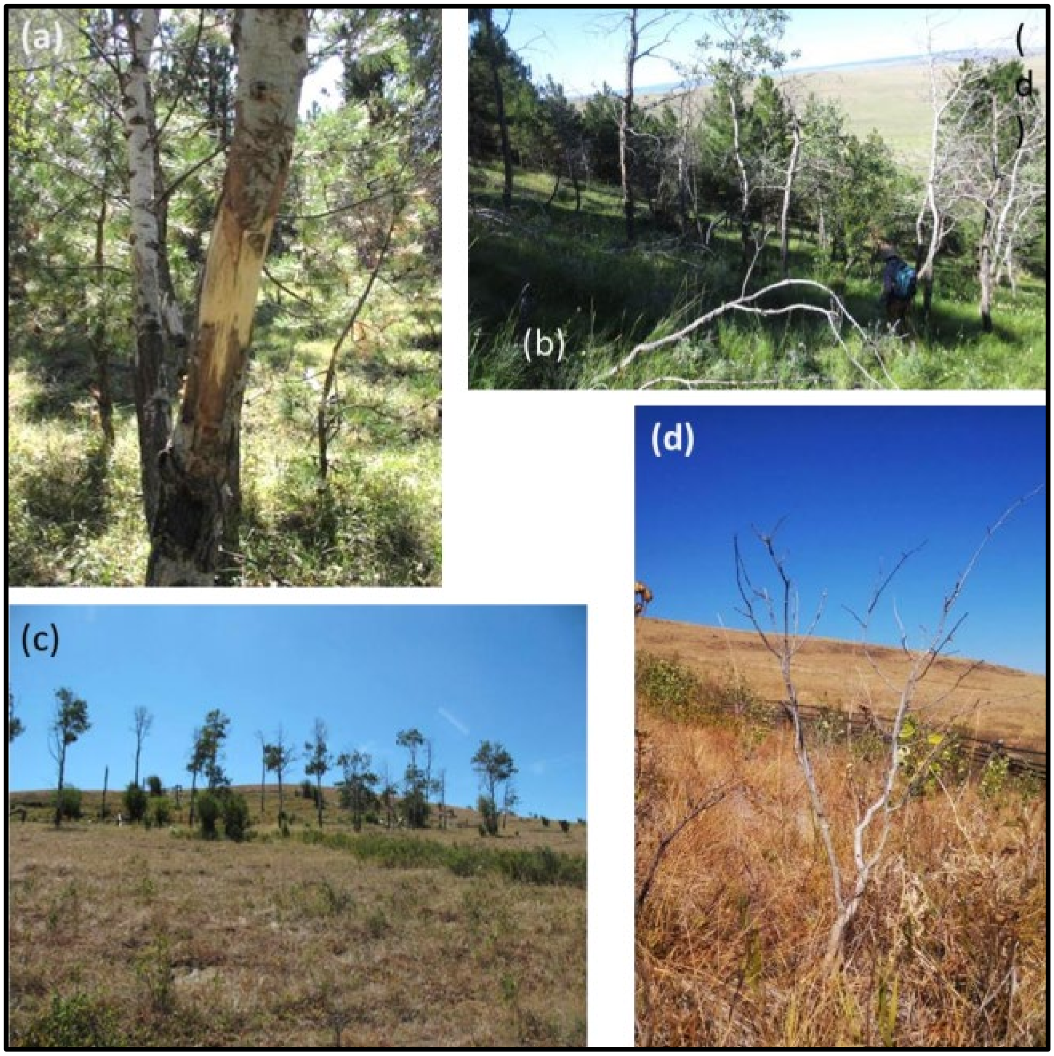


Figure 33. Aspen stands can be affected by a) ungulates such as deer, elk, and livestock that may rub against aspen, causing damage, b) reduced fire frequency that can lead to conifer invasions of aspen stands, c) drought that can cause die-backs of established stands, and d) disease, which can kill young aspen suckers. Figure adapted from Taylor and Rossman (2013).

Table 3. Blooming plant and native bee community characteristics in prairie and quaking aspen sites at The Nature Conservancy's Zumwalt Prairie Preserve.

Habitat Type:	**Native Prairie**	**Aspen**
# of Blooming Species	55	73
# of Blooming Species Unique to Habitat	25	43
Dominant Blooming Species - June	• Spring draba (*Draba verna*) • Sheldon's milkvetch (*Astragalus sheldonii*) • Nineleaf biscuitroot (*Lomatium triternatum*)	• Nettleleaf giant hyssop (*Agastache urticifolia*) • White spirea (*Spiraea betuifolia*)
Dominant Blooming Species - July	• Sagebrush mariposa lily (*Calochortus macrocarpus*)	• Nettleleaf giant hyssop (*Agastache urticifolia*) • Northern bedstraw (*Galium boreale*) • Canada goldenrod (*Solidago canadensis*) • Common snowberry (*Symphoricarpos albus*)
Dominant Blooming Species - August	None	• Nettleleaf giant hyssop (*Agastache urticifolia*) • Canada goldenrod (*Solidago canadensis*) • Common snowberry (*Symphoricarpos albus*)
# of Bee Genera	11	14
# of Bee Genera Unique to Habitat	2	5
Dominant Bee Taxa	The abundance of sweat bees (*Halictus* and *Lasoglossum*) was three times higher in grassland sites compared to aspen sites and digger bees (*Anthophora*) were only found at grassland sites	Bumble bees were almost twice as abundant in aspen stands compared to grassland sites
# of Bumble Bee Species	8	9
Sex-ratio of Bumble Bees	Female-dominated	Male-dominated
Type of Male Bumble Bees	Species in which males are territorial; vision is important in detecting trespassing males and locating females; males have large eyes compared to females (Figure 34)	Patrolling-scent-marking species may deposit scent on trees to attract females

Figure 34. A male (left) and female (right) Nevada bumble bee (*Bombus nevadensis*). Males are territorial and have much larger and more protuberant eyes than females, an adaptation thought to aid males in defending territories. Males of these species were associated with grassland sites and not aspen sites (see Table 3).

The key findings about temporal and spatial variation in pollinator and blooming plant communities from the variety of studies covered in this section are outlined below.

Summary of Key Findings Related to Temporal and Spatial Variability in Pollinator and Plant Communities

- Bee communities vary among the region's grassland types, with distinctive communities in the major grassland types studied.
- The community composition of plants, which provide food and nesting resources for native pollinators, also varies significantly both at small and large spatial scales.
- Flowering plant and native bee community composition changes strongly through the growing season, with distinct early, mid, and late season communities. Peaks in flowering plant and bee species richness and diversity depend on weather and elevation.
- Inter-annual variation in flowering phenology and bee emergence and activity can be substantial and appears to be influenced by spring precipitation and spring/summer temperatures.
- Blooming plant richness and abundance drops precipitously at the end of the growing season and bee communities tend to be dominated by several common generalist sweat bees.
- Even within a grassland type, different habitats are associated with different bee communities. Isolated quaking aspen stands at The Nature Conservancy's Zumwalt Prairie Preserve were associated with different native bee and blooming plant communities relative to grassland sites.

Management Implications

The findings from the research described in this section lead to management implications that touch on a broad range of topics, including the timing of management actions, the design of monitoring programs, the conservation of sensitive habitats embedded in these larger grassland types, and the direction for future research.

Management Implications

- The timing of management actions that may influence pollinators should be considered. The earlier portion of the growing season supports the highest diversity of blooming plants and bee species, including several specialists, so reducing negative impacts on plants and bees in these periods is a higher priority than later in the season.
- Given inter-annual variation in precipitation and temperatures, long-term monitoring of bee populations should not necessarily occur on the same calendar date each year, but timed to occur at similar points in bee phenology. Using plant phenology cues that are tightly correlated to bee phenology may be an easier way to adjust timing of bee monitoring.
- Conserving aspen habitat not only benefits many other plants and vertebrates, but also native pollinators.
- Given the sensitivity of both flowering plant and bee communities to climatic conditions, further research is needed to understand how predicted changes in climate over the next several decades may affect native bee abundance and diversity and the consequences of phenological mismatches from both the plant and the pollinator perspective.

3. Relationships between Plants and Pollinators

As outlined above, all pollinators depend on plants at some point in their life cycle. Bees are one of the few groups in which both adults and larvae depend on flowers for all of their food. While adults and larvae consume both nectar and pollen, larval diets are primarily comprised of pollen and certain species of bees can be selective about what type of pollen they provide their offspring. Selective bee species – those that collect pollen from just a few plant genera, for example – are relative specialists (termed “oligolectic”). Bee species that are generalists with regard to pollen are called “polylectic.” Understanding native bee foraging preferences is key to guiding conservation and restoration strategies aimed at enhancing pollinator habitat.

Identifying flower species that are best at providing pollen for a variety of bee species can be challenging. A common approach to identifying key plants for bees is to observe or collect individuals foraging on flowers (Figure 35). Almost all studies described in this report (Table 1) collected information about bee visitors to flowers, with the species of both the pollinator and the plant identified (Figure 36). Over 15 years, this effort has resulted in over 4,000 observations of bees belonging to more than 220 bee species visiting over 150 plant species. Often, these relationships are summarized in pollinator networks – graphical representations that show which pollinator species visits which plant species. Recent advances in molecular ecology have provided additional tools to better understand plant-pollinator relationships.

Figure 35. A handnet is used to collect insects visiting flowers so that plant-insect relationships can be described. Photo: S. DeBano

Figure 36. Examples of bee-plant relationships at the three locations described in this report. Hunt's bumble bee (*Bombus huntii*) is a common visitor of rabbitbrush (*Chrysothamnus* spp.) at The Nature Conservancy's Boardman Preserve (Photo: T. Korner), the black-fronted turret bee (*Diadasia nigrifrons*) is a frequent visitor of Oregon checkerbloom (*Sidalcea oregana*) at the USFS Starkey Experimental Forest and Range (Photo: S. Mitchell), and the yellow bumble bee (*Bombus fervidus*) forages on the threatened Spalding's catchfly (*Silene spaldingii*) at The Nature Conservancy's Zumwalt Prairie Preserve (Photo: C. Strohm).

Key Findings

Results from studies focused on plant-pollinator relationships addressed four general areas. One area of research was understanding which blooming plant species are most useful for enhancing native bee habitat and therefore may be good candidates for restoration projects in interior PNW grasslands and riparian meadows. The second was to identify which pollinator species are likely key pollinators for a threatened plant species that occurs in the region – Spalding's catchfly (*Silene spaldingii*). The third area in which plant-pollinator data were used is identifying some of the plant species that are visited by the western bumble bee *(Bombus occidentalis*) – a species of conservation concern. The final area of research focused on testing a new molecular approach to identify which plants are important to native bees – using DNA metabarcoding on pollen collected from foraging bees.

Some Plants May Be Particularly Useful for Enhancing Pollinator Habitat

A high-priority question of many restoration practitioners who are attempting to enhance pollinator habitat is which species of plants can be used to maximize benefits to pollinators. Roof et al. (2018) examined this question in a two-year study conducted at the USFS Starkey Experimental Forest and Range. Specifically, they investigated which plants are commonly visited by bees and which bee species are visiting them, which species are preferred by bees, and whether the native status or plant traits (such as flower color and morphology) influence the types of bees visiting plants. They found that while many forb species had bee visitors, some plants had higher numbers and species richness of visitors than others. The 14 plant species with the highest number of bees visiting them are shown in Table 4. In addition to identifying commonly visited flower species, Roof et al. (2018) also looked at bee preferences for blooming species (i.e., flowers that are visited at a higher rate than would be expected given their abundance in the environment). They identified several highly preferred species, including bull thistle (*Cirsium vulgare*) and seep monkeyflower (*Mimulus guttatus*) (Figure 37). In addition, Roof et al. (2018) found that flower morphology was more important than native status or color in influencing the types of bees visiting plants. Flowers with nectar and pollen that were typically more difficult to reach (e.g., bilaterally symmetrical and tubular flowers) were associated with larger bees with longer tongues and smaller, easily accessible flowers attracted smaller bees with shorter tongues (Roof et al. 2018).

Additional studies have documented bee-flower relationships in riparian areas at Meadow Creek, with a focus on riparian shrubs used in restoration projects (Mitchell et al. 2022). That study is described in the restoration section below.

Table 4. The 14 species in Meadow Creek at the USFS Starkey Experimental Forest and Range with the highest number of bees collected on them, their native status, and the number of bee species visiting them. Plant species are arranged from species with the highest to lowest number of bee species recorded on them. See Roof et al. (2018) for lists of bee species.

Plant	**Native Status**	**# of Bee Species Visiting**
Slender cinquefoil (*Potentilla gracilis*)	Native	31
Missouri goldenrod (*Solidago missouriensis*)	Native	20
Bird vetch (*Vicia cracca*)	Non-Native	14
Bull thistle (*Cirsium vulgare*)	Non-Native	14
Western mountain aster (*Symphyotrichum spathulatum*)*	Native	13
Cows clover (*Trifolium wormskioldii*)	Native	9
Idaho gumweed (*Grindelia nana*)	Native	8
White clover (*Trifolium repens*)	Non-Native	8
Common yarrow (*Achillea millefolium*)	Native	7
Oregon checkerbloom (*Sidalcea oregana*)	Native	6
Tall ragwort (*Senecio serra*)	Native	5
Wild mint (*Mentha arvensis*)	Native	5
Mountain monardella (*Monardella odoratissima*)	Native	4
Parsnipflower buckwheat (*Eriogonum heracleoides*)	Native	4

* Because of difficulty in identifying, this taxon may include two other native species: Eaton's aster (*Symphyotrichum eatonii*) and giant mountain aster (*Canadanthus modestus*).

Figure 37. Two preferred forb species at Meadow Creek at the USFS Starkey Experimental Forest and Range – the non-native bull thistle (*Cirsium vulgare*) and native seep monkeyflower (*Mimulus guttatus*). Photos: S. DeBano and S. Roof.

Plants that Support Pollinator Species of Concern

Another high priority area of research is understanding which plants may be particularly important to pollinators of conservation concern. Since the discovery of the first robust populations of western bumble bee (*Bombus occidentalis*) at The Nature Conservancy's Zumwalt Prairie Preserve after its precipitous decline in the western PNW (Rao et al. 2011), data have been gathered at both the Zumwalt Prairie and the USFS Starkey Experimental Forest and Range about plants that western bumble bees visit. Thus far, the species has been recorded foraging on 8 species that include shrubs and forbs and native and non-native species:

- Lupine (*Lupinus* spp.)
- Seep monkeyflower (*Mimulus guttatus*) (Figure 37)
- Common snowberry (*Symphoricarpos albus*)
- Common mullein (*Verbascum thapsus*)
- Twin arnica (*Arnica sororia*)
- Wild mint (*Mentha arvensis*)
- Redosier dogwood (*Cornus sericea*)
- Missouri goldenrod (*Solidago missouriensis*).

Pollinators of a Threatened Plant Species: Spalding's catchfly

Many flowering species depend on insect pollinators, including plant species of conservation concern. In Oregon alone, over 75 plant species are listed as threatened or endangered by the state and/or federal governments (ODA 2024). Spalding's catchfly (*Silene spaldingii*), which is federally threatened and state endangered, is closely associated with Pacific Northwest Bunchgrass Prairie. Because >90% of the prairie was converted to agriculture beginning in the 19th century, the once widespread Spalding's catchfly declined, and now occurs only in isolated remnants of high-quality grasslands, including in the Zumwalt Prairie (Tubbesing et al. 2014).

A study by Tubbesing et al. (2014) of pollinators of this relatively late-flowering species at the Zumwalt Prairie found only two species visiting its flowers (Figure 38). One was the yellow bumble bee (*Bombus fervidus*), which accounted for 90% of visits, and the other was the white shouldered bumble bee (*Bombus appositus*), which accounted for 10% of visits. This research shows that Spalding's catchfly relies on a very narrow pool of pollinators, one of which is a species of concern (*Bombus fervidus*). Interestingly, about 50% of the bumble bees visiting flowers were males (Figure 39), which are generally viewed as less effective pollinators. However, in certain situations, males can transfer more pollen between flowers than females (Ostevik et al. 2010). In addition, bees showed a high degree of fidelity to Spalding's catchfly, even though other flowering plants were present. This video shows a bumble bee consecutively visiting several different catchfly plants at the Zumwalt Prairie. The greater the fidelity of a bee to a particular plant species, the more likely the bee will be an effective pollinator (Tubbesing et al. 2014).

Figure 38. A female bumble bee visiting Spalding's catchfly at The Nature Conservancy's Zumwalt Prairie Preserve. Photo: C. Strohm.

Figure 39. A male bumble bee visiting Spalding's catchfly at The Nature Conservancy's Zumwalt Prairie Preserve. Even though males are typically thought to be less efficient pollinators than females (because they don't spend their day collecting food for developing larvae), they have been found to be important pollinators in some cases and particularly later in the growing season, when they are more abundant. Photo: C. Strohm.

New Approaches for Understanding Plant-Pollinator Relationships

One limitation of the observational/hand-netting approach to quantifying plant-pollinator relationships is that it represents a brief snapshot of the bee's activity, essentially providing information on the bee's foraging behavior on one plant at one moment in time. But bees visit multiple flowers during a foraging trip, and so a single trip could involve visits to multiple plant species (van der Niet et al. 2020). A new molecular technique, DNA metabarcoding, offers the opportunity to obtain a more comprehensive understanding of the plants that bees and other pollinators forage on. Pollen loads can be removed from foraging bees, and brought into the laboratory, where the plant DNA can be extracted from the pollen load (Figure 40). Sequencing the DNA allows for the identification of all the plant species that contributed to the pollen load of an individual bee.

Figure 40. Katie Arstingstall readying pollen samples in the laboratory for DNA metabarcoding. Photo: E. Carlson

Arstingstall and colleagues used this technique on pollen from bees collected at all three locations described in this report and made a number of significant discoveries (Arstingstall et al. 2021, 2023). First, their work showed that many bees are not faithful to a particular species of plant on a foraging bout. For example, some individuals had pollen from up to 9 plant species in a single pollen load (Arstingstall et al. 2021). Because of this, the relationship between bees and the plants they visit is much more complex than behavioral observations would suggest (Figure 41). In addition, the project also showed that some bee species that appeared to be oligolectic based on observations were polylectic when their pollen was examined with DNA metabarcoding (Arstingstall et al. 2021).

In addition to adding knowledge about native bee and plant interactions in interior PNW grasslands and riparian meadows, Arstingstall and colleagues also investigated several technical issues related to using DNA metabarcoding to understand plant-pollinator networks that can help others apply the approach. First, pollen DNA metabarcoding results are much more accurate if sequencing data can be compared to DNA libraries that only include plants known to occur in the study area (Arstingstall et al. 2021). Arstingstall et al (2023) also showed that sequence read data are not quantitative, in the sense that more sequence reads of a particular plant in a pollen load does not mean that species made up more of the pollen load. It is also important to select sequence count removal thresholds with the goals of the study in mind. Threshold selection involves balancing tradeoffs between detecting rare species versus overestimating network complexity, and can have a major effect on conclusions drawn from studies using metabarcoding of bee pollen to study plant-pollinator interactions (Arstingstall et al. 2023).

