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# Pollinators of the Great Plains: Disturbances, Stressors, Management, and Research Needs

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ABSTRACT

Recent global declines of pollinator populations have highlighted the importance of pollinators, which are undervalued despite essential contributions to ecosystem services. To identify critical knowledge gaps about pollinators, we describe the state of knowledge about responses of pollinators and their foraging and nesting resources to historical natural disturbances and new stressors in Great Plains grasslands and riparian ecosystems. In addition, we also provide information about pollinator management and research needs to guide efforts to sustain pollinators and by extension, flowering vegetation, and other ecosystem services of grasslands. Although pollinator responses varied, pollinator specialists of disturbance-sensitive plants tended to decline in response to disturbance. Management with grazing and fire overall may benefit pollinators of grasslands, depending on many factors; however, we recommend habitat and population monitoring to assess outcomes of these disturbances on small, isolated pollinator populations. The influences and interactions of drought and increasingly variable weather patterns, pesticides, and domesticated bees on pollinators are complex and understudied. Nonetheless, habitat management and restoration can reduce effects of stressors and augment floral and nesting resources for pollinators. Research needs include expanding information about 1) the distribution, abundance, trends, and intraregional variability of most pollinator species; 2) floral and nesting resources critical to support pollinators; 3) implications of different rangeland management approaches; 4) effects of missing and reestablished resources in altered and restored vegetation; and 5) disentangling the relative influence of interacting disturbances and stressors on pollinator declines. Despite limited research in the Great Plains on many of these topics, consideration of pollinator populations and their habitat needs in management plans is critical now to reduce future pollinator declines and promote recovery.



## Introduction

Animal pollination is necessary for production of approximately 85% of flowering plant species (Klein et al. 2007; Ollerton et al. 2011). However, up to 40% of all pollinator species have declined globally during the past several decades due to a variety of factors including habitat destruction and degradation, pesticides, disease, and climate change (Winfree et al. 2009; Potts et al. 2010; IPBES 2016). In the Great Plains of the central United States (Fig. 1), a region dominated by rangelands and croplands, some pollinator species also have declined. For example, half of all bumble bee species in Illinois tallgrass prairies have been extirpated or contracted in range after large-scale agricultural intensification during 1940 to 1960 (Grixti et al. 2009), while tallgrass prairie-specialist

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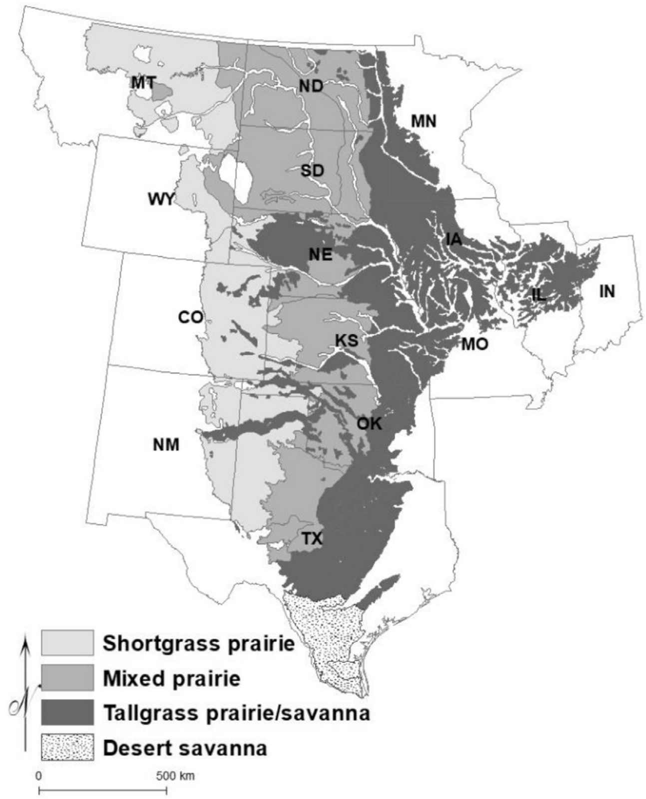


**Fig. 1.** General extent and ecosystem types of the Great Plains, modified from Kuchler et al. (1993).

**Table 1**
Examples of butterfly and bee species of concern in the Great Plains. Conservation status is relative to federal and state agencies and the International Union of Conservation of Nature (IUCN) Red List.

| Common name | Scientific name | Conservation status |
|---|---|---|
| Arogos skipper | *Atrytone arogos* | Endangered: IL<br>Threatened: MN<br>Species of concern: IA |
| Byssus skipper | *Problema byssus* | Threatened: IA |
| Dakota skipper | *Hesperia dacotae* | Endangered: IA<br>Threatened: USA, Canada, MN<br>Vulnerable: IUCN Red List |
| Ottoe skipper | *Hesperia ottoe* | Endangered: Canada |
| Regal fritillary | *Speyeria idalia* | Critically imperiled: CO, IN, OK<br>Imperiled: IA, IL, ND<br>Vulnerable: MN, MO, NE, SD, WY |
| American bumble bee | *Bombus pensylvanicus* | Vulnerable: IUCN Red List |
| Rusty patched bumble bee | *Bombus affinis* | Endangered: USA<br>Critically endangered: IUCN Red List |
| Southern Plains bumble bee | *Bombus fraternus* | Endangered: IUCN Red List |
| Variable cuckoo bumble bee | *Bombus variabilis* | Critically endangered: IUCN Red List |
| Yellow bumble bee | *Bombus fervidus* | Vulnerable: IUCN Red List |
| Yellow-banded bumble bee | *Bombus terricola* | Vulnerable: IUCN Red List |
| Western bumble bee | *Bombus occidentalis* | Vulnerable: IUCN Red List |

Source: Shepherd et al. 2005; NRC 2007; Hatfield et al. 2015; Lambe 2018.

butterfly species are now mostly confined to preserves (Swengel 1998; Swengel and Swengel 1999; Swengel et al. 2011). Numerous pollinator species of concern have been identified in the Great Plains, including many prairie-specialist butterflies and several bumble bee species (Table 1; Hatfield et al. 2012).