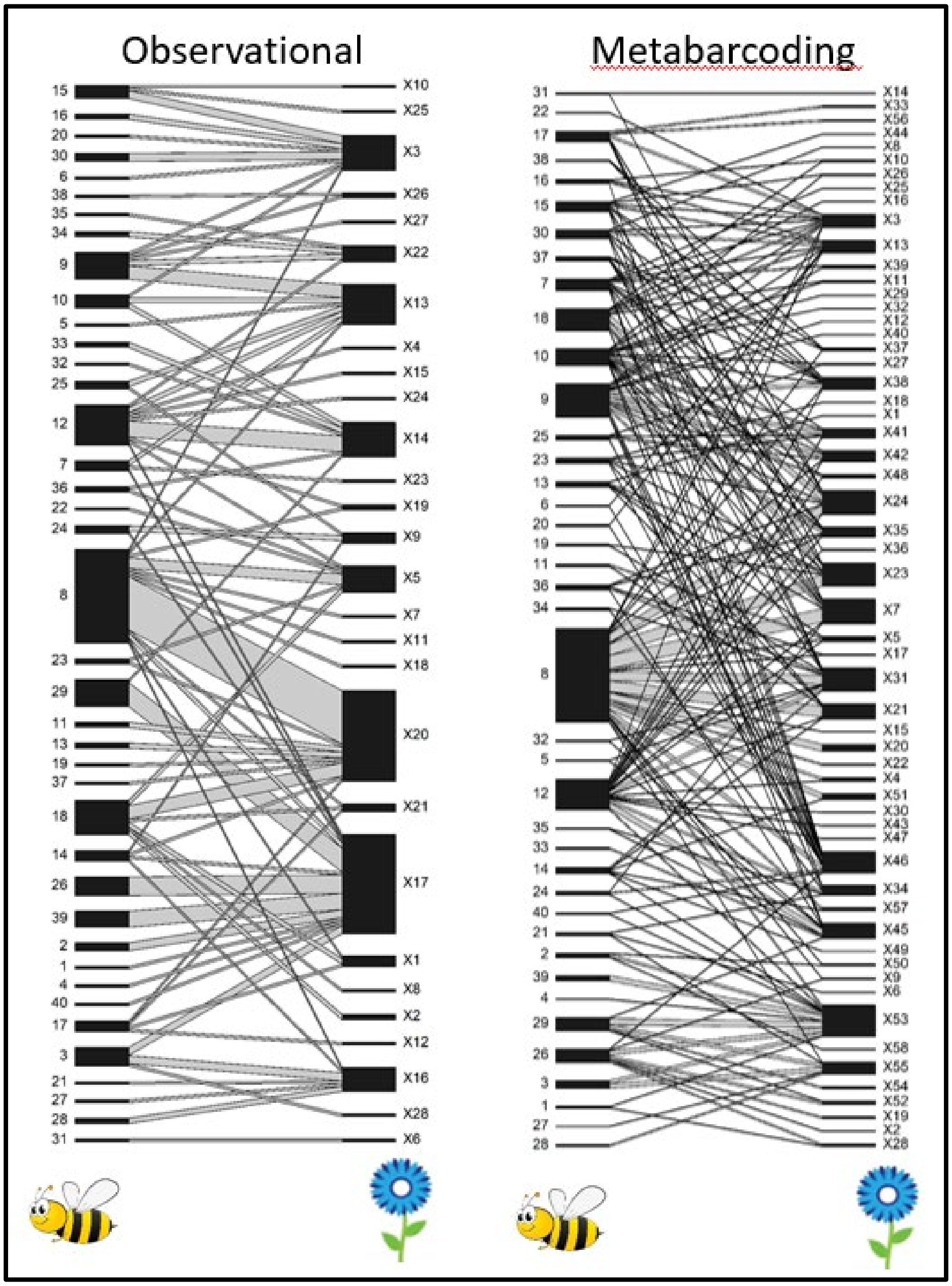


Figure 41. Plant–pollinator networks at the USFS Starkey Experimental Forest and Range created from bee foraging observations and DNA metabarcoding data. In each network, the left column represents bee species and the right column represents plant species. Thickness of the lines represents the frequency of the interactions. Adapted from Arstingstall et al. (2021); complete species listings for bees and plants can be found in Appendix 5 of that publication.

The body of work related to understanding plant-pollinator relationships described in this section are outlined below.

Summary of Key Findings on Relationships between Plants and Pollinators

- Certain forb and shrub species are used by many native bee species – serving as "floral work horses."
- Some forb and shrub species are preferred by native bee species – visited at a higher rate than expected given their availability in the environment – and essentially serve as "bee ice cream."
- Some bee species rely on a narrow set of plants.
- Some rare plant species rely on a very narrow group of pollinators.
- New techniques, like DNA metabarcoding of pollen, provide a more complete understanding of bee foraging behavior (Figure 42).

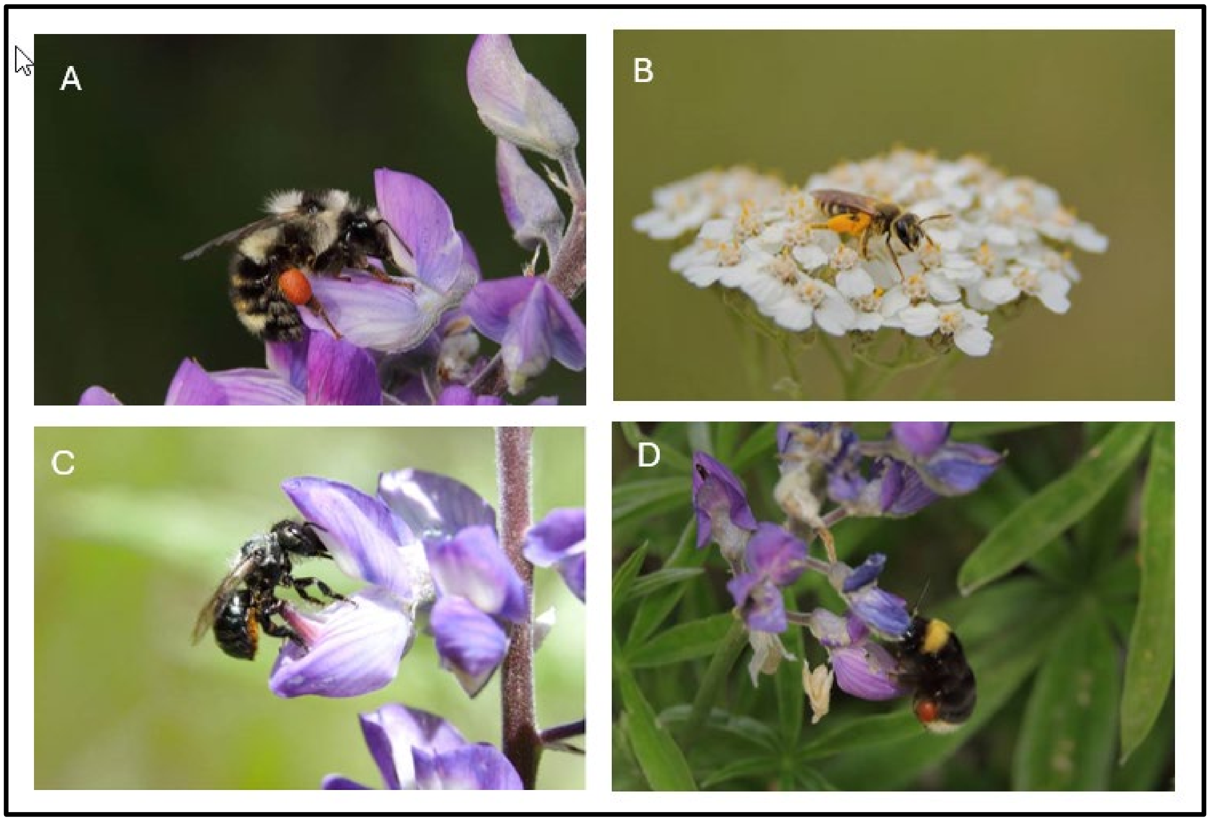


Figure 42. A female bumble bee foraging on lupine (A). Note the full pollen load in the corbicula or pollen basket on the hind leg. Bumble bees are considered pollen generalists. A female mining bee foraging on yarrow (B). Note the hind leg covered in pollen. Most mining bees are active early in the growing season and many species are pollen specialists. A female mason bee foraging on lupine (C). Mason bees are common early in the growing season. Note the pollen is stored on the underside of the abdomen for these types of bees. A female western bumble bee foraging on lupine (D). Because bumble bees are eusocial (i.e., have colonies with a queen and workers), foraging females of most species are common over much of the growing season. Photos: S. Mitchell.

Management Implications

Some of the key management implications arising from this work are outlined below.

Management Implications

- All flower species are not created equal in the eyes of a bee; the most effective restoration plantings to support the most bees will target plants used commonly by bees or preferred by bees.
- Increasing the diversity in the morphology of blooming plants is a key factor to consider when restoring areas for native bees.
- Information on flower use by western bumble bee can be used to inform plant selection aimed at restoring habitat to benefit the western bumble bee.
- Plant species that pollinator specialists rely on should be protected or enhanced through restoration efforts.
- Bee species that provide pollination services to rare plant species should be monitored regularly and habitat managed to support healthy populations of those species. For example, because Spalding's catchfly may be pollinated by just a few species of pollinators (one of which is a bee species of concern), the risk of pollination failure is higher. Thus, the continued maintenance of robust populations of these insect pollinators is a high priority for the conservation of this threatened plant species
- More research is needed to document pollinator networks to better understand their temporal and spatial stability and the consequences of various management actions.

B. Management Effects on Native Pollinators and Floral Communities

Documenting spatial and temporal diversity of flowering plant and bee communities and their relationships with each other forms a foundation for a better understanding of how human activities can influence pollinator communities and the resources they depend on. This understanding is the ultimate goal of pollinator research in northeastern Oregon – to work with stakeholders in the region to coproduce actionable science (i.e., science that can be used to support natural resource management (Beier et al. 2017)). The research described in this report was initiated because of interest by The Nature Conservancy in working with their neighbors and the larger ranching community to develop sustainable grazing practices that not only provide for livelihoods associated with livestock production and support rural economies, but also enhance habitat for diverse plant and animal communities, including native plants, grassland birds, and invertebrates such as pollinators. Since those earliest studies, research on interactions between ungulates and pollinators has continued and expanded to other areas beyond the Zumwalt, and broadened to examine a wider range of management practices (e.g., fire, restoration) and challenges (e.g., non-native plant invasions) (Table 1). Each are described in more detail in the following sections, where key findings are highlighted with a description of the underlying research that supports those findings.

1. Ungulate Herbivory

Productive rangelands rely on high quality forage, which include not only grasses, but also a diversity of forbs (Figure 43). Insect pollinators contribute to rangeland health because they pollinate many of the forbs that form important components of livestock diets (Black et al. 2011). Rangelands in the interior PNW benefit pollinators as well, by providing large tracts of undeveloped land that often support floral resources for native pollinators and provide nesting and overwintering habitat, including bunchgrass tussocks, bare ground, plant stems, and other structures.

However, ungulates can affect pollinators to the degree that their activities alter the availability of food, nesting, shelter, and/or overwintering habitat needed by pollinators (Hanberry et al. 2021). The pathways by which ungulate herbivory affects pollinators can be complex, involving a variety of direct and indirect effects. The direction and magnitude of effects are influenced by multiple factors (Table 5), including the specific pollinator in question, the type of grazer, the intensity of grazing, the type of habitat being grazed, the timing of grazing, the grazing system, climate, and herbivory's interaction with other management actions (e.g., prescribed fire) and disturbances (e.g., invasive grass invasions). In addition, the evolutionary history of the grassland can play a role in determining responses of vegetation and invertebrates to herbivory. Grasslands that evolved in the presence of large herds of grazing ungulates, such as American bison (*Bison bison*), are expected to be more resilient to livestock grazing (Kimoto et al. 2012b) than grasslands that do not have such an association. Because grasslands in the Pacific Northwest are believed to have been outside the main historic range of American bison, they are expected to be more sensitive to livestock grazing than areas in the Midwest, for example (Kimoto et al. 2012b).

All pollinators rely on the availability of floral products at some point in their lifecycle, including nectar, pollen, and/or floral oils. In addition, the immature stages of some taxa (e.g., moths and butterflies) also feed on vegetative tissue of plants (e.g., stems, leaves). The degree to which ungulate herbivory influences these resources depends on the dietary overlap between ungulates and pollinators. Understanding the extent of dietary overlap requires knowledge of both pollinator preferences (see flower-pollinator relationship section above) and ungulate foraging preferences. DeBano et al. (2016) conducted a literature review examining the potential degree of dietary overlap between native bees and cattle, elk, and deer relative to common blooming plant species found in riparian areas in the region. By reviewing published ungulate diet studies and lists of "bee-friendly" plants available in governmental technical reports, they determined that the preferences of many of those ungulates overlapped broadly with the species that native bees are believed to prefer. While cattle, elk, and deer all feed on graminoids, forbs, and browse (including flowering shrubs), they vary in the relative proportions of each in their diets. Elk and cattle generally prefer graminoids, but can also eat substantial amounts of forbs. One study found about half of elk diets may consist of forbs, and 20% of livestock diets (Cook 2002; Stewart et al. 2003; Findholt et al. 2005; Christianson and Creel 2010). Since that review, much work has been conducted to document native bee foraging preferences in the region (see “Relationships between Plants and Pollinators” section above), improving our understanding of potential dietary overlap.

Ungulates can also influence pollinators through effects on nesting, overwintering, and sheltering habitat (Hanberry et al. 2021). Effects of ungulates on the nesting habitat of bees has received the most attention. Work in other regions has found that ungulates can affect bees that nest in the ground or in stems if ungulate activity influences soil properties, soil cover, or vegetation structure (Thapa-Magar et al. 2020; Hanberry et al. 2021; Bruninga-Socolar et al. 2022). Trampling or wallowing actions associated with ungulates that typically forage in large herds can alter soil properties, and soil effects have been documented in response to not only cattle and bison (Knapp et al. 1999; Schmalz et al. 2013) but also to elk (Binkley et al. 2003). While more compact soils may influence some ground nesting bees negatively, other bee species may be positively affected by increased compaction. For example, some sweat bees prefer to nest in bare and compacted soils (Potts and Willmer 1997, 1998; Vulliamy et al. 2006). Stem-nesting bees can also be affected by ungulates, especially by those that prefer to browse on shrubs, such as deer (DeBano et al. 2016a, Stewart et al. 2021). Ungulate grazing may also negatively affect grass tussocks that bumble bees can use as nesting sites (Hanberry et al. 2021).

Figure 43. The Nature Conservancy's Zumwalt Prairie Preserve supports productive rangelands, abundant wildlife populations, and diverse plant and pollinator communities. Photo: L. Ketchum.

One high priority area of research in the interior PNW is investigating the effectiveness of grazing practices that minimize any negative effects that might be associated with livestock (Figure 44). Because a key way in which livestock can impact native pollinators is by consuming or trampling plants that are important food sources for pollinators, identifying ways to reduce these impacts is a high priority. A relatively recent approach to livestock management is targeted grazing (Launchbaugh and Walker 2006). Targeted grazing is an approach that involves manipulating the timing, frequency, location, and/or intensity of grazing in a way that also helps accomplish other management goals (Launchbaugh and Walker 2006). For example, targeted grazing can be employed to reduce invasive weed populations or increase native plant diversity in rangelands (Marchetto et al. 2021; Porensky et al. 2021). This approach can potentially also be used to improve pollinator habitat by focusing on timing grazing to avoid phenological windows in which blooming plants and pollinators may be particularly sensitive to grazing. Mitchell et al. (2023) termed this grazing strategy as "phenologically targeted grazing" and identified early season as being a key phenological window. Like many insects, the beginning of the growing season is a challenging time for pollinators because the weather is often unpredictable and food sources can be limited (Mitchell et al. 2022). During this time, queens of many large, social insects, such as bumble bees, emerge from overwintering and search for nesting sites to start their colonies. These queens need to find enough food (especially pollen) to start and grow their colonies, and previous research shows that colony size and reproductive numbers can be limited by a lack of sufficient nutrition (Rotheray et al. 2017). In addition, more oligolectic bee species are active early in the season compared to later in the season. These specialist species rely on a limited number of flowering plant species. If blooms of these species are unavailable because they have been removed by grazing, these specialist bees may not be able to reproduce. Phenologically targeted grazing is one potential way to minimize these effects by delaying the onset of grazing in high quality pollinator habitat – perhaps by just a week or two – and would be a practical option if alternative sites with fewer flowers (e.g., old fields, grasslands with low forb diversity) were available for livestock use during that period instead.

Table 5. Factors that may influence how ungulate herbivory affects pollinators.

Factor	Examples	Studies
Pollinator type	Major flower visiting group (e.g., butterflies, bees, flies, wasps, beetles); Type of bee (e.g., sweat bees, bumble bees)	Kimoto 2011; Kimoto et al. 2012b; DeBano et al. In Prep.
Type of grazer	Domestic ungulates (e.g., cattle, sheep) vs. native ungulates (deer, elk)	DeBano et al. In Prep.
Intensity of Grazing	Stocking rate, utilization	Kimoto et al. 2012b
Habitat being grazed	Uplands, grasslands, shrublands	Mitchell et al. 2023
Timing of grazing	Early season, late season	Mitchell et al. 2023
Grazing system	Deferred rotational grazing	--
Climate	Temperature, drought, precipitation	--
Interaction with other disturbances/activities	Grazing and fire Grazing and non-native plant invasions	Watson et al. 2021; Morris et al. In Prep; DeBano et al. In Prep.

Figure 44. Cattle using a stock pond in The Nature Conservancy's Zumwalt Prairie Preserve. Livestock grazing is a common use of grasslands in the interior Pacific Northwest. Photo: M. McCaskey.

Description of Studies

Studies of ungulate effects on pollinators in the region have been conducted at both The Nature Conservancy's Zumwalt Prairie Preserve and the USFS Starkey Experimental Forest and Range. All involved manipulations of herbivory either through varying livestock stocking rates and/or excluding ungulates from areas. At the Zumwalt Prairie, the earliest research involved a large-scale manipulation in which TNC erected fencing to create 16 40-ha pastures on a plateau in the center of the preserve (Figure 45). The studies associated with this experimental setup were collectively termed "The Grazing Food Web Study" because the original impetus of the project was to conduct a multi-disciplinary study examining how livestock grazing intensity affected grassland soils, vegetation, invertebrates (particularly those important in the diets of grassland birds), and ground-nesting bird communities. In addition to these initial aims and the research that resulted from them (e.g., Johnson et al. 2011, 2012; Schmalz et al. 2013; Wyffels and DelCurto 2020), two additional projects related to pollinators – one focused on native bees and one on butterflies – were added on to the original scope of work to take advantage of the infrastructure and the implementation of the grazing treatments, as well as data collection on soils and vegetation (Table 1). In 2007 and 2008, four treatments were applied to the 16 pastures in a randomized block design (Figure 45). Because the goal of the project was to manipulate grazing intensity, four different stocking rates were used – high (24 cow-calf pairs, medium (16 cow-calf pairs), low (8 cow calf pairs), and no cattle. Cattle were rotated through the pastures from May 20 to July 2 in 2007 and May 28 to July 8 in 2008. To quantify the effect of stocking rates on vegetation in each pasture, utilization (percent aboveground biomass removed by grazers) was estimated for each pasture within a week after cattle were removed.

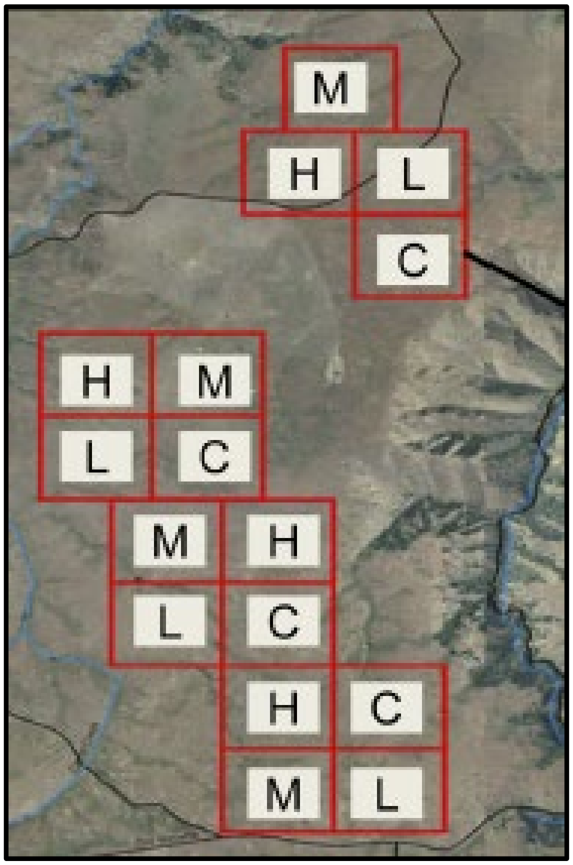


Figure 45. Set up of the first Zumwalt grazing experiment (the “Grazing Food Web Study”). Each of the 16 pastures is 40 ha.

Bees were sampled two times during the growing season in 2007 and bees and flowering plants were sampled three times in 2008. Butterflies were sampled once each growing season in 2007 and 2008. Bees were sampled using vane traps and butterflies by visual counts. Plants were sampled using the same overall approach to studying floral resource availability used in all the other projects described in this technical report but one (Watson et al. 2021). This approach involves quantifying the number and types of flowers blooming at the same location and time in which pollinators are sampled. To do this, the number of blooming stems were counted along five 20-m long, 0.3-m wide belt transects, each separated by 15 m. The same person conducted all counting in all studies, helping to control for observer biases relative to both detecting a bloom and defining a stem, making estimates of floral resource availability across treatments and studies more comparable.

A second set of experiments at the Zumwalt also investigated effects of livestock grazing on pollinators and focused on bees specifically. The purpose of this study, conducted in 2018 and 2019, was to examine not only livestock grazing effects, but also fire effects, and the interaction between fire and grazing. The design included some of the same pastures as the original "Grazing Food Web Study" – four grazed pastures ("grazed only") and four control pastures ("no grazing and no fire") – as well as eight pastures in two additional treatments – a "fire only" treatment and a "fire and grazing" treatment (Figure 46). In this study, stocking rate for grazed sites was targeted for a moderate level for the area and ranged between 0.27 – 0.30 AUM/acre in 2018 and 0.24-0.51 AUM/acre in 2019. The eight ungrazed sites had not been grazed since 2004 or 2005 (depending on the specific site). As in the previous experiment on the Zumwalt, cattle were rotated through the pastures, although relative to the first experiment, the cattle turn out and removal dates were approximately 3-4 weeks later (June 19 to August 9 in 2018 and June 16 to August 9 in 2019).

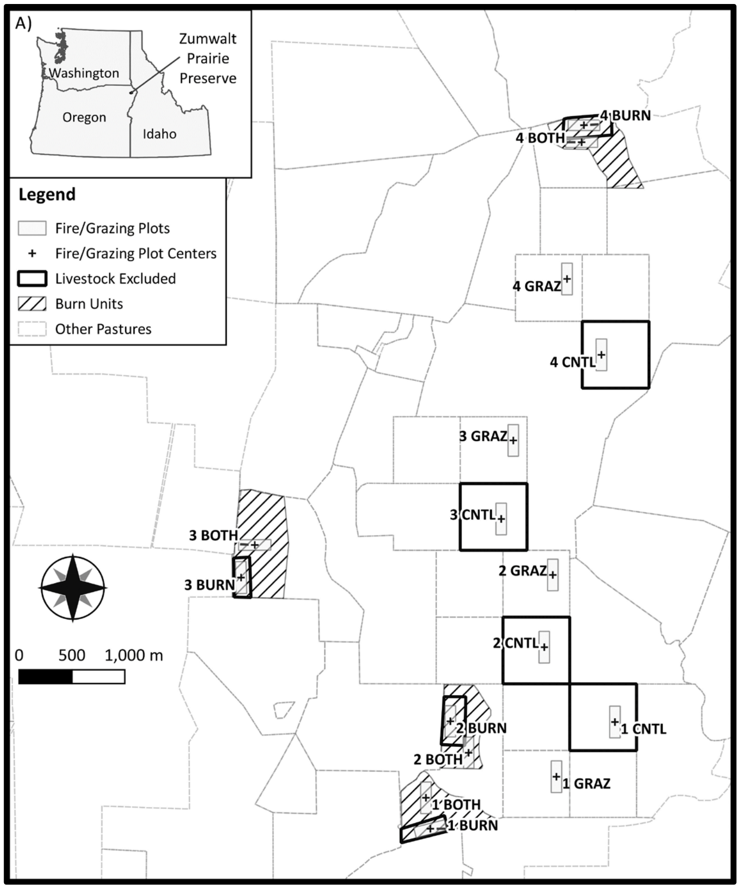


Figure 46. Sites used in the Zumwalt Prairie native bee study conducted in 2018 and 2019. Eight sites used in this study were also used in the "Grazing Food Web Study" (see Figure 45).

A third livestock-focused study, conducted at the Zumwalt Prairie from 2008 to 2021, examined longer-term responses of plant communities to livestock grazing and fire, including responses of forbs (regardless of blooming status). The treatment types and 12 of the 16 sites used in the study were the same as the 2018/2019 livestock grazing study. The only alteration in the design was that the four "grazed only" sites differed (Figure 47). The grazed sites for this study were selected to correspond with a long-term

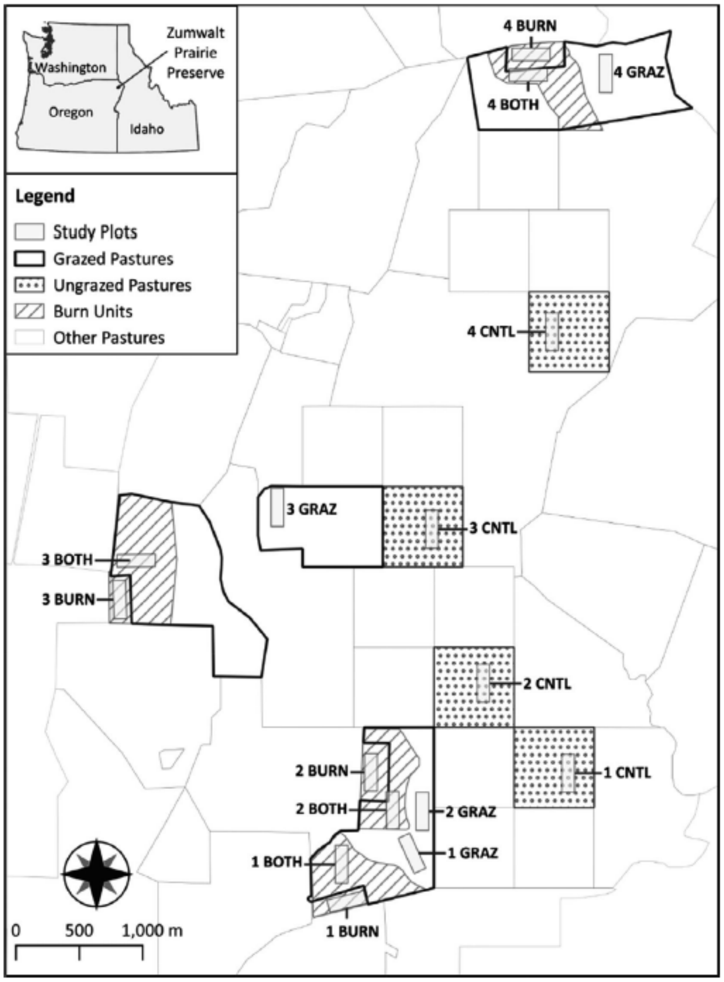


Figure 47. Study design of long-term study of vegetation responses to livestock grazing and fire. All sites, except the four grazed sites, are the same set used in the 2018/2019 study (see Figure 46).

vegetation sampling efforts and allowed for comparing vegetation trends over a decade, with sampling occurring in 2008, 2010, 2016, 2018, and 2021. In this study, vegetation was sampled along six 100-m parallel transects, spaced 50 m apart. Line-point intercept methods were used to quantify foliar cover of all plant species, with measurements taken every 3 m. Sampling occurred before cattle were turned out.

In addition to the three herbivory experiments conducted at the Zumwalt Prairie, a six-year study was also conducted in the Meadow Creek riparian system at the USFS Starkey Experimental Forest and Range. This study involved 12 riparian sites located in three larger pastures. Each pasture had four sites (Figure 48). The USFS also implemented an enclosure/exclosure system that allowed scientists to study the relative effects of both livestock and native ungulates [mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*)] on aquatic and riparian systems and their inhabitants, including native bees and flowering plants.

In the first three years of the study (2014-2016), the research focus was examining how exposure to native ungulate herbivory influenced native bees and floral resources. During those years, there were no livestock in the system and half the sites were exposed to herbivory by native ungulates (deer (*Odocoileus* spp.) and elk (*Cervus canadensis*)) and half were protected from herbivory by a 2.4 m fence (Figure 49).

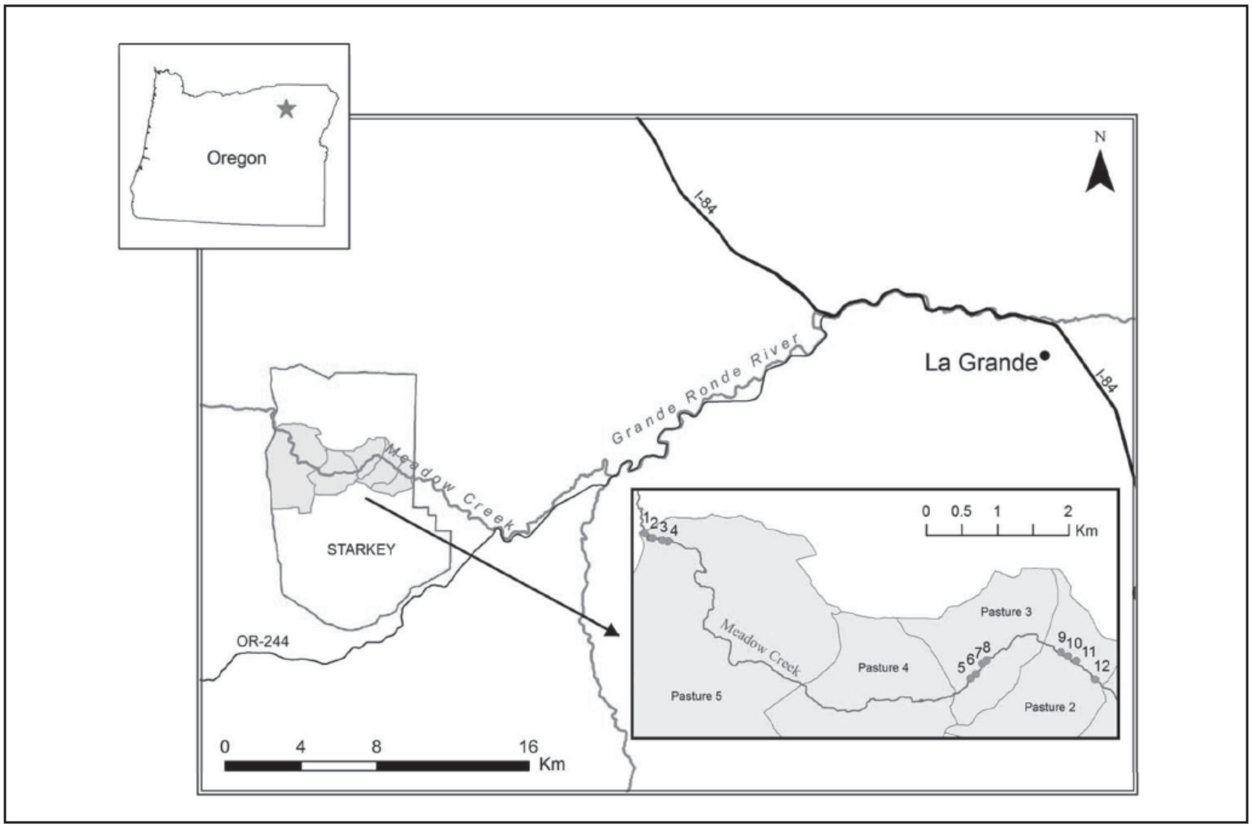


Figure 48. Location of the USFS Starkey Experimental Forest and Range in Oregon and the 12 study sites for sampling native bee and floral resources along.

Bees and native plants were sampled three times in 2015 and four times in 2014 and 2016 during the growing season. Bees were sampled with vane taps and pan traps. In the final three years of the study (2017-2019), the focus of the study was to quantify both cattle and native ungulate herbivory and investigate any interactions between the two types of herbivores. To do this, four treatments were implemented (one of each type in each pasture): no ungulates (livestock and native ungulates excluded), cattle only (deer and elk excluded), native ungulates only (cattle excluded), and all ungulates (unprotected areas). Bee and plant sampling occurred in the same manner as the first three years, except that each site was sampled four times during the growing season each year. Cattle were managed in a way consistent with common practices in riparian areas in mixed conifer forests of eastern Oregon.

Although stocking rates varied widely (e.g., 0.03 to 0.9 AUM/acre in 2018), the variation was due to differences in the sizes of the areas, as well as the duration for which they were grazed. In fact, actual utilization among livestock grazed sites was estimated to be similar and consistent with riparian areas in grazing allotments in the Pacific Northwest, especially those near streams and rivers that support salmonids. Specifically, cattle were moved out of each area when stubble height reached 19 cm.

Figure 49. The enclosure/exclosure system that allows for the manipulation of herbivory by deer, elk, and cattle along Meadow Creek at Starkey (Photo: S. DeBano)

Key Findings

The key findings of the four studies that focused on ungulate grazing describe the influence of ungulate herbivory on floral resources, nesting habitat, and pollinator groups. They also relate to the benefits of quantifying grazing intensity with utilization for livestock studies, the sensitivity of riparian areas to grazing compared to grasslands, and the potential of using phenologically-targeted grazing to minimize negative effects of livestock production on pollinators.

Influence of Ungulate Herbivory on Floral Resources

Results from empirical studies in the region are consistent in finding effects of ungulate grazing on the availability of floral resources used by bees and other pollinators. Much of this work has focused on livestock. Kimoto (2011) found that the number of blooming stems of two common forb species – hoary balsamroot (*Balsamorhiza incana*) and twin arnica (*Arnica sororia*) – decreased with increased utilization in the Zumwalt Prairie. These findings are consistent with other work that has shown balsamroot species are desired forage for cattle (Ogle and Brazee 2009) and arnica species are of moderate forage value for cattle (Reid 1942). Likewise, Watson et al. (2021) found total cover of forbs decreased with long term exposure to cattle grazing. Mitchell et al. (2023) also found riparian meadow sites that were grazed by cattle had lower blooming forb abundance, species richness, and diversity than areas where cattle were excluded, even though the onset of cattle grazing was delayed and occurred after peak bloom. However, Mitchell et al. (2023) found no effect of delayed onset livestock grazing on the availability of forbs at the Zumwalt Prairie.

Research in the interior PNW has shown that native ungulates can also decrease the abundance of blooms of plant species they prefer (DeBano et al. 2016a; DeBano et al. In Review). DeBano et al. (In Review) found that riparian meadow sites in which elk and deer were excluded for three years had more blooming stems of forbs preferred by elk, the most common herbivore in the system, compared to sites exposed to native ungulate herbivory.

Influence of Ungulate Activity on Nesting Habitat

One of the earliest pollinator studies at the Zumwalt Prairie examined how livestock grazing intensity influenced several variables associated with nesting habitat for native bees. Kimoto et al. (2012b) found that increased livestock grazing intensity, as measured by utilization, significantly reduced vegetation structure, soil stability, and herbaceous litter and significantly increased soil compaction and bare ground (Kimoto et al 2012b). Some of these effects, like increased soil compaction and bare ground, can enhance nesting habitat for some bees; for example, some sweat bees prefer compacted soils for nesting, and many ground-nesting bees prefer bare ground. Conversely, decreases in vegetation structure and stem availability may decrease nesting habitat for stem-nesting bees.

Interestingly, a more recent study found that the effect of livestock grazing on litter cover had shifted. In the 2018-2019 study on fire and grazing effects on native bees (Table 1), DeBano et al. (In Prep) found that litter was significantly higher in sites grazed by livestock compared to ungrazed sites. They hypothesized that this change may be driven by the increase of the invasive annual grass, *Ventenata dubia*, in the system. Ventenata has low palatability for livestock and produces large amounts of litter (Jones et al. 2020; Ridder et al. 2021) compared to other grasses common in PNW bunchgrass prairie. This, combined with ventenata cover being associated with livestock grazing, may explain the increase in litter production in grazed areas. Regardless, more litter may result in less bare ground available for ground-nesting bees.

Sensitivity of Pollinator Groups to Ungulate Grazing

Some of the earliest work in interior PNW grasslands demonstrated that not all pollinator species are affected by livestock grazing in the same way (Kimoto 2011; Kimoto et al. 2012b). Among native bees, bumble bees appear to be particularly sensitive to grazing intensity, showing strong negative responses in abundance and species richness with higher utilization (Kimoto et al. 2012b). In contrast, other bee species appeared to be relatively insensitive to livestock grazing, and yet other bee groups, such as sweat bees, tended to be more abundant with increased grazing intensity (Kimoto 2011).

In the same experimental study, butterflies in the Zumwalt Prairie showed similar responses to livestock grazing as bumble bees, with decreased adult abundance and species richness with increased utilization associated with earlier season grazing. This pattern may be due to overall reductions in blooming plant availability, which nectar generalists such as adult butterflies rely on, or the pattern may be due to reductions in plants on which caterpillars of some species rely on as specific host plants. Interestingly, responses of bumble bees and butterflies differed from responses of ground-nesting grassland birds found in the Zumalt “Grazing Food Web Study” (Johnson et al. 2011). Increased grazing intensity resulted in linear decreases in abundance and species richness of bumble bees and butterflies, while negative effects of grazing on grassland songbirds were only observed at high grazing intensities.

Work at the USFS Starkey Experimental Forest showed that native ungulates can also affect bees. Native bees in riparian areas exposed to native ungulate herbivory at Starkey showed decreased bee species richness relative to protected sites in some months (DeBano et al. In Review). Evidence suggested that oligolectic bees may be particularly vulnerable. For example, oligolectic species in the genus *Diadasia* rely on mallows (e.g., *Sidalcea* spp.). Mallows are also a preferred forage species of elk, and work at Starkey showed that bloom counts of elk-preferred species were reduced in areas exposed to elk relative to protected areas (DeBano et al. In Review). These differences were tied to low bee species richness, and one common species of *Diadasia* (*Diadasia nigrifrons*) that relies on *Sidalcea oregana* was an indicator species of sites protected from deer and elk.

Utilization is a More Useful Metric of Grazing Intensity than Stocking Rate

The earliest study examining the effects of livestock grazing on pollinators at the Zumwalt Prairie was one of the first to look at the intensity of grazing rather than just a dichotomy of “grazed” vs “non-grazed” (Kimoto et al. 2012b). The goal of the study was to use three stocking rates to implement “high,” “moderate,” and “low” grazing treatments (see methods above for details on stocking rates for each treatment). However, stocking rates do not always translate to cattle use given the heterogenous use of landscapes by cattle, variation in animal condition and preferences, and composition of vegetation in pastures. To more directly quantify overall pasture use, utilization (i.e., the percentage of aboveground biomass removed by grazers) was measured at 36 points throughout each pasture. A key finding of this early work at the Zumwalt Prairie was that utilization is a more accurate way of quantifying grazing intensity than stocking rate. Stocking rates did not always reflect actual use by livestock, as shown in Figure 50; utilization values for pastures with a particular stocking rate are sometimes higher than utilization values for other pastures in the next higher stocking rate category. These results suggest that using utilization in studies focused on understanding livestock effects on pollinator habitat will lead to a greater understanding of these systems.