Multiple interacting factors are linked to pollinator declines, but drivers causing declines vary across regions (Winfree et al. 2009; Potts et al. 2010; Vanbergen et al. 2013; Koh et al. 2016; Fig. 2). Although grasses are the dominant biomass in the Great Plains, forbs (i.e., herbaceous flowering plants) contribute most to species richness and diversity and exhibit the greatest responses to environmental change (Glenn and Collins 1990; Howe 1994; Steuter et al. 1995). Settlement, agriculture, intensive grazing, urbanization and roads, and invasive plant species have diminished area and diversity of grasslands, particularly tallgrass prairie (> 95% loss; Steinauer and Collins 1996). Historical natural disturbances of herbivory, fire, and drought have been altered during the past century or more, potentially decreasing pollinator foraging and nesting resources. In addition to these disturbances, pollinators face stresses from climate change, pesticides, and non-native bees.

Given the importance of pollination and recent declines of some pollinators, a pressing need exists for region-specific information to guide rangeland management to support pollinators. Here, after a brief overview, we examine disturbances and stressors, management, and research needs. We summarize the current state of knowledge about responses of Great Plains pollinators and their resources in sections about herbivory and fire and about changed climate and drought, pesticide use, and introduction of non-native bees. We then examine the status of pollinators in riparian areas, which are unique ecosystems embedded in grasslands that may provide an abundance of different resources for pollinators, such as flowering shrubs, and review restoration

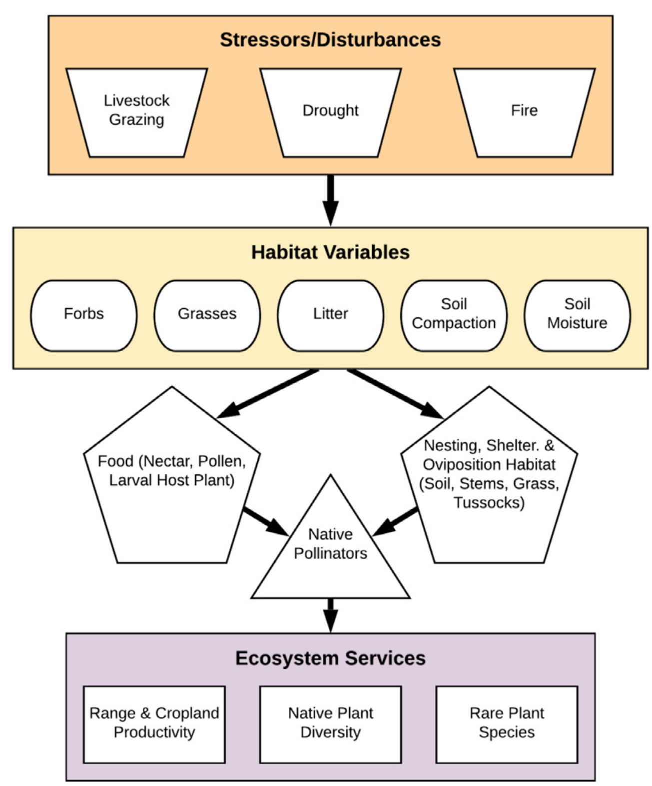


**Fig. 2.** Conceptual model of the effects of drought, livestock grazing, and fire on native pollinators and resources in Great Plains systems.

practices to restore degraded grasslands for pollinators. Although challenging given the lack of basic information about species distribution, abundance, and responses to disturbances for many species, effective pollinator management is key to conserving this valuable group and benefiting other wildlife species, biodiversity, and ecosystem resilience and resistance in Great Plains grasslands and other regions (McKnight et al. 2018).

## Overview of pollinators and resources in the Great Plains

Similar to many regions, distributions, abundances, and trends of most Great Plain pollinator species are generally unknown and information often is derived from uncoordinated, short-term, small-scale sampling focusing on bees and butterflies. Bee (Hymenoptera: Apoidea) communities of the Great Plains are diverse, with hundreds of species in some areas (summarized in table 6 of Kimoto et al. 2012a). Moth and butterfly (Lepidoptera) communities are also species rich, despite declines (Opler 1981; Johnson 1986; Panzer et al. 1995). Collinge et al. (2003) found that tallgrass prairie sites supported the greatest number of individuals and species of butterflies, whereas shortgrass prairie sites had the fewest individuals and species. In addition, at least eight beetle families, two fly families, and one wasp family contain species that have been identified as pollinators in Great Plains systems, with substantial contributions to maintaining native plant diversity (Travers et al. 2011). The diversity of pollinating taxa and their roles in pollination are likely underestimated due to limited research.

Bees are the most important pollinators in the Great Plains, followed by beetles, flies, and wasps, with butterflies and ants carrying the least pollen (Larson et al. 2018). Honey bees *(Apis mellifera)* are a major crop pollinator, but this domesticated species is not native to North America (Whitfield et al. 2006) and may play a more limited role in pollinating native plants while potentially benefitting reproduction of invasive nonnative plants (Barthell et al. 2001; Goulson 2003; Hatfield et al. 2018). Some moths and butterflies visit flowers primarily to feed on nectar and may have little direct contact with pollen (Larson et al. 2018), but other Lepidoptera contribute to native plant diversity. For example, several species of hawkmoths (Family Sphingidae) pollinate the threatened Great Plains white-fringed orchid (*Platanthera praeclara;* Travers et al. 2011; Fox et al. 2013). Among vertebrates, common bat species in the Great Plains are insectivorous and therefore do not contribute to pollination (Benedict et al. 1996), and the ruby-throated hummingbird (*Archilochus colubris*) is the only common pollinating bird species in the region.