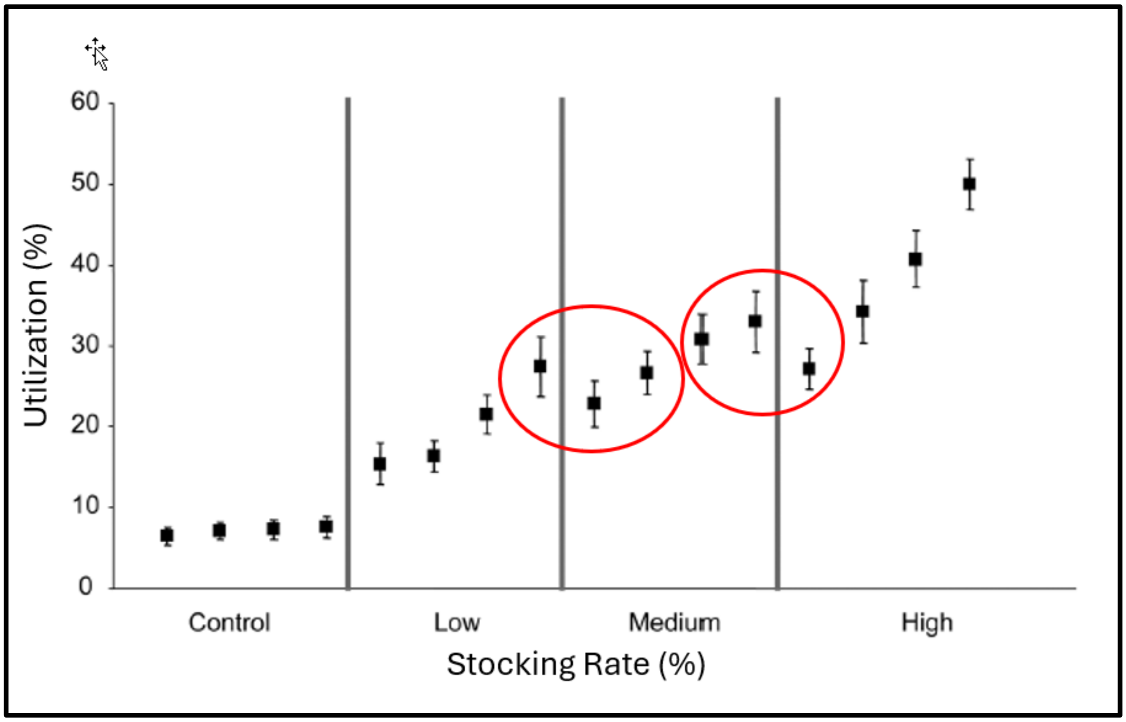


Figure 50. The relationship of stocking rate and utilization in 16 pastures at The Nature Conservancy's Zumwalt Prairie Preserve in 2007. The red circles show where utilization values for pastures with a particular stocking rate are higher than values for other pastures in the next higher stocking rate category. Figure adapted from Kimoto et al. (2012b).

Sensitivity of Pollinator Habitat Types to Livestock Grazing

Certain habitat types are expected to be more sensitive to livestock grazing than others, given differences in resistance and resilience to ungulate herbivory. Variation in resistance and resilience may be influenced by various factors, including vegetation communities, soil conditions, and microhabitat temperature and moisture differences between habitat types. Mitchell et al. (2023) examined blooming plant and native bee sensitivity to livestock grazing in bunchgrass prairie sites at the Zumwalt Prairie and in riparian meadow sites at Meadow Creek at Starkey, comparing responses during the same months and the same years. They found that vegetation in riparian meadows was more sensitive to livestock grazing than bunchgrass prairie, with the bloom abundance, richness, and diversity lower in sites grazed by cattle compared to ungrazed sites (Figure 51; Mitchell et al. 2023). However, native bees were equally abundant and diverse at grazed and ungrazed sites at both locations, potentially because grazing occurred relatively later in the season (see next section on “Phenologically Targeted Grazing”).

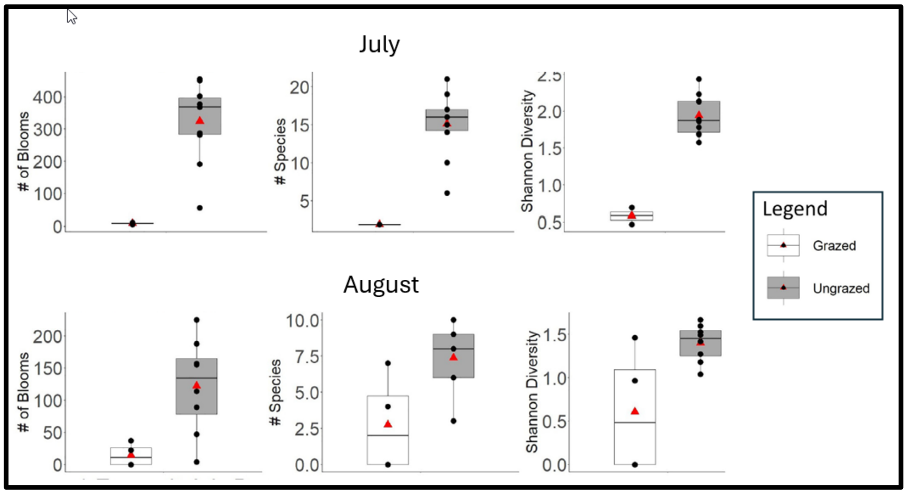


Figure 51. Differences in number of blooming plant stems, species richness, and Shannon diversity in sites grazed by cattle and ungrazed riparian sites at Meadow Creek in the USFS Starkey Experimental Forest and Range in July and August of 2018. Adapted from Mitchell et al. (2023).

Potential Benefits of Employing Phenologically-Targeted Grazing

One study conducted at The Nature Conservancy's Zumwalt Prairie Preserve and at Meadow Creek riparian areas in the USFS Starkey Experimental Forest and Range examined "phenologically" targeted grazing. In the 2018-2019 study (Table 1), cattle were turned out several weeks later than past studies (Mitchell et al. 2023). This resulted in grazing commencing largely after peak bloom. Mitchell et al. (2023) found fewer effects on blooming flower availability than detected in previous studies with normal onset times and no detectable negative effects on bee communities at either location.

Together, these results provide a body of work that sheds light on numerous aspects of ungulate herbivory effects on pollinators, as outlined below.

Summary of Key Findings on Ungulate Herbivory and Pollinators

- Ungulate herbivory can influence the availability of floral resources for pollinators, with effects partially depending on the dietary preferences of the ungulate species.
- Ungulate activity may enhance nesting habitat for some pollinators and decrease nesting habitat for others; however, the recent spread of the invasive annual grass, ventenata, may reverse previously positive effects of grazing on nesting habitat.
- Bumble bees and butterflies may be particularly sensitive to livestock grazing.
- Utilization is a more useful metric of grazing intensity than stocking rate when attempting to understand livestock effects on pollinator habitat.
- Riparian meadows may be more sensitive to livestock grazing than other types of grasslands.
- Livestock grazing occurring after peak bloom (i.e., phenologically targeted grazing) may have less impact on flower availability and decrease negative effects on native bee communities.

Management Implications

The body of research on ungulate grazing conducted in these interior PNW grasslands and riparian meadows have provided results that lead to the management implications outlined below. Information obtained from this research can aid natural resource managers and livestock producers in developing strategies that maintain healthy rangelands and pollinator populations. However, additional research is necessary to understand how emerging issues such as climate change and invasive annual grass invasions may alter best management practices in the future.

Management Implications of Ungulate Studies

- Bumble bees and butterflies, especially species of conservation concern, should be monitored carefully in rangelands.
- Decreasing stocking rates and keeping utilization <40% may benefit rangeland pollinator species.
- Using approaches that increase habitat heterogeneity (i.e., result in small patches of different types of habitats) may be the best approach to conserving native pollinator habitat. Examples include high-density short-duration approaches, rest and rotation systems, or having some areas that are not grazed by livestock.
- Management of riparian meadows for healthy pollinator habitat should take into account not only impacts of cattle, but also native ungulates like deer and elk.
- Phenologically-targeted grazing (i.e., commencing grazing after peak bloom) may reduce negative effects on bee communities in areas that include high quality bee habitat. This approach may be particularly useful if managers are able to use alternative locations (e.g., old fields, more intensively managed pasture) until after peak bloom. In the Zumwalt Prairie region, pollinators may benefit if grazing high quality sites can be delayed a few weeks, after peak bloom of these species (Figure 52):
    - Biscuitroot or desertparsley (*Lomatium* spp.)
    - Larkspur (*Delphinium* spp.)
    - Balsamroot (*Balsamorhiza* spp.)
    - Elkweed (*Frasera speciosa*)
    - Woodland-star (*Lithophragma* spp.)

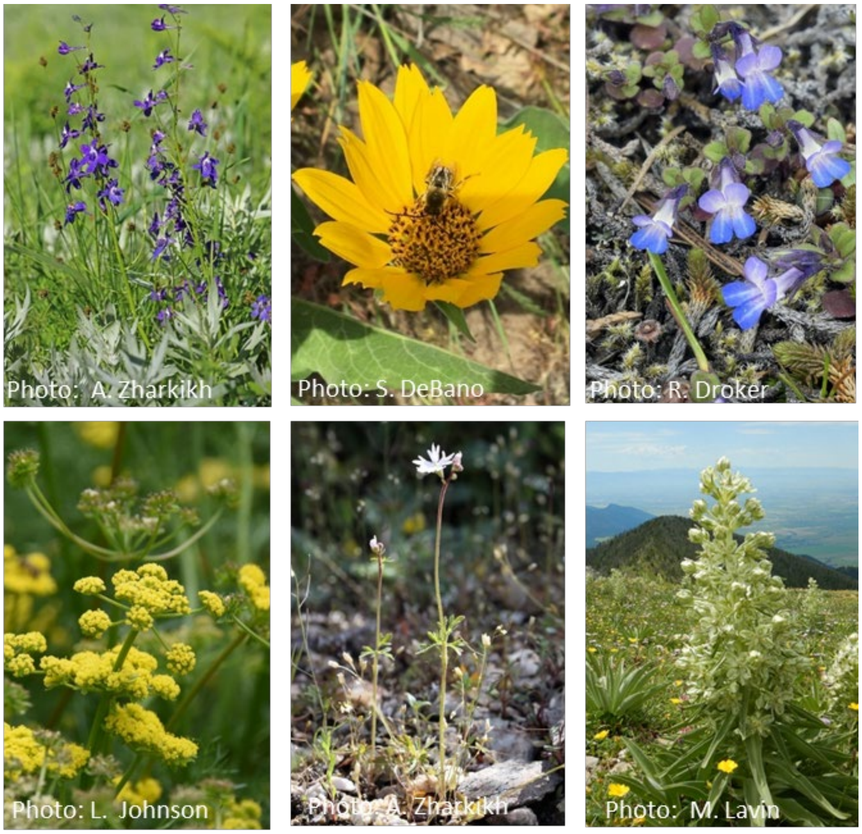


Figure 52. These common forbs can serve as general guides to help time grazing onset in the Zumwalt Prairie region. When these species are blooming, avoiding or delaying grazing may benefit sensitive pollinators. [Clockwise from top left: larkspur (*Delphinium* spp.), balsamroot (*Balsamorhiza* spp.), small flowered blue eyed Mary (*Collinsia parviflora*), giant frasera (*Frasera speciosa*), woodland-star (*Lithophragma* spp.), and biscuitroot (*Lomatium* spp.)]. Grazing high quality sites after these species have largely stopped blooming may reduce impacts of livestock grazing on native bees. Although these flowers were selected for the Zumwalt Prairie region, the approach can be used in other regions by identifying common plant species that are closely tied to sensitive pollinator phenology.

2. Fire Effects

While fires can be destructive, they can also be a useful tool for maintaining diverse grassland systems. Wildfire is ubiquitous across the US, with both the severity and prevalence increasing as the climate changes (Schoennagel et al. 2017). For example, in 2022, over 3 million ha in the US were consumed by wildfire, often with disastrous effects (NICC 2022). However, fire can also be a beneficial management tool in many grasslands, helping to limit woody species encroachment, reduce fuels, and potentially decrease non-native species, like invasive annual grasses (Hanberry et al. 2021).

Pollinators are predicted to be sensitive to fire, both through direct and indirect effects and responses are expected to vary with the time since fire (Potts et al. 2001, 2003; Love and Cane 2016; Carbone et al. 2019, 2025). Fire can cause direct mortality to animals, including insects (Figure 53), with the most vulnerable individuals being those with limited flight ability and those occurring on the soil surface or associated with vegetation (Hanberry et al. 2021). However, while certain pollinators, such as butterfly and moth larvae, may be likely to experience mortality, many pollinators are expected to be primarily influenced by fire's short-term and long-term effects on vegetation and nesting habitat (Carbone et al. 2019).

Figure 53. Fire can cause immediate mortality in many insect species, especially those with limited flight capacity, like this grasshopper burned in a wildfire at The Nature Conservancy's Boardman Conservation Area. Photo: S. DeBano

Studies at The Nature Conservancy's Boardman Conservation Area and the Zumwalt Prairie Preserve have focused on the effects of both wildfire and prescribed burning on grassland flowering plant and native bee communities (Smith DiCarlo et al. 2019; Watson et al. 2021, DeBano et al. In Prep.).

Key Findings

Wildfire

Little was known about how pollinators respond to fire in interior PNW grasslands until a serendipitous opportunity to examine wildfire effects on pollinators occurred at the Boardman Conservation Area (BCA) in 2015. In June of that year, a fire broke out in a neighboring agricultural area and spread into the BCA (Figure 54). The timing coincided with the second year of a three-year study focusing on grassland restoration effects on native bees (Smith DiCarlo et al. 2019, 2020). Approximately one-third of the study sites burned (Figure 55), allowing for the study of fire effects on bees and flowering plants using a before-after-control-impact design (Figure 56).

Figure 54. The initial stages of a wildfire that spread quickly to a large area of The Nature Conservancy's Boardman Conservation Area in June 2015. Photo: S. DeBano

At the BCA, numerous responses varied one year after the fire (Table 6). Plant communities differed between burned and unburned areas, overall forb abundance increased in burned sites, and certain forbs flourished in burned areas (Smith DiCarlo et al. 2019; Table 6). Bee species richness and Shannon diversity were higher in burned areas, and some bee species (primarily generalist species) were associated with burned areas (Table 6; Figure 57). In contrast, one species was associated with unburned areas (Table 6, Figure 58). Responses in bee communities may have been driven by a combination of factors including increased forb abundance, changes in forb community composition, and by more bare ground and other nesting resources (e.g., charred wood) (Smith DiCarlo et al. 2019).

Burned areas also showed decreased cover of two common invasive annual grasses – cheatgrass and medusahead. However, biological soil crust cover also decreased, making these areas potentially more vulnerable to cheatgrass invasion in the future (Smith DiCarlo et al. 2019).

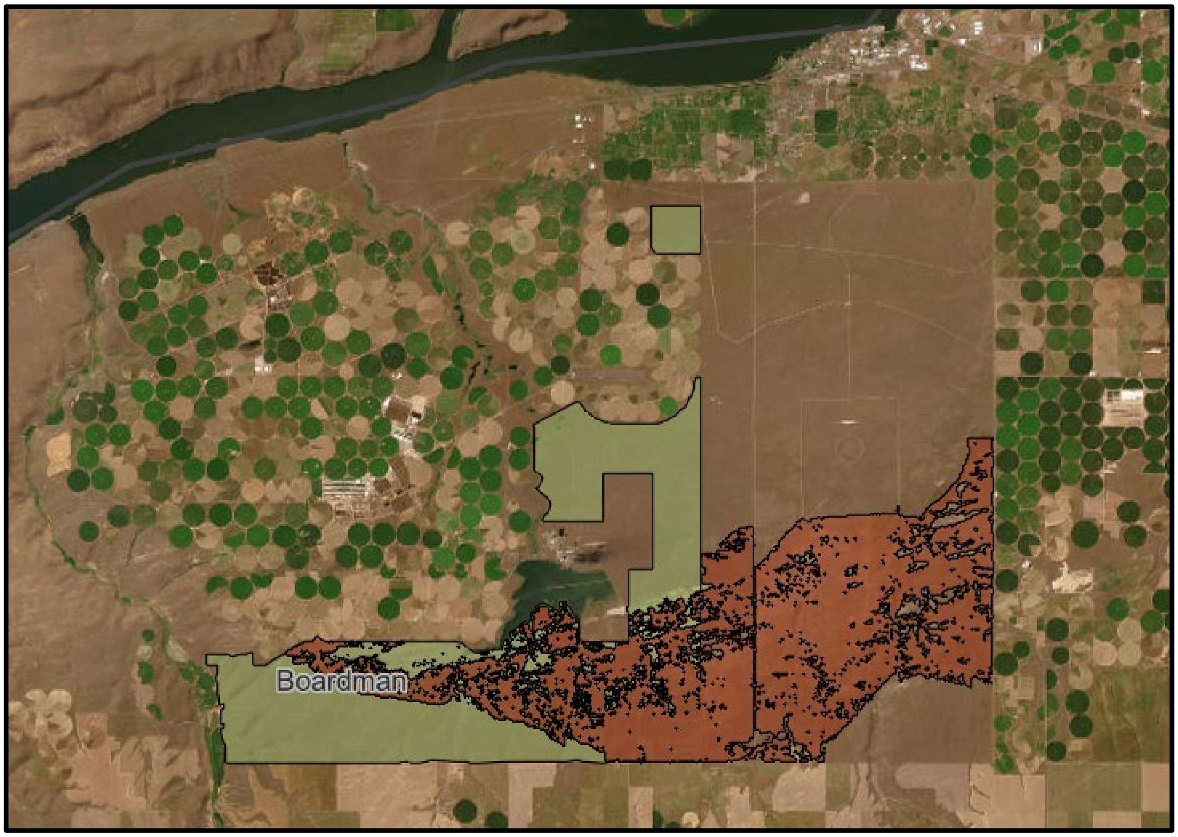


Figure 55. Map showing the area of The Nature Conservancy's Boardman Conservation Area that burned in a wildfire in June 2015. The orange area indicates the burned portion of the area.

Figure 56. A site at The Nature Conservancy's Boardman Conservation Area in 2014, which burned the following year (A); a burned site in 2015, one-week post-fire, showing moderate to severe surface burning (B); and a burned site in 2016 showing vegetation regrowth one-year postfire. Photo: L. DiCarlo Smith.

Table 6. Differences between unburned and burned sites at The Nature Conservancy's Boardman Conservation Area one year after a 2015 wildfire.

	Unburned	**Burned**
Associated Non-Native Blooming Plant Species	• Yellow star-thistle (*Centaurea solstitialis*)	• Prickly Russian thistle (*Salsola tragus*)
Associated Native Blooming Plant Species	• Rubber rabbitbrush (*Ericameria nauseosa*)	• Douglas' knotweed (*Polygonum douglasii*), • Canadian horseweed (*Conyza canadensis*) • Hoary tansyaster (*Machaeranthera canescens*) • Tall annual willowherb (*Epilobium brachycarpum*)
Changes in Cheatgrass Cover	• Cheatgrass cover increased in unburned sites	• Cheatgrass cover decreased in burned sites
Changes in Biological Soil Crust	• Soil crusts decreased less* in unburned sites than in burned sites	• Soil crusts decreased more* in burned sites than in unburned sites
Associated Bee Species	• Rival long-horned bee (*Melissodes rivalis*)	• Urbane digger bee (*Anthophora urbana*), • Western honey bee (*Apis mellifera*) • Wide-legged sweat bee (*Agapostemon femoratus*) • Two species of nomad bees (*Nomada* spp.) • Coquillett's leafcutter bee (*Megachile coquilletti*) • Tripartite sweat bee (*Halictus tripartitus*)

*Biological soil crusts decreased at all types of sites over the course of the three-year study.


Photo: L.H. Robinson

Photo: S. Galley

Figure 57. Two bee species associated with burned areas at The Nature Conservancy's Boardman Conservation Area: the wide-legged sweat bee (*Agapostemon femoratus*) and the tripartite sweat bee (*Halictus tripartitus*).


Photo: The Nature Guy, iNaturalist

Figure 58. The rival long-horned bee (*Melissodes rivalis*) was associated with unburned areas at The Nature Conservancy's Boardman Conservation Area.