Pollinators use diverse resources for feeding, nesting, overwintering, ovipositing, sheltering, and mating (see Fig. 2). Almost all pollinators require nectar or pollen, or both, as adults, and many species also consume pollen and nectar as larvae (bees) or feed on host plants as larvae (moths and butterflies). Pollinator feeding specificity for pollen, nectar, and host plants varies. Harmon et al. (2011) estimated about one-third of Great Plains native bee species are specialists regarding the family of plants they visit for pollen and two-thirds are generalists. Nesting sites are also diverse; more than 80% of North American bee species are estimated to nest in the ground, whereas other bees nest in wood, pithy stems, and grass tussocks (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; Cane et al. 2007, Harmon-Threatt 2020). While little is known about preferred sites for overwintering, these sites may be very different from foraging or nesting sites for pollinator 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).

## Herbivory, fire, and pollinators

Two major drivers in the evolution of Great Plains grasslands were herbivory and fire. Acting both individually and together, these disturbances shaped the development of Great Plains grassland systems and continue to influence present-day flora and fauna of the region. Understanding how each driver currently influences pollinators in systems that have been highly altered relative to historical conditions is key to developing effective conservation and management plans for pollinators.

Ungulate herbivory, particular grazing by 30–60 million bison, exerted a strong selective force on Great Plains vegetation, and plants in the region evolved characteristics that helped them withstand high grazing pressure (Mack and Thompson 1982; Milchunas et al. 1998; Gates et al. 2010). Dominant herbivores in the region are now livestock, primarily cattle (Derner et al. 2009). Because of the historical importance of bison and other ungulates in Great Plains grasslands, livestock grazing is a management tool often used to recreate the functional role of disturbance historically associated with bison (Steinauer and Collins 1996; Fuhlendorf and Engle 2001; Derner et al. 2009). Some of these roles may benefit pollinators, including increasing habitat heterogeneity and plant diversity that may result from selective feeding on grass, preferential grazing on recently burned areas, and patchy excrement deposition (Steinauer and Collins 1996; Hickman et al. 2004). Other effects of livestock may positively or negatively influence pollinators, including alteration of blooming flower abundance and diversity, physical structure of vegetation, soil characteristics, and microhabitat temperature and moisture (see Fig. 2; Fleischner 1994; DeBano 2006b; Kimoto et al. 2012b; Schmalz et al. 2013; Moranz et al. 2014; Buckles and Harmon-Threatt 2019).

It is unclear whether pollinator communities in systems that evolved with large herds of ungulate grazers are less sensitive to or benefit from livestock grazing compared with systems that evolved in their absence. While some studies conducted in areas with an evolutionary history that included large herds of ungulates have found positive or no effects of livestock grazing on pollinator diversity, others have found negative effects, including two studies of bees in the Great Plains (Kearns and Oliveras 2009; Buckles and Harmon-Threatt 2019; Table 2). Variation in responses suggests that livestock grazing effects on pollinator communities are modulated by a variety of factors beyond evolutionary history with large ungulate grazers, including type of grazers, grazing intensity and duration, plant and pollinator community composition, climate, and interactions with other disturbances (Kimoto et al. 2012b; Moranz et al. 2014). A more useful approach to understanding and managing grazing and Great Plains pollinators may be to focus less on community level responses and more on particular species that comprise pollinator communities of interest. Depending on life histories, even species within one community may respond positively or negatively or be unaffected by grazing. For example, Vogel et al. (2007) found responses of different butterfly species to grazing and fire in the Great Plains were highly variable, even within the same specialist guild.

Varying responses of pollinator species to grazing may be caused by differences in the dietary overlap between grazers and pollinators (Moranz et al. 2014; DeBano et al. 2016). For example, adults of the Dakota skipper *(Hesperia dacotae),* a federally listed Great Plains butterfly, prefer flower species that can be reduced or eliminated by cattle grazing and do not use other plant species that are typically avoided by cattle (e.g., some milkweeds, *Asclepias;* dogbane, *Apocynum;* McCabe 1981). Another Great Plains butterfly, the regal fritillary *(Speyeria idalia),* relies heavily on pale

**Table 2**
Summary of studies describing effects of grazing and fire on Great Plains pollinators.

| Disturbance | Taxa | Location | Effect |
|---|---|---|---|
| **Grazing** | | | |
| Buckles and Harmon-Threatt, 2019 | Native bees | Tallgrass prairie, MO | Decreased abundance and nesting[1] |
| Kearns and Oliveras, 2009 | Native bees | Shortgrass prairie, CO | Decreased abundance |
| **Fire** | | | |
| Decker and Harmon-Threatt, 2019 | Native bees | Tallgrass prairie, IL | Increased abundance[2] |
| Henderson et al., 2018 | Regal fritillary butterfly (*Speyeria idalia*) | Tallgrass prairie, WI | Positive long-term effect[3] |
| Panzer and Schwartz, 2000 | Butterflies | Tallgrass prairie, IL, IN, WI | Positive effect on abundance and species richness |
| Panzer, 2002 | Butterflies | Tallgrass prairie, IL, IN, WI | Variable |
| **Grazing and fire** | | | |
| Delaney et al., 2016 | Butterflies | Tallgrass prairie, MO, IA | Positive effect of fire and grazing for sites dominated by non-native vegetation[4] |
| McCabe, 1981 | Dakota skipper butterfly (*Hesperia dacotae*) | Tallgrass prairie, ND, MN | Both fire and grazing negative[5] |
| Moranz et al., 2012 | Butterflies | Tallgrass prairie, MO, IA | Variable[6] |
| Moranz et al., 2014 | Regal fritillary butterfly *(Speyeria idalia)* | Tallgrass prairie, MO | Higher butterfly densities at sites with rotational burning compared with sites recently burned and grazed[7] |
| Swengel et al., 2011 | Prairie-specialist butterflies | Tallgrass prairie, oldfields, and barrens, IA, IL, MN, WI | Fire has negative effect; grazing positive |
| Vogel et al., 2007 | Butterflies | Tallgrass prairie, IA | Variable[8] |

[1] Compared three treatments: 1) patch-burn grazed, 2) hayed, and 3) burned. Abundance and nesting were lower in recently patch-burn grazed and hayed plots relative to burned plots.