Prescribed Burning

Research on the effects of fire continued at The Nature Conservancy's Zumwalt Prairie Preserve and examined longer term effects of prescribed fire in combination with grazing. This 10-year study found that fire was more influential than grazing in affecting forb community composition (Watson et al. 2021). Forb communities changed in response to fire, with more fire-adapted perennial forbs associated with burned areas. Three native species were indicators of burned sites: aspen fleabane (*Erigeron speciosus*), whitestem frasera (*Frasera albicaulis*), and pleated gentian (*Gentiana affinis*) (Watson et al. 2021). Burned areas also had more bare ground and less litter, soil moisture, and compaction – all characteristics that may benefit some groups of ground-nesting bees. In fact, burned areas had more species of bees two years after the fire than unburned areas (DeBano et al. In Prep). Unfortunately, other work at the Zumwalt has shown that fire does not reduce the abundance of the most problematic annual invasive grass in the Zumwalt – ventenata (*Ventenata dubia*) (Ridder et al. 2021, 2022).

Research at The Nature Conservancy's Zumwalt Prairie Preserve and Boardman Conservation Area have provided rare opportunities to examine both short- and long-term responses of native bees to prescribed burning and wildfires. Some of the key findings of this research are summarized below.

Summary of Key Findings Related to Fire Effects on Pollinators

- Short-term responses to wildfire included changes in flowering plant communities, with some forb species increasing in burned areas, and an overall increase in forb abundance.
- Bee species richness and diversity increased in burned areas the year following wildfire, with some bee species (primarily generalist species) associated with burned areas.
- Responses in bee communities may have been driven by a combination of factors including increased forb abundance, changes in forb community composition, and by more bare ground and nesting resources (e.g., charred wood).
- Burned areas in low-elevation grasslands showed a short-term decrease of invasive annual grasses (cheatgrass and medusahead). However, biological soil crust cover also decreased, making these areas potentially more vulnerable to cheatgrass invasion in the future.
- Longer-term effects of prescribed fire include changes in forb composition, with some species of fire-adapted forbs associated with burned areas. Bee richness increased two years after prescribed burning.
- Prescribed burning can have both short- and longer-term beneficial effects on bees by increasing select floral resources and creating more nesting habitat.
- Fires may be helpful in reducing some invasive annual grasses in the short term, but longer-term effects of fire on invasive grasses are less clear and may depend on the severity and season of burning, as well as the specific species involved.

Management Implications

Several management implications arise from the research conducted at The Nature Conservancy's Boardman Conservation Area and the Zumwalt Prairie Preserve (see below). However, more research is needed to guide future fire management for pollinator conservation in grasslands, especially in the face of the increasing prevalence of invasive annual grasses and climate change.

Management Implications

- Prescribed burning may be a useful tool to increase forb species that benefit some pollinator species and to enhance nesting habitat for bees that nest in ground or charred wood.
- Burning smaller patches of larger landscapes may benefit pollinator conservation in interior PNW grasslands and meadows.
- While fire may result in short-term decreases in some invasive annual grasses (e.g., cheatgrass and medusahead), there is little evidence that fire reduces other annual grasses in the long-term (e.g., ventenata). Thus, negative effects of annual grasses like ventenata on pollinator habitat should not necessarily be expected to improve with prescribed burning.
- Effects of fire on biological soil crust may be a key management consideration for pollinator conservation, if loss of soil crusts increases future annual grass invasion potential. Long-term monitoring after fires is necessary to investigate the effects of losses of biological soil crusts and associated annual grass invasions.

3. Non-Native Annual Grass Invasions

Non-native annual grass invasions are an increasing problem in PNW grasslands and riparian meadows. Although non-native annual grasses, such as cheatgrass, have been a problem in western grasslands for many decades, the rapid spread of other types of annual grasses in previously uninvaded systems is concerning (Jones et al. 2018, 2020). For example, the Zumwalt Prairie has experienced a dramatic increase in the prevalence of ventenata [also known as North Africa grass (*Ventenata dubia*)] – a relative newcomer from North Africa (Averett et al. 2020; Endress et al. 2020; Ridder et al. 2021). In fact, ventenata has increased from less than 5% cover in 2008 to more than 35% cover in 2018 in plots sampled at the Zumwalt Prairie Preserve (Watson et al. 2021; Figure 59). In some years, ventenata is the most dominant plant, in terms of cover, on the prairie. Ungulate activity may potentially aid in the spread of ventenata, which often establishes in disturbed areas like cattle and game trails (Figure 60), and recent work at the Zumwalt shows that ventenata cover is higher on sites grazed by cattle than sites not grazed by cattle (Schmalz et al. In Prep).

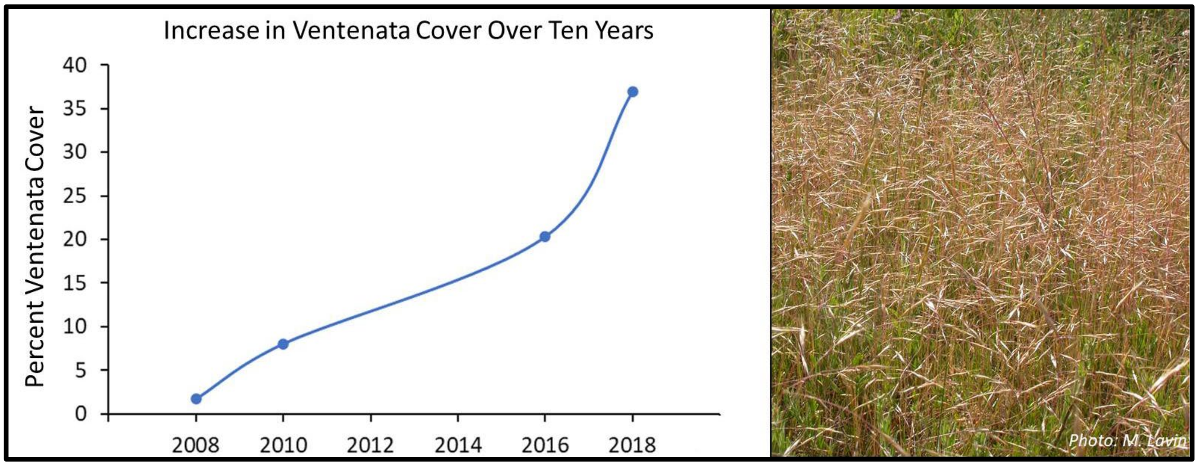


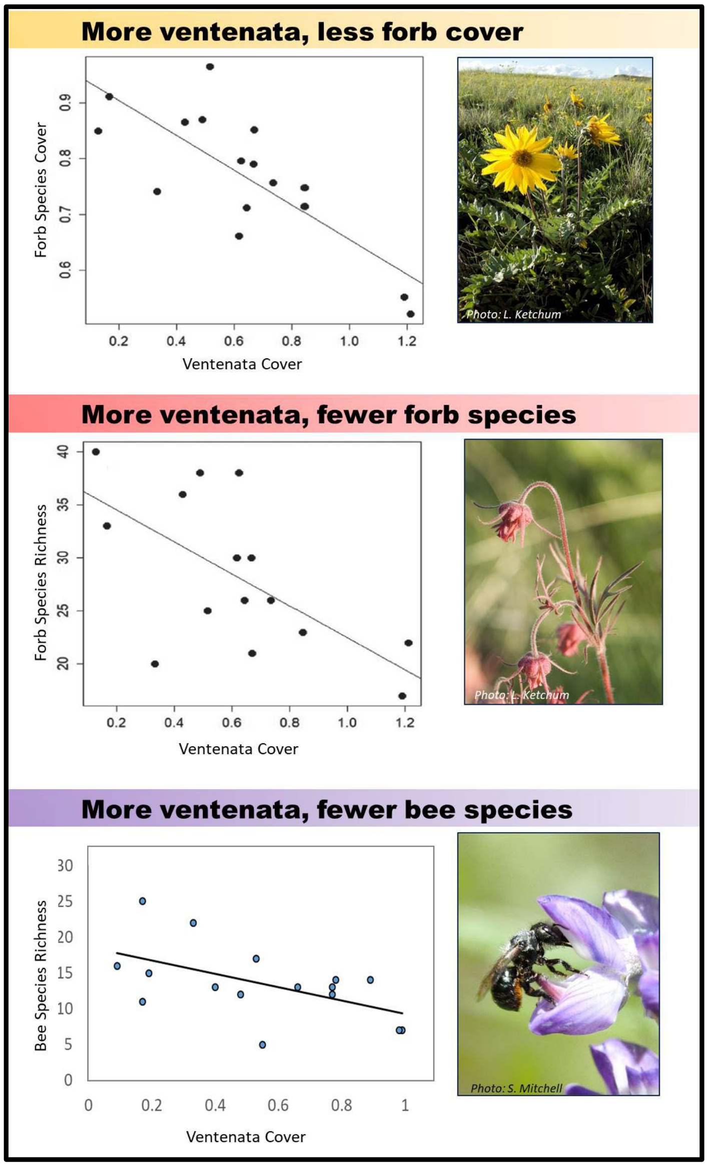
Figure 59. Increase in ventenata cover since 2008 at The Nature Conservancy's Zumwalt Prairie Preserve.

Not only is ventenata a threat to livestock producers because it reduces livestock carrying capacity, but it also increases fine fuel loads because of the large amount of litter it produces (Jones et al. 2020; Ridder et al. 2021). This can, in turn, lead to more intense fires. Unfortunately, prescribed burns have not been found to be an effective method of controlling ventenata thus far (Ridder et al. 2021, 2022). Given the magnitude of the problem and the potential seriousness of annual grass invasions on native flowering plant communities that provide food for many pollinators, a number of studies have been conducted at The Nature Conservancy's Zumwalt Prairie Preserve to investigate how the spread of annual invasive grasses, such as ventenata, affect native bees and their habitat (Table 1).

Figure 60. Cattle amid a large patch of *Ventenata dubia* at the Nature Conservancy's Zumwalt Prairie Preserve. Photo: M. McCaskey.

Key Findings

Research at The Nature Conservancy’s Zumwalt Prairie Preserve has shown that the spread of ventenata affects both blooming flowers that bees use, and the bees themselves. Watson et al. (2021) showed that as the cover of ventenata increased, forb cover and the number of forb species decreased (Figure 61). These results are consistent with previous work (Averett et al. 2020). In addition, ventenata litter covers bare soil, and decreases nesting habitat for bees that prefer bare soil (Figure 62). Not surprisingly, the number of bee species decreased with increased ventenata cover (Figure 61).



More ventenata, less forb cover

Photo: L. Ketchum

More ventenata, fewer forb species

Photo: L. Ketchum

More ventenata, fewer bee species

Photo: S. Mitchell

Figure 61. Response of forb cover, forb richness, and native bee richness to increased cover of ventenata at The Nature Conservancy's Zumwalt Prairie Preserve. Top two panels adapted from Fig. 4 in Watson et al. (2021).

Figure 62. Documenting the consequences of invading ventenata on pollinator habitat at The Nature Conservancy's Zumwalt Prairie Preserve.

Work thus far at The Zumwalt Prairie Preserve suggests that one highly invasive annual grass (*Ventenata dubia*) is having an impact both on pollinator floral resources and nesting habitat, and on native bees themselves, as summarized below.

Summary of Key Findings Related to Non-Native Annual Grass Invasions on Pollinators and Their Habitat

- As ventenata increased, forb cover and the number of forb species decreased.
- Ventenata litter reduced the availability of bare soil, decreasing habitat for ground-nesting bees.
- The number of bee species decreased with increased ventenata cover.

Management Implications

Studies in The Nature Conservancy's Zumwalt Prairie Preserve have shown that ventenata has successfully invaded the prairie and dramatically increased over the last decade. The species' effect on pollinator habitat needs more study, but research so far suggests that it negatively impacts native bees by decreasing flowering forb abundance and species richness and decreasing the availability of bare ground important to ground-nesting bees. The management implications of this work are outlined below.

Management Implications

- To safeguard pollinator habitat, preventing further spread of non-native annual grasses is a high priority.
- Limiting actions that may disturb biological soil crusts, where they remain intact, may be key to preventing annual grasses from expanding their distribution.
- Further research into measures that effectively control (or at least slow) non-native invasive annual grasses is a top priority. These measures may include new herbicides, developing new burning and grazing strategies that effectively control or limit invasions, or combinations of actions.

4. Restoration

Grassland and riparian areas are a common focus of restoration projects in the interior Pacific Northwest, partially because of their history of conversion and disturbance, but also because of their importance in supporting high levels of biodiversity and as habitat for many sensitive species (DeBano et al. 2016a). Although vertebrate species are often the focus of grassland and riparian restoration efforts (e.g., the greater sage-grouse (*Centrocercus urophasianus*), grassland songbirds, listed salmonids (*Oncorhynchus* spp.)) (Kennedy et al. 2009; Averett et al. 2017; Haab et al. 2023), many natural resource managers are also interested in how these restoration efforts influence pollinator habitat (DeBano et al. 2016a).

Because grasslands have been impacted primarily by conversion to cropland or pastures with planted non-native forage species for livestock, the aim of managers is often to restore the prairie to some semblance of pre-settlement conditions. In the interior PNW grasslands, this typically means a system dominated by native bunchgrass and a diversity of forb species (Figure 63). Restoration of abandoned cropland or seeded pasturelands can occur passively (removal of disturbance only) or actively (removal of disturbance and planted with desired species). Choosing one method or another may involve trade-offs between biodiversity, ecosystem services, and cost (Smith DiCarlo and DeBano 2019).


Photo: L. Ketcham

Figure 63. Native prairie at The Nature Conservancy's Zumwalt Prairie Preserve.

The focus of riparian restoration efforts in the PNW is often improving habitat for listed salmonid species, such as threatened steelhead (*Oncorhynchus mykiss*) (Wooster et al. 2019; Walther et al. 2022). Because high water temperature is a common limiting factor for many of these cold-water anadromous species, riparian restoration projects often aim to increase woody riparian species that shade streams and keep temperatures cool (Figure 64; Averett et al. 2017; Wondzell et al. 2019). The potential effects of planting woody species in riparian areas on pollinators had not been studied in the PNW. Because many species selected for riparian projects in the PNW are flowering shrubs, planting shrubs could potentially be a win-win strategy to improve both fish and pollinator habitat.

Figure 64. Shrub plantings in Meadow Creek riparian areas the USFS Starkey Experimental Forest and Range. Photo: M. Rowland.

Several research projects described in this report have investigated various responses of native bees and flowering plants to grassland and riparian restoration in eastern Oregon (Table 1). These include several studies at The Nature Conservancy's Boardman Conservation Area and Zumwalt Prairie Preserve (Smith DiCarlo et al. 2020; Watson 2020; DeBano et al. In Prep.) and one study in Starkey riparian areas (Mitchell et al. 2023).

Key Findings

Grassland Restoration

At the Boardman Conservation Area (BCA), past last uses such as cultivation and livestock grazing resulted in parts of the conservation area being dominated by non-native invasive grasses and low forb diversity. In response, The Nature Conservancy undertook active restoration projects from 2006-2012 in which relatively large areas (23-41 ha) were treated with glyphosate and seeded with native bunchgrasses and a limited number of forbs. Smith DiCarlo et al. (2020) compared both these actively restored sites and others that were passively restored with high quality, intact native sites. They found that neither active nor passive restoration resulted in the abundant flowering resources or distinct bee communities that were associated with high quality sites. This work suggests that in systems like the BCA, passive restoration or even actively planting primarily grasses is insufficient for improving pollinator habitat. Instead, active planting of a variety of forbs may be key for pollinator-related restoration goals, especially in areas like the BCA that are surrounded by high-intensity agricultural production systems.

The history of land use at the Zumwalt Prairie Preserve differs from the BCA in that in the late 1800s, homesteaders began cultivating grasslands on the Zumwalt Prairie. However, the short growing season, severe winters, and poor soils led to abandonment of these efforts beginning in the 1930s (Bartuszevige et al. 2012). These abandoned fields (termed “old fields”) were often subsequently planted with perennial non-native forage grasses for livestock (Figure 65). This led to a mosaic of old fields surrounded by intact prairie (Figure 66).

Figure 65. Native prairie (left) and an old field (right) at The Nature Conservancy’s Zumwalt Prairie Preserve.

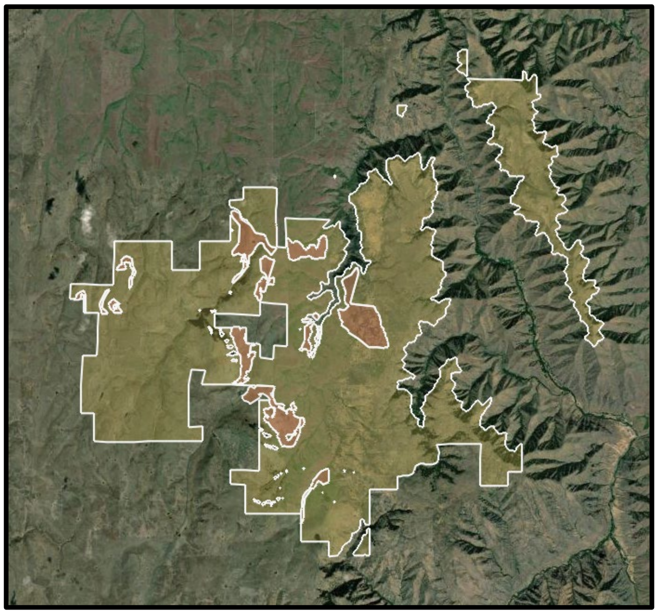


Figure 66. The location of old fields within native prairie at the Zumwalt. The white lines delineate the border of the Zumwalt Prairie Preserve, with old fields shown in orange.

Research showed that even after decades of passive restoration, seeded old fields had fewer flowering forbs and less bare ground compared to native prairie habitats (Table 7), and that many of the flowers that were absent or at low densities in old fields are species that are frequently visited or preferred by native bees in the region (Watson 2020). However, native bee communities did not differ between the two types of sites, potentially because large tracts of intact prairie adjacent to formerly cultivated grasslands compensated for decreased floral resources associated with those sites.

Table 7. Differences between old field and native sites at The Nature Conservancy's Zumwalt Prairie Preserve. Averages reported are per site, where plants were sampled along five 20-m transects per site, and bees were sampled at 15 locations per site.

	Old Field Sites	**Native Prairie**
Average # of Blooming Plant Species	16	24
Average # of Flowers	662	1,553
Common Flowering Species	• Idaho gumweed (*Grindelia nana*)	• Lupine (*Lupinus* spp.) • Meadow deathcamas (*Zigadenus venenosus*) • Thinleaved owl's-clover (*Orthocarpus tenuifolius*)
% Bare Ground	2.5%	8%
Average # of Bee Species	37	38
Bee Community Composition	Similar to native prairie sites	Similar to old field sites

Riparian Restoration

Interior PNW riparian areas, like those found along Meadow Creek at the USFS Starkey Experimental Forest and Range, have historically experienced a disproportionately high level of multiple disturbances, including road and railroad construction, flood control structures, timber harvesting, and replacement of native vegetation with forage grasses for livestock (DeBano et al. 2016). For this reason, they are often the focus of restoration efforts.

Efforts to restore riparian habitats take many forms and are often aimed at restoring conditions that improve habitat for aquatic species, like salmonids. At Meadow Creek within Starkey, the USFS, in conjunction with multiple partners (e.g., OWEB, Bonneville Power Administration, the Grand Ronde Model Watershed) undertook a large-scale restoration project in 2012-2013 that involved planting thousands of shrubs and trees to improve habitat conditions for threatened steelhead (*Oncorhynchus mykiss*) and Chinook salmon (*O. tshawytscha)*. To investigate how these shrubs may influence native bee habitat, Mitchell et al. (2022) conducted a two-year study investigating the use of riparian flowering shrubs by native bees (Figure 67).