[2] While burned treatments had higher bee abundance than unburned treatments, growing season burns had higher bee abundance than dormant season burns.

[3] Fire had negative short-term effects, so authors stressed unburned refugia are critical to maintaining populations.

[4] Compared grasslands sites dominated by non-native plants that were either patch-burned/grazed (one-third of pasture burned each year and entire pasture exposed to cattle) or grazed-and-burned (entire pasture burned every 3 yr and grazed each year) with reference sites dominated by native vegetation. The authors compared community composition of sites exposed to both treatments for 7 yr to reference sites and found butterfly communities in treated areas became more similar to native sites. Only two butterfly species showed statistically significant linear responses through time, with *Pyrisitia lisa* decreasing with respect to abundance in reference sites through time and *Speyeria idalia* increasing.

[5] Based on personal observations.

[6] Compared two types of grazing-burning treatments with a burn-ungrazed treatment; two prairie specialists (*Cercyonis pegala* and *Speyeria idalia*) and one generalist *(Danaus plexippus)* had the highest density in the burn-ungrazed treatment, while the density of one generalist *(Cupido comyntas)* was highest in one of the grazing-burning treatments.

[7] Compared patch-burn/grazed (rotational burning with cattle grazing) vs. rotational burning without cattle. Butterfly density was lower at recently burned sites that were grazed compared with recently burned, ungrazed sites.

[8] Compared grazed-only, burned-only, and burned and grazed treatments. Found butterfly abundance was highest on burned and grazed sites and lowest on burned-only sites. Species diversity was highest on burned-only sites. Individual species responses were highly variable.

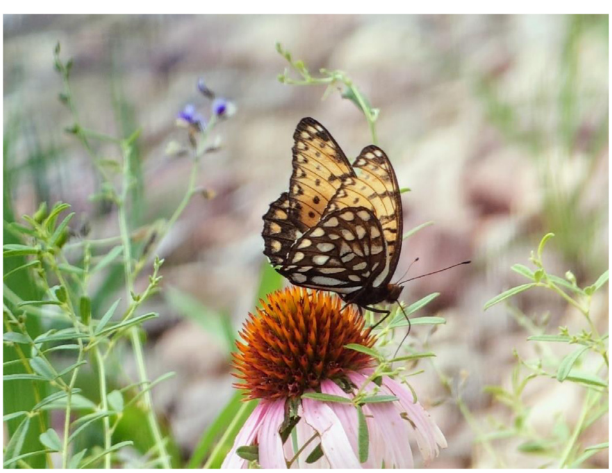

**Fig. 3.** The regal fritillary *(Speyeria idalia)* on pale purple coneflower *(Echinacea pallida)* during July in South Dakota. (Photograph courtesy of P. Hanberry.)

purple coneflower *(Echinacea pallida)* for nectar during June and July (Fig. 3). This coneflower is also frequently eaten by cattle, and the overlapping preference may be why, in one study, grazed areas had lower regal fritillary densities than ungrazed areas (Moranz et al. 2014; see Table 2). In contrast, if a specialist pollinator species with a narrow dietary breadth uses a plant species avoided by grazers, such as lupines *(Lupinus)* and milkvetches *(Astragalus)*, then grazing may not reduce food availability for the species. However, all plant species may be consumed at high stocking rates, even plants typically not preferred by livestock (Sugden 1985).

Pollinator species also respond to grazing-induced changes in nesting, sheltering, and ovipositing habitat. Livestock grazing effects on soils can have major impacts on bee communities, both directly by influencing nesting habitat and indirectly by altering vegetation. Buckles and Harmon-Threatt (2019) found that livestock grazing in a tallgrass prairie system was associated with higher soil moisture, lower soil temperature, and decreased bare ground. This last effect was possibly due to an altered plant community and the spread of invasive grasses, which were associated with decreased nesting by bees. Other studies outside of the Great Plains suggest that many ground-nesting bees prefer bare ground for nesting (Potts and Willmer 1997, 1998; Potts et al. 2005; Vulliamy et al. 2006; Harmon-Threatt 2020). Conversely, butterflies, male bees, and other pollinators often use shelters in stems, flowers, grass structure, brush piles, and leaf litter to escape unfavorable weather, and thus loss of physical structure may negatively affect them. Likewise, butterflies that oviposit in plants, especially prairie-specialists, can be particularly sensitive to grazing-induced changes in physical structure, with some specialist species preferring either taller or shorter vegetation (Vogel et al. 2007). However, at very high stocking rates, removal of most plant material may negatively affect even those species that prefer shorter-statured grasses, and intensive grazing has the added risk of increasing mortality through livestock consumption of oviposited eggs.