The study showed that, in spring, the majority of flower-visiting bees foraged on shrubs – particularly willows (*Salix* sp.), a commonly planted riparian shrub (Mitchell et al. 2022). This was true despite the fact that blooming forbs were more species-rich and abundant at the sites in spring. In addition, the community composition of bees visiting shrubs differed from those visiting forbs. Wax currant (*Ribes cereum*) and willow had the most diverse group of bees visiting in early spring and black hawthorn (*Crataegus douglasii*) and mallow ninebark (*Physocarpus malvaceus*) had the most diverse bee visitors later in the season (i.e., June – July) (Figure 68, Figure 69). Some bee species showed strong preferences for particular shrub species. For example, all *Andrena porterae* and *Anthophora pacifica* were observed only on wax currant, and all *Andrena flocculosa* were observed only on red osier dogwood (*Cornus sericea*). Wax currant and black hawthorn are also more resistant to ungulate herbivory than other common shrubs occurring in eastern Oregon.

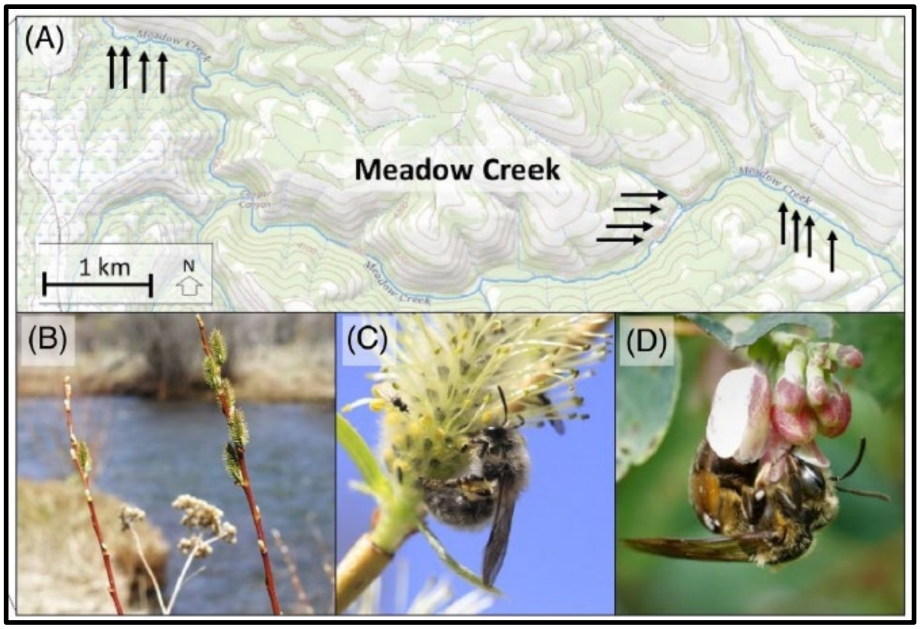


Figure 67. Study sites in the riparian area at Meadow Creek in the USFS Starkey Experimental Forest and Range with sites sampled indicated with black arrows (A), and examples of shrubs and native bees observed, including one-color willow (*Salix monochroma*) (B, C), a mining bee (*Andrena* sp.) foraging on willow in April (C), and another mining bee foraging on common snowberry (*Symphoricarpos albus*) in July (D). Adapted from Figure 1 in Mitchell et al. (2022). All photos: S. Mitchell.

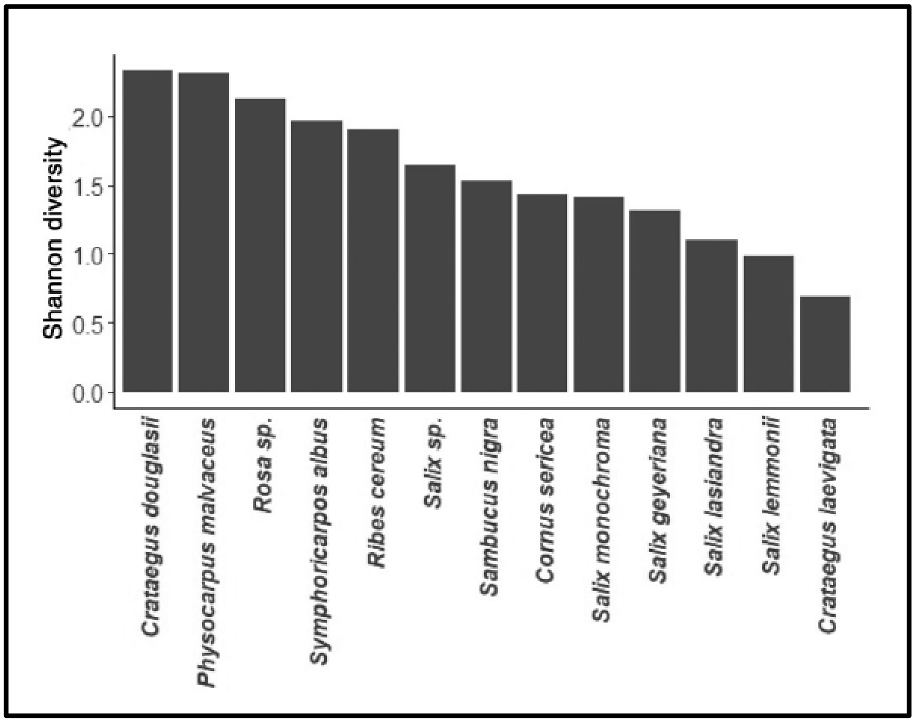


Figure 68. Shannon diversity of bee visitors to common shrub species occurring at Meadow Creek. Adapted from Figure 6 in Mitchell et al. (2022).

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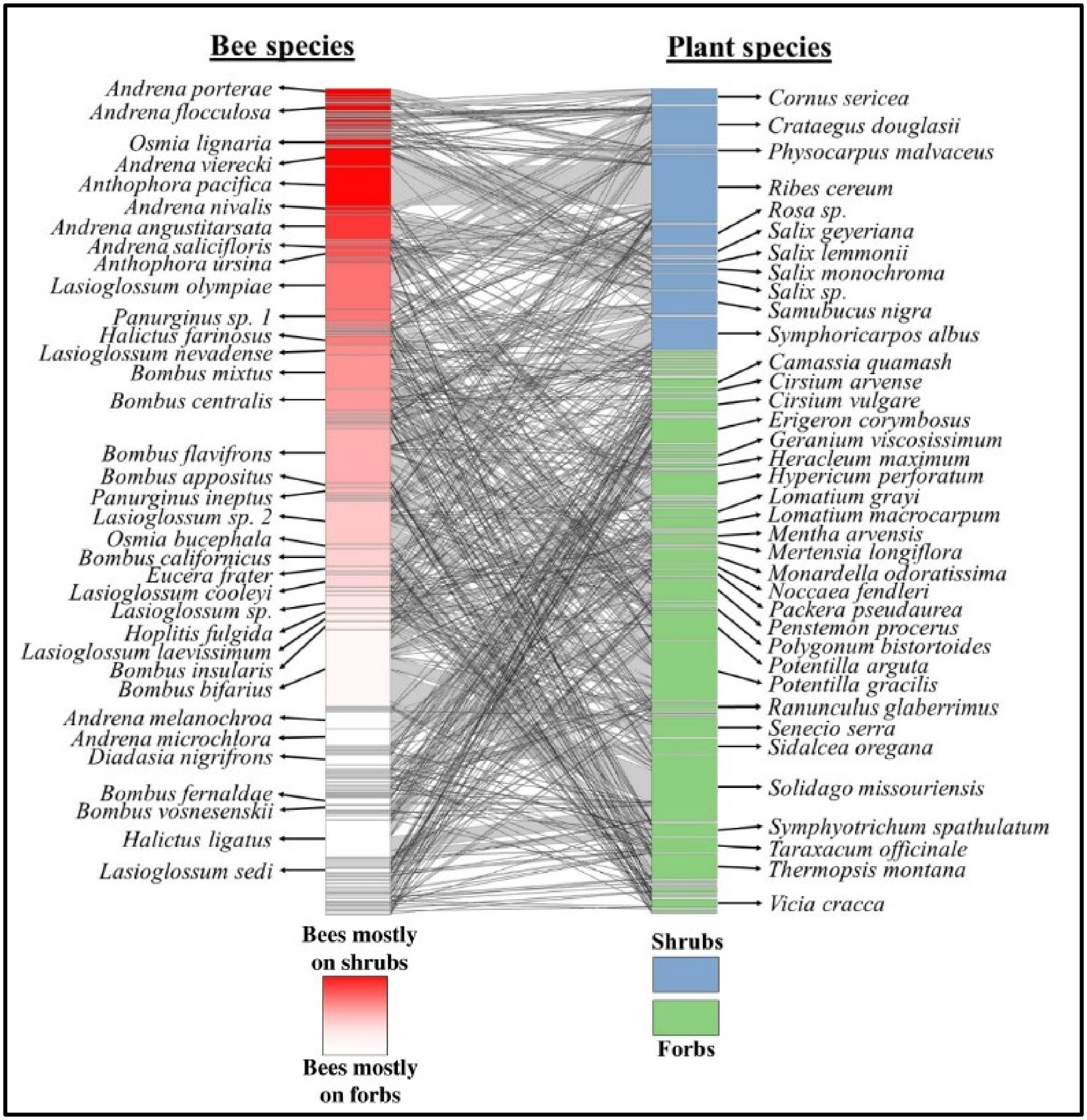

Figure 69. Network of bee and plant interactions for 150 bee species and 92 plant species (16 shrubs, 76 forbs) identified from observations of foraging bees from April to September, 2018–2019, at Meadow Creek. Box height and lines connecting bee and plant species are proportional to the number of observations. Adapted from Figure 8 in Mitchell et al. (2022).

Examining effects of restoration in grasslands at The Nature Conservancy's Boardman Conservation Area and at the USFS Starkey Experimental Forest and Range resulted in a number of key findings, summarized below.

Summary of Key Findings of Restoration Studies

Grasslands:

- Active and passive restoration in low elevation grasslands did not result in the abundant flowering resources or distinct bee communities that were associated with high quality sites.
- Passive restoration of seeded old fields had fewer flowering forbs and less bare ground compared to native prairie habitats and many of the flowers that were absent or at low densities in old fields are species that are frequently visited or preferred by native bees in the region.
- Native bee communities did not differ between old field and native sites at the Zumwalt prairie, potentially because large tracts of intact prairie adjacent to formerly cultivated grasslands compensated for decreased floral resources associated with those sites.

Riparian Areas:

- In spring, the majority of flower-visiting bees foraged on shrubs – particularly willows (*Salix* sp.), a commonly planted riparian shrub. This was true despite the fact that blooming forbs were more species-rich and abundant at riparian sites in spring.
- The species composition of bees visiting shrubs differed from those visiting forbs.
- Wax currant and willow had the most diverse group of bees visiting in early spring and black hawthorn and mallow ninebark had the most diverse bee visitors later in the season.
- Some bee species showed strong preferences for particular shrub species.

Management Implications

The body of work examining effects of grassland and riparian restoration on pollinators in the interior PNW leads to some broad management implications, outlined below. Although more work is needed, especially with regard to non-bee pollinators, this work forms a foundation to expand our knowledge of restoration effects in these key habitats.

Management Implications

Grasslands

- Passive restoration may not be sufficient to restore flowering plant and pollinator communities in many PNW grasslands, especially in those surrounded by highly modified landscapes.
- Active restoration of interior PNW grasslands should include not only planting native bunchgrasses (that provide nesting habitat for bumble bees) but also flowering forbs.
- Pollinator-focused restoration should aim to provide season-long floral resources that include plant species with different flower shapes.
- While controlling non-native annual grasses alone is insufficient for restoring bee habitat, it can help improve nesting habitat for ground nesting bees by increasing bare ground. This is because many non-native annual grasses (e.g., cheatgrass and ventenata) produce abundant litter that covers bare ground and also serves as fine fuels for fire.

Riparian Areas

- Riparian restoration practitioners that plant shrubs may not only improve stream health by shading and stabilizing banks but may also provide forage to a diverse group of pollinators.
- Considering phenology in pollinator-plant relationships is recommended when restoring structure and function of degraded systems.
- Planting wax currant and black hawthorn may be especially useful in PNW restoration projects because they provide forage for diverse native bees and are relatively resistant to ungulate herbivory.
- Planting bee-friendly shrubs in interior PNW riparian restoration projects is an effective strategy to accomplish multiple restoration goals, including improving fish and pollinator habitat and leveraging limited restoration funding.

VI. Broader Implications, Knowledge Gaps, and Research Priorities

Understanding Interior PNW Pollinator Communities

Although the three locations described in this report represent a range of habitats that occur in the interior PNW, the region is large and diverse. As the research presented here shows, even the best-studied pollinator group – native bees – varies tremendously over a variety of spatial and temporal scales. While this work provides a foundation upon which to build future efforts, effective pollinator management and conservation depends on understanding the distribution and abundance of pollinating species throughout the region. The volunteer-driven research of the Oregon Bee Atlas has dramatically increased our knowledge of bee distributions throughout Oregon, and shed light on the relationships of many groups of bees with flowers. However, systematic studies of focal habitats that 1) describe the species composition of communities and how they vary seasonally and 2) investigate variables underlying patterns in abundance and diversity remain a high priority. Management and restoration activities that target groups of conservation concern (e.g., bumble bees) and sensitive pollinator species (e.g., the western bumble bee) depend on our ability to predict where diversity hot spots occur and to understand which habitat factors are associated with occurrences of these hot spots and the presence of sensitive species.

In addition, the need to broaden our understanding of non-bee pollinator groups is pressing. For example, the work at The Nature Conservancy’s Zumwalt Prairie Preserve shows that moth diversity is high, but little is known about which species may be important pollinators, which plants may depend upon them, and how management and restoration affects them. The importance of examining non-bee pollinator diversity is especially true for locations like the ones described here, which are relatively large and undisturbed compared to much of the land in the inland PNW. The conservation value of these lands is likely particularly high because of their isolation from stressors such as light pollution and pesticide exposure. If patterns for non-bee pollinators are similar to those observed with native bees, these lands are expected to not only harbor high levels of diversity in these non-bee insect groups but also species of conservation concern.

Investigating Plant-Pollinator Relationships

The body of work presented in this report clearly shows the importance of understanding the relationship between pollinators and the plant species they depend upon, as well as the challenges inherent in their study. Bees illustrate the interdependent and complex nature of insect pollinators and the plants they visit. Understanding which plant species support pollinators can inform the selection of plant material and seed mixes for restoration. Not only is it important to understand which plants are useful to most pollinators, but it is also a high priority to understand which plants support specialist pollinators. Conversely, understanding which pollinators are key for the reproduction of plant species of conservation concern is equally important, as the study of Spalding’s catchfly at The Nature Conservancy’s Zumwalt Prairie demonstrates.

One high priority area for future study is understanding how stable pollinator networks are through time and space. This information would allow managers and restoration practitioners to understand how applicable knowledge about pollinator-plant relationships is from one location to another, and how sensitive these relationships are to perturbations associated with species loss and climate-induced changes in phenology. Another high priority area is examining which insect species serve as pollinators for culturally significant plants, including First Food roots and berries used by indigenous people.

Managing and Restoring Habitats for Pollinators

The research described here shows that the management of ungulates, fire, and weeds can all influence native bee communities, both through effects on floral resources and nesting habitat. In addition, the effects of several different approaches to grassland and riparian restoration on bees have been examined, and this research has identified strategies that may result in benefits to pollinators (e.g., planting more forb species in grassland restoration, incorporating "bee-friendly" shrubs in riparian restoration). However, more work is needed in four areas. First, more research should aim to untangle the mechanisms responsible for observed responses of pollinators to management and restoration. New methods, such as DNA metabarcoding, are helping identify floral resources important to pollinators. However, assessing how management and restoration affect nesting and overwintering habitat for most pollinators remains particularly challenging.

Second, more work is needed to examine the effects of alternative or innovative management and restoration strategies on pollinator responses. For example, the use of prescribed burns in inland PNW systems to improve pollinator habitat is not well-studied, and little is known about ideal burn intervals and sizes of prescribed burns relative to pollinator benefits. Work in the Midwest suggests that both interval and the size of the burned area can strongly influence some butterflies (Hanberry et al. 2021). In addition, further research on targeted grazing strategies, including phenologically targeted grazing and the use of virtual fencing, are needed to help rangeland managers and producers graze livestock in ways that reduce any potential negative effects on pollinators.

Innovative restoration techniques in streams and riparian areas are also high priority research topics. The popularity of low-tech process-based restoration approaches in PNW streams has increased dramatically in the last decade. These low-tech process-based restoration projects (e.g., beaver dam analogs) increase floodplain connectivity and may strongly influence riparian condition in ways that improve habitat for native bees and other pollinators. In addition, new approaches to large-scale watershed restoration that involves both upland and riparian areas are planned for the USFS Starkey Experimental Forest and Range and surrounding regions in the coming years. Plans are underway to monitor a wide variety of responses to this restoration effort, and previous pollinator work at Starkey in both riparian areas and uplands would help quantify the benefits of these efforts for pollinators.

Third, further research is needed on the response of a wider variety of pollinator groups to management and restoration in inland PNW grasslands and riparian areas. With the exception of bees and butterflies, no work has been conducted in the region on responses of pollinating insects to management and restoration. Given the variation in life histories of the major pollinating groups, responses to management and restoration are expected to differ. This increases the likelihood that managers will have to balance tradeoffs when making decisions that impact pollinators, given that actions that benefit one pollinator group may not necessarily benefit others.

Interacting Factors Influencing Pollinators in a Changing Climate

Natural resource managers have had to consider multiple, interacting forces and shifting management priorities for decades (Figure 70). However, the number of factors impacting interior PNW grasslands and riparian areas is increasing, and the rate of change of several major stressors is rapidly expanding (e.g., the spread of invasive species, climate change). With these changes, the importance of examining the interaction of management and restoration is growing, and research on pollinators in the interior PNW has increasingly expanded to include multiple factors (Figure 71). Studies at all three locations described in this report have examined multiple factors simultaneously, including restoration and fire at The Nature Conservancy’s Boardman Conservation Area; fire, grazing, and annual grass invasions at The Nature Conservancy’s Zumwalt Prairie Preserve; and ungulate herbivory and restoration at USFS Stakey Experimental Forest and Range (Table 1). These projects and others show the potential for interactions between management and disturbances such as annual grass invasions. For example, previous work by Ridder et al. (2022) in the Zumwalt Prairie suggested fire and grazing may interact in their effects on ventenata cover. The authors suggested that fall prescribed fire may help reduce ventenata where livestock are grazed in this system, and that livestock grazing without prescribed fire may contribute to a higher abundance of ventenata in the Zumwalt Prairie. The consequences of these interactions on pollinators need more study, especially in the context of a changing climate.

Figure 70. Land management and restoration decisions and various stressors, including non-native annual grass invasions and climate change, interact in complex ways to affect native pollinators and the resources they depend upon.

A recurring theme of the projects described in this report is the inter-relatedness of disturbance, management actions, and restoration, all in the larger context of a changing climate. Changing climate can not only alter the players in the community (i.e., which species persist in given locations and at what levels), but also the relationships between them and quickly changing abiotic variables (e.g., soil moisture). For example, climate change may exacerbate negative effects of ventenata and other invasive annual grass invasions. As these grasses increase fine fuel loads, and as summers become hotter and drier, fires that once contributed to sustaining healthy rangelands may be more likely to become catastrophic fires that fundamentally alter grassland composition. Climate change may mean that management practices that were effective in the past may no longer be. Changing temperature and precipitation can have direct and indirect effects on insect pollinators. Indirect effects include impacts on phenology, soil moisture, fire severity and frequency, biological soil crusts, and ungulate foraging behavior, which may all affect pollinators of inland PNW grassland and riparian areas. A high priority in dealing with this complexity is developing predictive models that include direct and indirect effects of climate change on key variables expected to influence pollinators.