As with herbivory, reoccurring fire played a key role in the development and maintenance of Great Plains herbaceous plant communities and their associated pollinators (Samson et al. 2004). Historically, fire intervals may have ranged from 1 to 5 yr, preventing encroachment of woody vegetation into grasslands, but due to fire exclusion, currently only 0.1–2.0% of grasslands burn each year on public lands managed by the US Forest Service in the northern Great Plains (Samson et al. 2004). Tallgrass prairie remnants are often burned on a 2- to 5-yr rotation, with 20–50% of the area burned per site (Swengel 1998). Fire's effect on floral resources used by pollinators varies relative to fire characteristics, such as extent, severity, and timing, and will change through time post-fire (Moranz et al. 2014; see Fig. 2). Work in other regions has shown that pollinator diversity and richness can peak after fire with increased forb abundance and/or richness and then steadily decrease with time, in response to plant community change (e.g., Potts et al. 2003b). Fire also can enhance habitat for some species by increasing bare ground or aboveground-nesting resources, such as charred wood (see Fig. 2; Potts et al. 2003b; Decker and Harmon-Threatt 2019; Smith DiCarlo et al. 2019). For some specialist species, fire may be necessary to maintain flowering plant density (Henderson et al. 2018). Nevertheless, fire may no longer be beneficial in certain circumstances, and nonfire alternatives may be preferable for some species where current conditions may be too altered due to changes in vegetation and small patch size of remnant prairies (e.g., McCabe 1981; Opler 1981; Panzer 1988; Swengel 1998; Panzer and Schwartz 2000; Swengel et al. 2011; Symstad and Leis 2017). The extent and timing of fire influence pollinator response (Moranz et al. 2014). For example, if a small prairie is burned in the spring in its entirety, spatial and temporal refuges will be limited compared with burning a fraction during the dormant season.

Studies and reviews of fire effects on Great Plains pollinators show varied responses by species, family, and order, with few definitive trends (see Table 2; see also Reed 1997 for a wide range of insect response). Butterflies have received the most attention. Several Great Plains studies suggest that fire may increase the density and diversity of flowering plants, at least in the short-term, including species crucial to butterfly specialists, and lead to increases in the density of butterflies (Moranz et al. 2014; Henderson et al. 2018). However, some prairie specialist butterflies may be negatively affected by frequent burning in tallgrass prairie remnants (Swengel et al. 2011 and references therein). While Swengel et al. (2011) concluded that many tallgrass prairie butterfly specialists are not adapted to current fire regimes, Vogel et al. (2007) concluded that differential butterfly responses to fire are not explained by the degree of habitat specialization, but rather a combination of natural history characteristics, including type of overwintering sites or location of host plants.

While comparatively little work has been conducted on the effect of fire on native bees in the Great Plains, Decker and Harmon-Threatt (2019) concluded that fire may benefit bees in tallgrass prairies. They found that tallgrass prairie exposed to growing and dormant-season fire had higher overall bee abundance relative to unburned sites, with sites exposed to growing season burns having the highest bee abundance. Burned sites had more bare ground but did not differ in characteristics of plant communities, suggesting increased nesting sites may be responsible for increased bee abundance. Work outside the Great Plains also suggests that bee community responses to grassland fire may be partially driven by increased nesting habitat for ground-nesting bees (Smith DiCarlo et al. 2019). A meta-analysis of the effects of different factors on bee communities at a global scale found that fire did not have a significant impact on abundance or richness (Winfree et al. 2009), but the small number of studies on fire and bees limited the statistical power to detect differences (Potts et al. 2010).

The variety of observed responses of pollinators to fire may be due to differences in attributes of the fire (e.g., duration, severity, seasonal timing, return interval intensity, depth of heat penetration into the soil), geographic location, grassland area (i.e., fragmentation), and characteristics of the plant and pollinator communities (e.g., species composition and their fire tolerance, population size and connectivity, colonizing ability, and life histories). Thus, as with grazing, one approach to understanding fire effects on Great Plains pollinators is to examine underlying mechanisms (i.e., how fire alters key environmental variables; see Fig. 2) or results in direct mortality, coupled with life history information about pollinator species in an area of interest. For example, a pollinator's vulnerability to injury or death is partially a function of its location (e.g., foraging, in a nest), stage of development, and life history (DeBano et al. 1998; Love and Cane 2016; Swengel 2001). Low temperatures and patchy patterns of grassland fires may leave undamaged basal portions of plants that provide protection from fire (Fig. 4; Hill et al. 2017 in Washington prairies). Some invertebrates may shelter from fire in soil holes and depressions, and in different ground substrates such as rocks, coarse plant debris, wetlands, and bison wallows. Bees that build shallow nests in the ground or aboveground nests are at a greater risk of mortality than species that nest deeper in the soil (Cane and Neff 2011). Direct mortality due to fire exposure for adults may be rare because they can leave or, for bees, take refuge in nests (Potts et al. 2003a; Cane and Neff 2011), although Swengel (2001) suggests that most aboveground insects that are present in vegetation die in fires. Immature stages (eggs, larvae, pupae) of invertebrate pollinators are less mobile and more vulnerable to fire (Reed 1997). Prairie skippers may show low mortality to early-season fire, when larvae are in burrows, but later fires can cause greater mortality because as larvae mature, they move to shelters on the soil surface (Reed 1997). Some pollinator populations in the Great Plains that decline in the months to years following fire (Swengel 2001) recover to preburn levels within 2–6 yr (Reed 1997; Panzer 2002; Vogel et al. 2010). Small populations of rare species in isolated remnants are particularly vulnerable to local extinction and may require extended time to rebuild numbers after fire in burned units (McCabe 1981).

*Management*

Despite a lack of information about the response of many Great Plains pollinators to livestock grazing, grazing may be a beneficial tool in Great Plains range management for some pollinators. For example, prairie-specialist butterfly species of the Great Plains depend on open habitats and may respond more positively to grazing and mowing than to fire as a way to prevent invasion by woody plants (Swengel et al. 2011). However, best livestock management for pollinators should consider both temporal and spatial scales. Historically, large areas of grasslands were not grazed by herds of herbivores in any given year, thus providing patches of intact habitat for species that do not tolerate intensely grazed conditions (Fuhlendorf and Engle 2001). Overgrazing in large areas and for prolonged periods will remove excessive amounts of floral resources and vegetation physical structure and increase the likelihood of direct mortality of pollinators through trampling and consumption of lepidopteran eggs deposited in plants. The spatial and temporal scales of livestock grazing may be adjusted depending on the life history and flight abilities of local pollinators. One strategy to reduce the likelihood of overgrazing is to focus on utilization rates of forbs and host plants rather than stocking rates, as the same stocking can result in different grazing pressure depending on area, weather, and other disturbances (Allison 1985).

**Fig. 4.** Surface fire is often light and patchy, leaving both unburned areas and herbaceous plant bases. Images from the Legion Lake fire in Custer State Park, South Dakota that burned 218 km$^2$ during December 2017. By April 2018, no evidence of fire was present except for scorched trees due to vegetation re-growth. (Photographs courtesy of P. Hanberry.)

Fire is a useful tool in the Great Plains for maintaining grasslands and grassland-dependent species, and most negative short-term effects of burning may be ameliorated by long-term benefits of maintaining high-quality grassland habitat and enhancing native plant species (Panzer 1988; Hartley et al. 2007; Symstad and Leis 2017). No management or disturbance favors all species, but because fire is a historical part of grassland ecosystems, many grassland pollinators may be able to tolerate fire and benefit from maintenance of grassland ecosystems by fire (particularly grassland specialists). However, determining whether management is optimal for pollinators also should be based on monitoring pollinator species rather than solely based on vegetation responses. Swengel et al. (2011) found that in preserves that applied management involving fire, butterfly species of conservation concern declined more than in areas that did not use the approach. In these cases, species-specific management that incorporates pollinator life history traits and responses of specific plants and pollinators to fire to inform management is preferable to assuming certain responses to fire based on the species association with a particular ecosystem (Swengel 2001). As not all communities respond similarly to wildfire due to geographic location, grassland area and population fragmentation, timing of sampling (short-term vs. long-term), and other fire-related factors, monitoring should be conducted at a suitably broad spatial scale and at both short- and long-term intervals.

In cases where fire is deemed suitable, managers must determine the appropriate frequency. While historical fire regimes may provide some guidance about how frequently to burn, the more that grasslands have been fragmented and degraded, the less relevant historical fire regimes become in determining frequencies for management. Variable burn cycles of 3–10 yr or longer, depending on pollinator recovery time, may support pollinators better than annual or biennial burns, particularly on fragmented grasslands. Preferably, adjacent unburned units also will be at a recovery point after fire to provide enough individuals to reestablish populations. For example, if mean fire frequency is 10 yr, then sites adjacent to a burn treatment can be maintained approximately at 5 yr post fire. Although generalist grassland butterfly species may be less sensitive to regularly occurring fire, single, occasional wildfires may be better for specialists than regular rotational burning (Swengel 1998).

Area of burn units will vary on the basis of the objectives of restoration of degraded grasslands versus maintenance of grasslands, total management area, conditions of surrounding land, pollinator species present, and nectar and host plant distribution. Retention of unburned areas as refugia is critical, particularly for species of conservation concern. Managers should plan conservatively, by assuming 100% mortality of pollinators in the burn unit (Moffat and McPhillips 1993). Swengel et al. (2011) advise protecting at least 20% of a site from fire and only using fire at small sites (<5 ha) in unusual circumstances, with careful monitoring. However, in degraded grasslands, with few inventoried grassland species of concern and with extensive woody encroachment, the best use of resources may entail frequent, nearly complete burns to restore plant species (Reed 1997; Symstad and Leis 2017).

Finally, managers should consider how fire interacts with other disturbances. Fire and grazing are not independent disturbances in grasslands, particularly in the past when large herbivores such as bison were free-ranging. Vegetation regrowth post fire attracts most herbivores, increasing grazing intensity ("pyric herbivory"; Fuhlendorf et al. 2009). Pyric herbivory or patch-burn grazing can result in landscapes of shifting mosaics of burned-grazed areas interspersed with unburned–lightly grazed areas. The spatial and temporal heterogeneity produced in plant height may benefit invertebrates relative to more homogenous use of livestock in the absence of fire (Engle et al. 2008). However, Moranz et al. (2012) found that butterfly species richness did not vary between plots that were only burned and plots exposed to two types of burning and grazing treatments. The authors suggest that historical overgrazing combined with heavy grazing may not generate structural heterogeneity under coupled patch-burn grazing management (Moranz et al. 2012). The few other studies of grazing and fire in the Great Plains have shown varied results (see Table 2).

*Research needs*

While existing research about grazing and fire effects on pollinators for the Great Plains has helped to formulate general guidelines for management, more research is needed to inform management given the variability in Great Plains habitat types and pollinator diversity. Although butterflies have been most thoroughly studied, followed by bees, even these groups have been examined in relatively few Great Plains habitats (see Table 2). Numerous studies have demonstrated the danger of generalizing responses to disturbances or stressors and management for one group of pollinators to others (e.g., DeBano 2006a; Davis et al. 2008; Sjödin et al. 2008). In addition, grazing and fire may interact in ways that are not necessarily predictable based on knowledge of each individual disturbance alone (Wisdom et al. 2006). While research on pyric herbivory management approaches on Great Plains pollinators is growing (see Table 2), efforts should be expanded to include more focal taxa and habitat and to examine how past land uses and current conditions influence the effectiveness of these approaches (Swengel et al, 2011). For example, it is unclear whether reintroducing fire and grazing in systems dominated by non-native species will be sufficient to improve habitat for pollinators. Moranz et al. (2012) suggested that historical land use that reduced native plant cover and increased non-native plant cover superseded effects related to fire and grazing treatments, and that restoring native plants may be equally important as reintroducing historical disturbances. In contrast, Delaney et al. (2016) found evidence that both fire and grazing treatments applied to highly invaded grasslands over 7 yr resulted in butterfly communities becoming more similar to those found in native prairies.