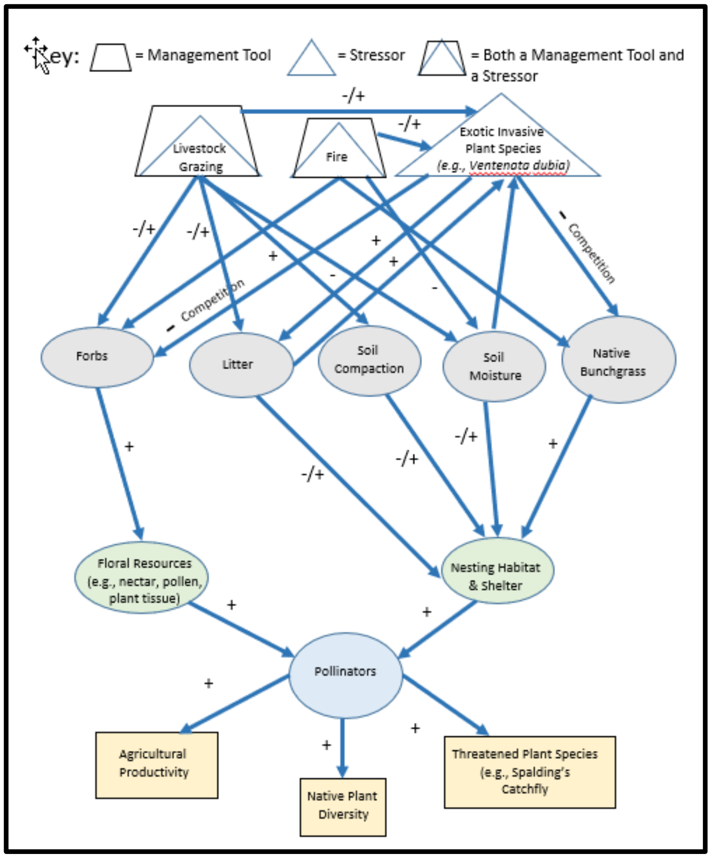

Figure 71. Hypothesized effects of management and potential stressors on select habitat variables (in gray) that influence pollinators (in blue) and the ecosystem services they provide (in orange) through their effect on food, nesting, and shelter (in green). For simplicity, not all possible relationships are depicted.

Finally, until a more comprehensive understanding of complex ecological interactions of pollinators in PNW grasslands and riparian areas is achieved, the best approach may be to manage for habitat heterogeneity and with the precautionary principle in mind. Management and restoration actions that maintain as many components of systems as possible and keep interactions among players intact are most likely to lead to healthy pollinator communities. Success will also be more likely with greater Investment in researching win-win strategies for multiple users. Finally, as this report illustrates, the protection of natural areas like the Zumwalt Prairie and other hotspots of biodiversity will be important in ensuring the conservation of pollinators and the ecosystem services they provide.

Figure 72. A long and winding road to understanding pollinators in interior PNW grasslands and riparian areas. Photo: L. Ketchum

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Appendix A: Publications and Other Products Associated with Pollinator Research in Eastern Oregon

Journal Articles

Arstingstall, K.A., S.J. DeBano, X. Li, D.E. Wooster, M.M. Rowland, S. Burrows, and K. Frost. 2021. Capabilities and limitations of using DNA metabarcoding to study plant-pollinator interactions. Molecular Ecology 30: 5266-5287.

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Appendix B: Bee Species Documented at The Nature Conservancy's Zumwalt Prairie Preserve, The Nature Conservancy's Boardman Conservation Area, and Meadow Creek at the USFS Starkey Experimental Forest and Range

Bee species collected when pollinator studies were conducted at each of the three study locations: The Nature Conservancy's Zumwalt Prairie Preserve (Zumwalt), The Nature Conservancy's Boardman Conservation Area (Boardman), and at Meadow Creek in the USFS Starkey Experimental Forest and Range (Starkey). All species determinations were made by Skyler Burrows except those indicated with an asterisk. Asterisked species were determined by Robbin Thorp (University of California Davis) or Andy Moldenke (Oregon State University). Lists include species collected using vane traps, pan traps, and hand-netting. The number of years and sites of study at each location varied, with one year of data from 16 sites and two years of data from 30 sites at the Zumwalt, three years of data from 18 sites at Boardman and 6 years of data from 12 sites at Starkey.

Zumwalt (209 species)	**Boardman** (85 species)	**Starkey** (285 species)
Agapostemon femoratus	*Agapostemon femoratus*	*Agapostemon femoratus*
Agapostemon texanus	*Agapostemon texanus*	*Agapostemon texanus*
Agapostemon virescens	*Agapostemon virescens*	*Agapostemon virescens*
Andrena amphibola	*Andrena prunorum*	*Andrena amphibola*
Andrena angustitarsata	*Anthophora curta*	*Andrena angustitarsata*
Andrena astragali	*Anthophora exigua*	*Andrena astragali*
Andrena buckelli	*Anthophora urbana*	*Andrena barbilabris*
Andrena candida	*Apis mellifera*	*Andrena birtwelli*
Andrena cressonii	*Bombus fervidus*	*Andrena caerulea*
Andrena cyanophila	*Bombus griseocollis*	*Andrena candida*
Andrena evoluta	*Bombus huntii*	*Andrena crataegi*
Andrena gordoni	*Bombus nevadensis*	*Andrena cressonii*
Andrena lawrencei	*Coelioxys octodentata*	*Andrena cupreotincta*
Andrena medionitens	*Coelioxys rufitarsis*	*Andrena cyanophila*
Andrena melanochroa	*Colletes annae*	*Andrena evoluta*
Andrena merriami	*Colletes compactus*	*Andrena flocculosa*
Andrena microchlora	*Colletes fulgidus*	*Andrena hamulata*
Andrena miranda	*Colletes phaceliae*	*Andrena hippotes*
Andrena nigrocaerulea	*Colletes gypsicolens*	*Andrena laminibucca*
Andrena nivalis	*Diadasia enavata*	*Andrena lupinorum*
Andrena pallidifovea	*Dianthidium pudicum*	*Andrena medionitens*
Andrena prunorum	*Dianthidium ulkei*	*Andrena melanochroa*
Andrena raveni	*Eucera edwardsii*	*Andrena microchlora*
*Andrena rufosignata**	*Eucera speciosa*	*Andrena milwaukeensis*
Andrena salicifloris	*Halictus farinosus*	*Andrena miranda*
Andrena scutellinitens	*Halictus ligatus*	*Andrena nigrihirta*
Andrena shoshoni	*Halictus rubicundus*	*Andrena nigrocaerulea*

Zumwalt (continued)	**Boardman** (continued)	**Starkey** (continued)
Andrena sp. 5	*Halictus tripartitus*	*Andrena nivalis*
Andrena sp. A	*Hoplitis grinnelli*	*Andrena nothocalaidis*
Andrena thaspii	*Hylaeus rudbeckiae*	*Andrena pallidifovea*
Andrena transnigra	*Lasioglossum albohirtum*	*Andrena pallidiscopa*
Andrena venata	*Lasioglossum brunneiventre*	*Andrena porterae*
Andrena vicinoides	*Lasioglossum ebmerellum*	*Andrena prunorum*
Andrena vierecki	*Lasioglossum hyalinum*	*Andrena salicifloris*
Andrena washingtoni	*Lasioglossum incompletum*	*Andrena schuhi*
Andrena w-scripta	*Lasioglossum kincaidii*	*Andrena scurra*
*Anthidiellum notatum**	*Lasioglossum lusorium*	*Andrena scutellinitens*
Anthidium atrifrons	*Lasioglossum macroprosopum*	*Andrena shoshoni*
Anthidium utahense	*Lasioglossum perpunctatum*	*Andrena sladeni*
Anthophora affabilis	*Lasioglossum prasinogaster*	*Andrena* sp. 2
Anthophora bomboides	*Lasioglossum pruinosum*	*Andrena* sp. 4
Anthophora pacifica	*Lasioglossum sisymbrii*	*Andrena* sp. A
*Anthophora terminalis**	*Lasioglossum sp. 2*	*Andrena* sp. B
Anthophora urbana	*Lasioglossum titusi*	*Andrena* sp. C
Anthophora ursina	*Lasioglossum trizonatum*	*Andrena* sp. D
Ashmeadiella bucconis	*Megachile apicalis*	*Andrena* sp. stylopized
Ashmeadiella californica	*Megachile coquilletti*	*Andrena subtilis*
Ashmeadiella difugita	*Megachile montivaga*	*Andrena surda*
*Ashmeadiella sculleni**	*Megachile nevadensis*	*Andrena thaspii*
*Atoposmia sp.**	*Megachile onobrychidis*	*Andrena topazana*
Bombus appositus	*Megachile parallela*	*Andrena transnigra*
Bombus bifarius	*Megachile perihirta*	*Andrena venata*
Bombus californicus	*Megachile umatillensis*	*Andrena vicinoides*
Bombus centralis	*Megachile wheeleri*	*Andrena vierecki*
*Bombus fernaldae**	*Melissodes agilis*	*Andrena walleyi*
Bombus fervidus	*Melissodes bimatris*	*Andrena w-scripta*
Bombus flavifrons	*Melissodes lupinus*	*Anthidiellum robertsoni*
Bombus griseocollis	*Melissodes lutulentus*	*Anthidium atrifrons*
Bombus huntii	*Melissodes microstictus*	*Anthidium formosum*
Bombus insularis	*Melissodes pallidisignatus*	*Anthidium mormonum*
Bombus mixtus	*Melissodes perlusus*	*Anthidium utahense*
Bombus nevadensis	*Melissodes rivalis*	*Anthophora bomboides*
Bombus occidentalis	*Melissodes saponellus*	*Anthophora curta*
Bombus rufocinctus	*Melissodes semilupinus*	*Anthophora pacifica*
*Bombus vagans**	*Melissodes sp. 1*	*Anthophora terminalis*
Bombus vosnesenskii	*Melissodes subagilis*	*Anthophora urbana*
Ceratina acantha	*Melissodes tristis*	*Anthophora ursina*
Ceratina nanula	*Nomada* sp. 1	*Apis mellifera*
Ceratina pacifica	*Nomada* sp. 2	*Ashmeadiella bucconis*
Chelostoma phaceliae	*Nomada* sp. 3	*Ashmeadiella cactorum*
Coelioxys rufitarsis	*Nomada* sp. 4	*Ashmeadiella californica*
Colletes fulgidus	*Nomada* sp. 6	*Ashmeadiella cubiceps*
Colletes nigrifrons	*Osmia brevis*	*Ashmeadiella difugita*
Colletes phaceliae	*Osmia integra*	*Atoposmia abjecta*

Zumwalt (continued)

*Colletes simulans**
Diadasia enavata
Diadasia nigrifrons
Dianthidium pudicum
*Dianthidium singulare**
Dianthidium subparvum
Dufourea holocyanea
*Dufourea rufiventris**
Dufourea trochantera
Eucera edwardsii
Eucera frater
Habropoda sp.*
Halictus confusus
Halictus farinosus
Halictus ligatus
Halictus rubicundus
Halictus tripartitus
Hoplitis albifrons
Hoplitis fulgida
Hoplitis grinnelli
Hoplitis hypocrita
Hoplitis producta
Hylaeus coloradensis
Hylaeus conspicuus
Lasioglossum aberrans
Lasioglossum albipenne
Lasioglossum albohirtum
*Lasioglossum anhypops**
Lasioglossum brunneiventre
Lasioglossum cooleyi
Lasioglossum egregium
Lasioglossum glabriventre
Lasioglossum incompletum
Lasioglossum macroprosopum
Lasioglossum marinense
Lasioglossum nevadense
Lasioglossum olympiae
Lasioglossum ovaliceps
Lasioglossum perpunctatum
Lasioglossum prasinogaster
Lasioglossum pruinosum
Lasioglossum punctatoventre
Lasioglossum reasbeckae
Lasioglossum ruidosense
Lasioglossum sedi
Lasioglossum sisymbrii
Lasioglossum sp. 1

Boardman (continued)

Osmia trevoris
Perdita aridella
Perdita dubia
Perdita lingualis
Perdita oregonensis
Sphecodes sp. 03
Svastra obliqua
Triepeolus grindeliae
Triepeolus paenepectoralis
Triepeolus sp. 2
Xeromelecta californica

Starkey (continued)

Bombus appositus
Bombus bifarius
Bombus californicus
Bombus centralis
Bombus fernaldae
Bombus fervidus
Bombus flavifrons
Bombus griseocollis
Bombus huntii
Bombus insularis
Bombus mixtus
Bombus nevadensis
Bombus occidentalis
Bombus rufocinctus
Bombus vosnesenskii
Ceratina acantha
Ceratina nanula
Ceratina pacifica
Ceratina sequoiae
Coelioxys moesta
Coelioxys octodentata
Coelioxys porterae
Coelioxys rufitarsis
Colletes fulgidus
Colletes kincaidii
Diadasia diminuta
Diadasia enavata
Diadasia nigrifrons
Dianthidium heterulkei
Dianthidium parvum
Dianthidium pudicum
Dianthidium subparvum
Dianthidium ulkei
Dufourea dilatipes
Dufourea maura
Epeolus americanus
Epeolus compactus
Eucera actuosa
Eucera edwardsii
Eucera frater
Eucera hurdi
Habropoda cineraria
Halictus confusus
Halictus farinosus
Halictus ligatus
Halictus rubicundus
Halictus tripartitus

Zumwalt (continued)

Lasioglossum sp. 2
Lasioglossum sp. 3
Lasioglossum sp. 5
Lasioglossum sp. 6
Lasioglossum titusi
Lasioglossum trizonatum
Megachile apicalis
Megachile bradleyi*
Megachile brevis
Megachile coquilletti
Megachile dentitarsus*
Megachile latimanus*
Megachile lippiae
Megachile melanophaea
Megachile mellitarsus*
Megachile montivaga
Megachile nevadensis*
Megachile onobrychidis
Megachile parallela
Megachile perihirta
Megachile pugnata
Megachile relativa*
Megachile sublaurita
Megachile wheeleri*
Melecta pacifica
Melissodes ablusus
Melissodes agilis
Melissodes bicolorata*
Melissodes bimatris*
Melissodes confusa*
Melissodes lupinus
Melissodes metenua*
Melissodes microstictus
Melissodes rivalis
Melissodes robustior*
Nomada sp. 8
Osmia albolateralis
Osmia atrocyanea
Osmia austromaritima
Osmia bella
Osmia brevis
Osmia bruneri
Osmia bucephala*
Osmia californica
Osmia calla*
Osmia caulicola*
Osmia cobaltina*

Starkey (continued)

Heriades carinatus
Hoplitis albifrons
Hoplitis fulgida
Hoplitis grinnelli
Hoplitis hypocrita
Hoplitis plagiostoma
Hoplitis producta
Hoplitis sambuci
Hylaeus affinis
Hylaeus annulatus
Hylaeus basalis
Hylaeus conspicuus
Hylaeus episcopalis
Hylaeus modestus
Hylaeus rudbeckiae
Hylaeus verticalis
Hylaeus wootoni
Lasioglossum albipenne
Lasioglossum anhypops
Lasioglossum colatum
Lasioglossum cooleyi
Lasioglossum egregium
Lasioglossum glabriventre
Lasioglossum glabriventris
Lasioglossum incompletum
Lasioglossum leucozonium
Lasioglossum marinense
Lasioglossum mellipes
Lasioglossum nevadense
Lasioglossum olympiae
Lasioglossum ovaliceps
Lasioglossum pacificum
Lasioglossum prasinogaster
Lasioglossum punctatoventre
Lasioglossum reasbeckae
Lasioglossum ruidosense
Lasioglossum sandhousiellum
Lasioglossum sedi
Lasioglossum sisymbrii
Lasioglossum sp. 1
Lasioglossum sp. 2
Lasioglossum sp. 3
Lasioglossum sp. 4
Lasioglossum sp. 5
Lasioglossum sp. 6
Lasioglossum sp. 7
Lasioglossum tegulare

Zumwalt (continued)

Osmia coloradensis
*Osmia cyanella**
*Osmia cyaneonitens**
Osmia ednae
Osmia indeprensa
*Osmia juxta**
Osmia kincaidii
Osmia longula
Osmia melanopleura
*Osmia montana**
*Osmia nanula**
Osmia nemoris
*Osmia nifoata**
Osmia nigrifrons
*Osmia pellax**
*Osmia pentstemonis**
Osmia pusilla
Osmia raritatis
*Osmia regulina**
*Osmia sculleni**
Osmia sp. 2
Osmia sp. 3
Osmia subaustralis
Osmia tanneri
Osmia thysanisca
Osmia trevoris
*Osmia tristella**
Osmia vandykei
Panurginus atriceps
Panurginus gracilis
Panurginus ineptus
Panurginus torchio
Perdita lingualis
*Perdita oregonensis**
Perdita wyomingensis
Pseudopanurgus didirupa
Sphecodes sp. 01
Stelis sp.*
Triepeolus heterurus
Triepeolus paenepectoralis
*Xeromelecta californica**

Starkey (continued)

Lasioglossum tenax
Lasioglossum titusi
Lasioglossum trizonatum
Megachile angelarum
Megachile fidelis
Megachile gemula
Megachile lippiae
Megachile melanophaea
Megachile montivaga
Megachile onobrychidis
Megachile parallela
Megachile perihirta
Megachile pugnata
Megachile relativa
Megachile sublaurita
Megachile wheeleri
Melecta pacifica
Melecta separata
Melecta thoracica
Melissodes agilis
Melissodes bimatris
Melissodes confusus
Melissodes lupinus
Melissodes microstictus
Melissodes pallidisignatus
Melissodes rivalis
Nomada sp. 1
Nomada sp. 2
Nomada sp. 3
Nomada sp. 4
Nomada sp. 5
Nomada sp. 7
Nomada sp. 8
Nomada sp. A
Nomada sp. B
Nomada sp. C
Nomada sp. D
Nomada sp. E
Nomada sp. F
Nomada sp. G
*Nomad*a sp. I
Nomia melanderi
Osmia albolateralis
Osmia atrocyanea
Osmia bella
Osmia brevis
Osmia bruneri

Starkey (continued)
Osmia bucephala
Osmia californica
Osmia calla
Osmia cobaltina
Osmia coloradensis
Osmia cyanella
Osmia cyaneonitens
Osmia densa
Osmia ednae
Osmia exigua
Osmia giffardi
Osmia grindeliae
Osmia indeprensa
Osmia inermis
Osmia juxta
Osmia kincaidii
Osmia lignaria
Osmia longula
Osmia melanopleura
Osmia montana
Osmia nemoris
Osmia nigrifrons
Osmia obliqua
Osmia pusilla
Osmia raritatis
Osmia simillima
Osmia sp. 1
Osmia sp. 2
Osmia sp. 3
Osmia sp. 4
Osmia sp. 5
Osmia sp. 6
Osmia sp. A
Osmia subaustralis
Osmia thysanisca
Osmia trevoris
Osmia tristella
Osmia vandykei
Panurginus atriceps
Panurginus gracilis
Panurginus ineptus
Panurginus sp. 1
Panurginus torchio
Perdita lingualis
Perdita wyomingensis
Sphecodes arvensiformis
Sphecodes sp. 01

Starkey (continued)
Sphecodes sp. 02
Sphecodes sp. 04
Sphecodes sp. 05
Sphecodes sp. 06
Sphecodes sp. 07
Sphecodes sp. A
Sphecodes sp. B
Sphecodes sp. C
Sphecodes sp. D
Sphecodes sp. E
Sphecodes sp. F
Sphecodes sp. G
Stelis holocyanea
Stelis montana
Stelis nitida
Stelis pavonina
Stelis sp. B
Stelis spined #6
Stelis subemarginata
Svastra obliqua
Triepeolus paenepectoralis
Triepeolus sp. 2
Xeromelecta californica

Appendix C: Butterfly Species Documented at the Zumwalt Prairie

List of butterfly species documented at The Nature Conservancy’s Zumwalt Prairie Preserve. Identification work was done by Cliff Ferris, Dana Ross, and Paul Hammond.