## Climate change and drought, pesticides, domesticated bees, and pollinators

In addition to alterations in historical disturbances of fire and grazing, pollinators are facing relatively new stressors, including climate change. Climate change includes warming temperatures, increasing precipitation variability within and among years, and shifting precipitation timing (Finch et al. 2016). These changes result in not only more drought (including frequent flash droughts, or a rapid intensification to drier conditions over a period of weeks to months; Finch et al. 2016), but also increased floods, more late frosts, reduced duration of snow cover, and potentially more freeze-thaw cycles that may impact growth, survival, and reproduction of pollinators and their plant-based resources and predators (Bale et al. 2002; Bale and Hayward 2010). Warming may have direct physiological impacts related to upper thermal tolerances and metabolism (Deutsch et al. 2008). Varying temperature and precipitation may reduce quantity or quality of flower and nectar resources for pollinators (Thomson 2016; Ogilvie et al. 2017).

Warming temperatures may affect pollinators through differential range shifts or phenologies that disrupt plant-pollinator relationships in space or time. Kerr et al. (2015) detected failure of bumble bees to shift in range with warming at northern range limits, although perhaps due in part to similar failure to migrate by plants. Therefore, suitable resources may not be available north of the current range of some Great Plains pollinators and nectar corridors or stopping points of plant resources that facilitate movement may be absent. In many species of plants and insect pollinators, development responds to growing degree days, a measure of heat accumulation. Warming may lead to asynchrony between flowering and pollination when plant and pollinator phenologies change at different rates or plant-pollinator pairs use different cues (e.g., if pollinators respond to temperature while early spring flowering plants respond to snow melt). While studies of some species suggest that the timing of plant flowering and insect emergence have remained synchronous as temperatures have increased in recent decades (Bartomeus et al. 2011), phenological responses to warming temperature are variable across species and the magnitude of future disruption on plant-pollinator communities as a result of phenological change remains unknown (Rafferty and Ives 2011).

Recent shifts in climatic patterns during the past decades have resulted in increased precipitation in the northern Great Plains and decreased precipitation in the southern Great Plains (Finch et al. 2016), affecting the frequency and duration of drought, a disturbance in the Great Plains. Drought, a moisture deficit on the landscape with consequent effects on natural resources, occurs relatively frequently in the Great Plains due to the naturally low (<75 cm on average) and variable precipitation levels in this region (Finch et al. 2016). Drought is considered a major threat to the abundance and diversity of pollinator communities (Brown et al. 2016). Drought-induced physiological stress or mortality of vegetation can reduce the quality and quantity of floral resources available to pollinators and the ability of pollinators to locate floral resources within the landscape (e.g., Halpern et al. 2010; Gallagher and Campbell 2017). Reductions in the quality and availability of pollinators' food resources, or in their ability to locate such resources, ultimately can lead to population declines (e.g., Roulston and Goodell 2011; Baude et al. 2016; Carvell et al. 2017) in butterflies (Ehrlich et al. 1980; WallisDeVries et al. 2011; Robinson et al. 2012; Oliver et al. 2015) and bees (Minckley et al. 2013; Thomson 2016). Studies of pollinator community diversity during droughts in nonarid environments have shown that pollinators specialized to feed on drought-sensitive plants are more likely to decline than generalist species, shifting communities toward a greater proportion of widespread generalist species and fewer specialists (Gutbrodt et al. 2011; WallisDeVries et al. 2011; Settele et al. 2016; DePalma et al. 2017). In arid and semiarid environments, specialist species may respond to low growing season moisture cues by remaining in diapause (Minckley et al. 2013), thereby potentially avoiding unfavorable conditions and food shortages. Soil moisture deficits may negatively affect the quality of nesting and oviposition sites. Studies of ground-nesting and dwelling invertebrates have shown that low soil moisture levels can inhibit the development of eggs and larvae and reduce their survival rates (Ellis et al. 2004; Staley et al. 2007).

Another stressor faced by pollinators of the Great Plains is exposure to toxic chemicals. Insecticides, along with other pesticides, may be directly toxic or reduce survival and reproduction of pollinators in the Great Plains and elsewhere. Neonicotinoids, organophosphates, pyrethrins, phenylpyrazoles, and carbamates are broad-spectrum insecticides that generally target insect nervous or muscular systems. Pollinators are exposed to a range of agrochemicals in grasslands due to a matrix of croplands in the eastern Great Plains and embedded agricultural fields in wetter areas of the western Great Plains (e.g., Otto et al. 2016). For example, 12 pesticides and degradates were detected in 54 samples of native bee tissue in Colorado grasslands near wheat fields (Hladik et al. 2016). Herbicides are also used for control of non-native species or nonforage species, including roadside applications. In addition to agricultural and residential use of pesticides, municipalities in the Great Plains and elsewhere often have mosquito and tick abatement programs, with the potential to harm native insect pollinators (Ginsberg et al. 2017).

The Environmental Protection Agency assigns Toxicity Categories I and II for toxic pesticides to honey bees, although other pollinator species will have different sensitivities (Hooven et al. 2016). Synergistic effects of pesticides on pollinators caused by chemical interactions generally have not been evaluated (Goulson et al. 2015). Inert ingredients of pesticides also may interact with active ingredients, increasing toxicity (Cox and Surgan 2006) or potentially be more toxic than the active ingredient (Zhu et al. 2014). Neurotoxic insecticides can have sublethal effects on pollinating insects including cognitive impairment leading to reduced foraging and homing success and immune suppression that may increase susceptibility to disease and parasites (Hladik et al. 2016).

Among non-native bees, honey bees were introduced to North America in the early 1600s (Whitfield et al. 2006). North Dakota, South Dakota, Minnesota, Montana, and Texas are five of the top seven US state producers of honey (ERS 2018). Although historical effects of non-native bees on native bees are not known, non-native bees may have brought new diseases to North America. Recent declines in North American wild bees are due partially to diseases, such as the fungal pathogen *Nosema bombi* and *Varroa destructor* mite and the deformed wing virus, that can be carried by imported commercial bumble bees; honey bees also can infect native bees with diseases and shared floral resources may be an important route for transmission (Graystock et al. 2016; Alger et al. 2019). Competition for limited resources may occur between non-native bees and native bees, with honey bees outcompeting native bees (53% of 78 studies, Mallinger et al. 2017; Cane and Tepedino 2017; Hatfield et al. 2018). Even though non-native bees may continue to limit the populations of native pollinators, non-native bees appear to favor non-native plants, and enhancing native plant resources may help reduce competition (Otto et al. 2017).