Family	**Scientific Name**	**Common Name**
Hesperiidae	*Amblyscirtes vialis* (W. H. Edwards)	Common roadside-skipper
	Burnsius communis communis (Grote)	Common checkered-skipper
	Erynnis persius ssp. (Scudder)	Persius duskywing
	Hesperia colorado idaho (W. H. Edwards)	Western branded wkipper
	Hesperia juba (Scudder)	Juba skipper
	Ochlodes sylvanoides sylvanoides (Bdv.)	Woodland skipper
	Pyrgus ruralis nr. *ruralis* (Bdv.)	Two-banded checkered-skipper
Lycaenidae	*Callophrys affinis* (W.H. Edwards)	Western green hairstreak
	Callophrys eryphon eryphon (W. H. Edwards)	Western pine elfin
	Celastrina echo ssp. (Cramer)	Spring azure
	Euphilotes heracleoides (Kohler & A. Warren)	Cascadia blue
	Glaucopsyche lygdamus columbia (Scudder)	Silvery blue
	Glaucopsyche piasus toxeuma (W. H. Edwards)	Arrowhead blue
	Icaricia acmon (W. H. Edwards)	Acmon blue
	Icaricia icarioides pembina (W. H. Edwards)	Boisduval's blue
	Icaricia saepiolus rufescens (Bdv.)	Greenish blue
	Plebejus melissa ssp. (W. H. Edwards)	Melissa blue
	Tharsalea editha nr. *editha* (Mead)	Edith's copper
	Tharsalea helloides (Bdv.)	Purplish copper
	Tharsalea heteronea rava (Bdv.)	Blue copper
Nymphalidae	*Aglais milberti* (Godart)	Milberts tortoisesheell
	Cercyonis oetus oetus (Bdv.)	Small wood nymph
	Cercyonis pegala nr. *ariane* (Behr)	Common wood nymph
	Chlosyne palla spp. (Bdv.)	Northern checkerspot
	Coenonympha california ampelos (W. H. Edwards)	Common ringlet
	Danaus plexippus plexippus (Linnaeus)	Monarch
	Erebia epipsodea epipsodea (P. Ehrlich)	Common alpine
	Euphydryas colon wallacensis (Gunder)	Snowberry checkerspot
	Euphydryas editha nr. *edithana* (Strand)	Edith's checkerspot
	Limenitis lorquini burrisonii (W. H. Edwards)	Lorquin's admiral
	Nymphalis antiopa (L.)	Mourning cloak
	*Nymphalis californica (*W. H. Edwards)	California tortoiseshell
	Phyciodes mylitta mylitta (W. H. Edwards)	Mylitta crescent
	Phyciodes pulchella owimba (W. H. Edwards)	Field crescent
	Polygonia satyrus neomarsyas (W. H. Edwards)	Satyr comma
	Speveria hesperis dodgei (W. H. Edwards)	Northwestern fritillary
	Speyeria bischoffii erinna (W. H. Edwards)	Mormon fritillary
	Speyeria callippe semivirida (McDunnough)	Callippe fritillary
	Speyeria cybele leto (Behr)	Great spangled fritillary
	Speyeria zerene picta (W. H. Edwards)	Zerene fritillary
	Vanessa atalanta rubria (Fruh.)	Red admiral
	Vanessa cardui (L.)	Painted lady

Family	Scientific Name	Common Name
Papilionidae	*Papilio eurymedon* (Lucas)	Pale swallowtail
	Papilio multicaudata pusillus (W. H. Edwards)	Two-tailed swallowtail
	Papilio rutulus (Lucas)	Western tiger swallowtail
	Papilio zelicaon zelicaon (W. H. Edwards)	Anise swallowtail
	Parnassius smintheus magnus (W. H. Edwards)	Rocky Mountain parnassian
Pieridae	*Anthocharis julia sulfuris* (W. H. Edwards)	Pacific orangetip
	Colias alexandra edwardsii (W. H. Edwards)	Queen Alexandra's sulphur
	Colias eriphyle (W. H. Edwards)	Clouded sulphur
	Colias eurytheme (Boisduval)	Orange sulphur
	Euchloe ausonides transmontana (Lucas)	Large marble
	Pieris rapae rapae (L.)	Cabbage white
	Pontia occidentalis occidentalis (Reakirt)	Western white
	Pontieuchloia beckerii (W. H. Edwards)	Becker's white

Appendix D: Moth Species Documented at The Zumwalt Prairie

Families and species of moths collected using a black light at night from May to September 2017. Samples were collected at the bottom of a canyon with a riparian corridor. Vegetation was native bunchgrass and forbs, interspersed with annual grasses, on canyon slopes and mixed native and non-native species in riparian areas with canopies of cottonwood and alder on canyon bottom. Sampling alternated irregularly between riparian, canyon edge, and an open area (driveway). Samples were retrieved in the morning, placed in plastic resealable bags and frozen until identification.

Family	***Species***
Cossidae	*Acossus populi*
	Prionyxtus robiniae
Crambidae	*Chalcoela iphitalis*
	Chrysoteuchia topiarius
	Crambus leachellus
	Evergestis pallidata
	Fumibotys fumalis
	Microtheoris ophionalis
	Mimoschinia rufofascialis
	Pediasia trisecta
	Petrophila confusalis
	Pyla fusca
	Pyrausta fodinalis
	Pyrausta grotei
	Pyrausta nexalis
	Pyrausta semirubralis
	Saucrobotys fumoferalis
	Udea ?profundalis
Drepanidae	*Ceranemota tearlei*
	Drepana arcuata
Erebidae	*Caenurgina erechtea*
	Catocala neogama
	Catocala semirelicta
	Crambidia casta
	Cycnia oregonensis
	Dasychira vagans
	Drasteria adumbrata
	Drasteria divergens
	Drasteria edwardsii
	Drasteria ochracea
	Drasteria perplexa
Erebidae	*Drasteria sabulosa*
	Grammia nevadensis
	Grammia ornata
	Hypena humuli
	Hyphantria cunea
	Idia americalis
	Orgyia pseudotsugata
	Phobolosia anfracta
	Pyrrharctia isabella
	Spilosoma vagans
	Spilosoma vestalis
	Zale lunata
	Zale minerea
Euteliidae	*Marathyssa inficita*
Geometridae	*Aplocera plagiata*
	Chlorochlamys triangularis
	Cyclophora pendulinaria
	Digrammia californiaria
	Digrammia curvata
	Digrammia decorata
	Digrammia modocata
	Digrammia neptaria
	Digrammia nubiculata
	Digrammia sexpunctata
	Digrammia ubiquitata
	Ectropis crepuscularia
	Ennomos magnaria
	Euchlaena johnsonaria
	Euchlaena madusaria
	Euchlaena mollisaria
	Eumacaria madopata

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Family	*Species*
Geometridae	*Eupithecia olivacea*
	Eupithecia agnesata
	Eupithecia misturata
	Eustroma semiatrata
	Glena nigricaria
	Hesperumia sulphuraria
	Horisme intestinata
	Idaea demissaria
	Idaea dimidiata
	Iridopsis clivinaria
	Macaria aemulataria
	Macaria decorata
	Perizoma costiguttata
	Pero mizon
	Pero occidentalis
	Pero spp
	Protitame subalbaria
	Scopula junctaria
	Scopula luteolata
	Stergomataea delicatum
	Synchlora aerata
	Tetracis cervinaria
	Venusia pearsalli
	Xanthorhoe defensaria
	Zenophleps lignicolorata
Lasiocampidae	*Malacosoma californica*
	Malacosoma disstria
	Phyllodesma americana
	Tolype distincta
Noctuidae	*?Mniotype ducta*
	Abagrotis duanca
	Abagrotis erratica
	Abagrotis forbesi
	Abagrotis placida
	Abagrotis reedi
	Abagrotis scopeops
	Abagrotis trigona
	Abagrotis variata
	Acerra normalis
	Acronicta americana
	Acronicta parallela
	Adelphagrotis indeterminata
	Admetovis n. sp.
	Admetovis similaris
	Agrochola purpurea
Noctuidae	*Agrotis venerabilis*
	Agrotis vetusta
	Anagrapha falcifera
	Apamea acera
	Apamea amputatrix
	Apamea antennata
	Apamea cinefacta
	Apamea cogitata
	Apamea devastator
	Apamea inordinata
	Apamea longula
	Apamea niveivenosa
	Apamea occidens
	Apamea scoparia
	Apamea sordens
	Apamea spaldingi
	Aseptis binotata
	Aseptis fumosa
	Autographa californica
	Autographa metallica
	Caradrina meralis
	Condica discistriga
	Condica mersa
	Cryphia cuerva
	Cucullia similaris
	Dichagyris variabilis
	Egira curialis
	Egira hiemalis
	Egira perlubens
	Egira rubrica
	Enargia decolor
	Enargia infumata
	Epidemas cinerea
	Epidemas obscurus
	Eueretagrotis perattentus
	Euxoa albipennis
	Euxoa altens
	Euxoa atomaris
	Euxoa bicollaris
	Euxoa bochus
	Euxoa brunneigera
	Euxoa catenula
	Euxoa comosa
	Euxoa divergens
	Euxoa hollemani

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Family	Species
Noctuidae	*Euxoa infausta*
	Euxoa infracta
	Euxoa messoria
	Euxoa munis
	Euxoa obeliscoides
	Euxoa oliviae
	Euxoa punctigera
	Euxoa satis
	Euxoa septentrionalis
	Feltia jaculifera
	Fishia discors
	Hecatera dysodea
	Heliothodes phloxiphaga
	Homorthodes communis
	Homorthodes furfurata
	Hypocoena rufostrigata
	Lacinipolia acutipennis
	Lacinipolia comis
	Lacinipolia olivacea
	Lacinipolia pensilis
	Lacinipolia sareta
	Lacinipolia stricta
	Lacinipolia strigicollis
	Leucania farcta
	Litholomia napaea
	Lithophane dilatocula
	Mesogona olivata
	Mythimna oxygala
	Nedra stewarti
	Neoligia tonsa
	Nephelodes minians
	Noctua pronuba
	Oligia divesta
	Oligia rampartensis
	Orthodes noverca
	Orthodes obscura
	Orthosia hibisci
	Parabagrotis exsertistigma
	Parabagrotis insularis
	Parabagrotis sulinaris
	Pleromelloida bonuscula
	Pleromelloida conserta
	Polia piniae
	Ponometia semiflava
	Properigea albimacula
	(continued in next column)
Noctuidae	*Protolampra rufipectus*
	Protoperigea posticata
	Protoperigea umbricata
	Protorthodes curtica
	Protoschinia nuchalis
	Raphia frater
	Rhyacia clemens
	Schinia guarae
	Schinia oleagina
	Spaelotis bicava
	Spaelotis clandestina
	Spodoptera praefica
	Stretchia plusiiformis
	Sympistis parvanigra
	Sympistis stabilis
	Tarache areli
	Tholera americana
	Tyta luctuosa
	Ufeus satyricus
	Xestia c-nigrum
	Xestia infimatis
	Xylena cineritia
	Zotheca tranquilla
Nolidae	*Nycteola cinereana*
Notodontidae	*Datana ministra*
	Furcula cinerea
	Gluphisia septentrionis
	Gluphisia severa
	Oligocentria semirufescens
	Pheosia rimosa
	Schizura conspecta
	Schizura ipomaeae
Oecophoridae	*Agonopteryx spp.*
	Ethmia marmorata
Pyralidae	*Ambesa laetella*
	Dioryctria spp.
	Melitara subumbrella
	Pima fulvirugella
	Pyla ssp.
	Toripalpus trabalis
Saturniidae	*Antheraea polyphemus*
Sphingidae	*Hyles lineata*
	Pachysphinx occidentalis
	Paonias excaecatus
	Paonias myops
	(continued in next column)

Family	Species
Sphingidae	*Smerinthus ophthalmica* *Sphinx drupiferarum* *Sphinx vashti*
Tortricidae	*Choristoneura rosaceana* *Eana argentata* (continued in next column)
Tortricidae	*Pelochrista ?ridingsiana* *Pelochrista subflavana* *Pelochrista spp.* *Pelochrista subflavana*
Ypsolophidae	*Ypsolopha spp.*

Appendix E: Flowering Forbs and Shrubs at the Zumwalt Prairie Preserve, the Boardman Conservation Area, and Meadow Creek at the USFS Starkey Experimental Forest and Range

Blooming plant species found blooming on transects when pollinator studies were conducted at each of the three study locations: The Nature Conservancy's Zumwalt Prairie Preserve (Zumwalt), The Nature Conservancy's Boardman Conservation Area (Boardman), and at Meadow Creek in the USFS Starkey Experimental Forest and Range (Starkey). The number of years and sites of study at each location varied, with one year of data from 16 sites and two years of data from 30 sites at the Zumwalt, three years of data from 18 sites at Boardman and 6 years of data from 12 sites at Starkey.

Zumwalt (110 species)	**Boardman** (28 species)	**Starkey** (134 species)
Achillea millefolium	*Achillea millefolium*	*Achillea millefolium*
Agoseris glauca	*Aster* sp.	*Aconitum columbianum*
Agoseris heterophylla	*Astragalus* sp.	*Agastache urticifolia*
Allium acuminatum	*Calochortus macrocarpus*	*Agoseris glauca*
Allium fibrillum	*Centaurea diffusa*	*Allium acuminatum*
Allium tolmiei	*Centaurea solstitialis*	*Allium fibrillum*
Alyssum alyssoides	*Chondrilla juncea*	*Allium madidum*
Amsinckia menziesii	*Chrysothamnus viscidiflorus*	*Angelica arguta*
Antennaria anaphaloides	*Cirsium undulatum*	*Angelica canbyi*
Antennaria luzuloides	*Cirsium vulgare*	*Antennaria rosea*
Antennaria rosea	*Collinsia parviflora*	*Arabis holboellii*
Arenaria aculeata	*Conyza canadensis*	*Arenaria serpyllifolia*
Arenaria congesta	*Crepis atribarba*	*Arnica chamissonis*
Arnica sororia	*Descurainia pinnata*	*Arnica cordifolia*
Astragalus sheldonii	*Epilobium brachycarpum*	*Arnica sororia*
Balsamorhiza incana	*Ericameria nauseosa*	*Astragalus reventus*
Blepharipappus scaber	*Erigeron filifolius*	*Barbarea orthoceras*
Buglossoides arvensis	*Grindelia nana*	*Camassia quamash*
Calochortus eurycarpus	*Helianthus* sp.	*Camissonia subacaulis*
Camassia quamash	*Heterotheca villosa*	*Canadanthus modestus*
Camelina microcarpa	*Lactuca serriola*	*Castilleja cusickii*
Castilleja cusickii	*Linum lewisii*	*Castilleja lutescens*
Castilleja lutescens	*Machaeranthera canescens*	*Cerastium fontanum*
Castilleja tenuis	*Polygonum douglasii*	*Cerastium glomeratum*
Chrysothamnus viscidiflorus	*Salsola kali*	*Certica dioica*
Cirsium arvense	*Sisymbrium altissimum*	*Cirsium arvense*
Cirsium brevifolium	*Stephanomeria paniculata*	*Cirsium scariosum*
Cirsium vulgare	*Tragopogon dubius*	*Cirsium vulgare*
Clarkia pulchella		*Collinsia parviflora*
Clematis hirsutissima		*Collomia linearis*
Collinsia parviflora		*Crataegus douglasii*
Collomia linearis		*Delphinium depauperatum*

Zumwalt (continued)

Crepis spp.
Delphinium nuttallianum
Descurainia incana
Dianthus armeria
Draba verna
Epilobium brachycarpum
Erigeron chrysopsis
Erigeron corymbosus
Erigeron pumilus
Erigeron speciosus
Erigonum nudum
Eriogonum douglasii
Eriogonum heracleoides
Eriogonum strictum
Frasera albicaulis
Frasera speciosa
Galium boreale
Gentiana affinis
Geranium viscosissimum
Geum triflorum
Grindelia nana
Heuchera grossulariifolia
Hieracium cynoglossoides
Hypericum scouleri
Lactuca serriola
Linum lewisii
Lithophragma glabrum
Lithospermum ruderale
Lomatium cous
Lomatium triternatum
Lupinus caudatus
Lupinus leucophyllus
Lupinus sericeus
Lupinus spp.
Madia glomerata
Madia gracilis
Microseris nutans
Microsteris gracilis
Montia linearis
Myosotis stricta
Navarretia divaricata
Orthocarpus tenuifolius
Packera cana
Penstemon procerus
Perideridia gairdneri
Phlox hoodii
Phlox pulvinata

Starkey (Continued)

Descurainia sp.
Dianthus armeria
Dodecatheon pulchellum
Draba verna
Epilobium brachycarpum
Epilobium ciliatum
Erigeron speciosus
Eriogonum heracleoides
Eriophyllum lanatum
Erythronium grandiflorum
Fragaria vesca
Fragaria virginiana
Galium aparine
Galium boreale
Gentiana affinis
Gentianopsis simplex
Geum macrophyllum
Grindelia nana
Heracleum maximum
Horkelia fusca
Hydrophyllum capitatum
Hypericum anagalloides
Hypericum perforatum
Hypericum scouleri
Iris missouriensis
Lepidium campestre
Lithophragma glabrum
Lithophragma parviflorum
Lomatium ambiguum
Lomatium cous
Lomatium grayi
Lomatium macrocarpum
Lotus unifoliolatus
Madia glomerata
Madia gracilis
Maianthemum stellatum
Medicago lupulina
Mentha arvensis
Microsteris gracilis
Mimulus guttatus
Monardella odoratissima
Montia linearis
Myosotis stricta
Navarretia intertexta
Noccaea fendleri
Olsynium douglasii
Packera pseudaurea

Zumwalt (continued)

Phlox viscida
Polygonum douglasii
Polygonum polygaloides
Potentilla glandulosa
Potentilla gracilis
Potentilla recta
Pyrrocoma carthamoides
Rosa woodsii
Sagina decumbens
Saxifraga integrifolia
Sedum stenopetalum
Senecio integerrimus
Sidalcea oregana
Silene oregana
Silene scouleri
Silene spaldingii
Sisymbrium altissimum
Solidago missouriensis
Spergula arvensis
Stellaria longipes
Symphoricarpos albus
Taraxacum officinale
Tragopogon dubius
Trifolium hybridum
Trifolium macrocephalum
Triteleia grandiflora
Valeriana edulis
Veronica arvensis
Vicia villosa
Viola adunca
Zigadenus venenosus

Starkey (continued)

Penstemon procerus
Perideridia gairdneri
Platanthera dilatata
Polemonium occidentale
Polygonum bistortoides
Polygonum douglasii
Potentilla arguta
Potentilla glandulosa
Potentilla gracilis
Potentilla recta
Prunella vulgaris
Ranunculus glabierrimus
Ranunculus orthorhynchus
Ranunculus uncinatus
Ribes aureum
Ribes cereum
Ribes hudsonianum
Rosa nutkana
Rumex acetosella
Salix exigua
Sanguisorba canadensis
Saxifraga integrifolia
Saxifraga nidifica
Saxifraga oregona
Scutellaria angustifolia
Sedum stenopetalum
Senecio serra
Sidalcea oregana
Sisymbrium altissimum
Solidago missouriensis
Stellaria longipes
Symphoricarpos albus
Symphyotrichum eotonii
Symphyotrichum spathulatum
Taraxacum officinale
Thalictrum fendleri
Thermopsis montana
Thlaspi arvense
Tragopogon dubius
Trifolium eriocephalum
Trifolium plumosum
Trifolium pratense
Trifolium repens
Trifolium wormskioldii
Triteleia grandiflora
Urtica dioica
Valeriana dioica

Starkey (continued)
Veratrum californicum
Verbascum thapsus
Veronica americana
Veronica serpyllifolia
Vicia cracca
Viola adunca
Viola palustris
Viola vallicola