Interactions among changing climate and variable weather, competition from non-native bees, pathogens, and pesticide stressors are likely to impact pollinators of the Great Plains, compounded by synergistic effects due to nutritional stress from limited floral resources, intensive grazing, agriculture, fire, and drought (Vanbergen et al. 2013). Well-nourished bees may be more resistant to insecticides and diseases; where food resources are poor, insecticides depress the immune system, leading to infection, which requires increased food consumption, resulting in greater exposure to insecticides (Goulson et al. 2015).

### *Management*

Several types of management actions that can help mitigate many of these stressors have been identified. Maintaining floral resources throughout the growing season may help reduce climate change and drought effects, and providing additional resources north of current ranges may assist range shifts. Habitat restoration that lessens fragmentation may reduce the magnitude of pollinator population decreases in response to climate change and extreme drought events and aid in the recovery and resilience of pollinator communities (Oliver et al. 2013, 2015; Oliver and Morecroft 2014). Planting strips of drought-tolerant plants (Brown et al. 2016), such as perennial plants with deep root systems, or restoring habitat to ensure diverse flowering plant communities (Mallinger et al. 2016) may help mitigate drought effects and ensure production of floral resources during drought conditions. Reducing stocking rates of livestock during drought may help increase plant community resistance and resilience, as plants that have been overgrazed or cropped too frequently are less able to recover after drought (Hart and Carpenter 2005). Protection of topographical diversity (such as north-facing slopes) and wetlands may provide more refugia for drought-sensitive species (Oliver et al. 2010, 2013; Oliver and Morecroft 2014; Warriner and Hutchens 2016).

Best management practices for pesticide applications include integrated pest management that incorporates nonchemical control methods to reduce insecticide application and avoiding bee-toxic pesticides (Hooven et al. 2016; McKnight et al. 2018). Applications should occur when pollinators are not actively foraging (e.g., late in day) and should avoid flowers. Granules are preferable to liquids, but dust and powder formulations are most hazardous because they are similar in size to pollen and stick to bee hairs. Targeting infested areas and limiting drift of sprays and pesticide-coated seed dust can also decrease pollinator exposure (Nuyttens et al. 2013). Many herbicides, including 2,4-D and dicamba, produce drift-related damage to nontarget vegetation (NDSU 2018). Cool and wet conditions may increase duration of toxicity (McKnight et al. 2018). After herbicide application for non-native plant control, restoration with desired native plant species may be necessary to prevent another round of herbicide application.

One management approach to reduce negative effects of honey bees on native bees is creation of more habitat with diverse native plant species flowering at different times, which may reduce the risk of disease transfer at concentrated sites with shared floral resources and competition for scarce resources from honey bees. Land managers may consider restricting exposure of grasslands with high quality and quantity of native floral resources to commercial honeybee hives, due to competition for limited resources and prevalence of disease (Goulson and Hughes 2015; Hatfield et al. 2018; McKnight et al. 2018). Croplands are avoided by commercial beekeepers (Otto et al. 2016), but apiaries could be located in restored, seminatural lands (Otto et al. 2017). Although direct causal relationships for health issues resulting from exposure to non-native bees are difficult to establish, rapid decline of native bees in many areas suggests a range of precautionary responses to prevent disease (Goulson and Hughes 2015; Hatfield et al. 2018). Moreover, although wild bees contribute to crop pollination and also must compete with commercial bees in agricultural settings, increasing forage opportunities for honey bees in managed agricultural lands may reduce pressure on wild bees in natural areas (Wojcik et al. 2018), particularly given that rapid conversion of rangelands to biofuel crops has resulted in less pollinator habitat in the northern Great Plains (Otto et al. 2016).

### *Research needs*

Response of pollinator communities to drought remains relatively little studied (Minckley et al. 2013), particularly in the Great Plains. Research needs also include determining specific influences of pesticides, domesticated bees and pathogens, increasingly variable weather patterns, and warming temperatures on pollinators. Additionally, examination of multiple interactions and identification of the importance of each stressor for insect declines are areas of needed research.

## Riparian areas—pollinator habitat of special concern

Riparian areas represent an ecological transition at the interface between upland terrestrial ecosystems and streams or other bodies of water. Before Euro-American settlement, riparian areas in some parts of the Great Plains were forested by various species of deciduous trees, particularly cottonwood and willow (*Populus-Salix;* Johnson and Boettcher 2000; conversely, see Currier and Davis 2000) and numerous flowering shrubs and wildflowers (Ripple and Beschta 2007). Although riparian areas, and wetlands in general, typically represent a small percentage of landscapes, they are disproportionately productive and contain distinctive vegetation and wildlife communities, including pollinators (Johnson and Boettcher 2000; Hoover et al. 2001; Williams 2011; DeBano et al. 2016). Holloway and Barclay (2000) found that insect abundance tends to be greater along rivers in the Great Plains. For example, lepidopteran richness in woody riparian areas of prairie provinces in Canada was found to be greater than that in adjacent upland areas because the community includes *Populus*-feeding species, as well as some specialists (Pohl et al. 2014).

Relatively little work has examined the importance of riparian areas to insect pollinators in general (DeBano and Wooster 2003; Williams 2011; DeBano et al. 2016) or in the Great Plains, specifically (Pohl et al. 2014); however, patterns observed elsewhere likely apply to riparian systems of the Great Plains. Vegetation and abiotic conditions associated with riparian areas may enhance Great Plains pollinator diversity by providing a greater range of food, nesting, or mating habitat. Riparian areas may provide thermal refuges for larger species, like bumble bees, which can overheat in high summer temperatures (Heinrich 1975, 2004). Flowering shrubs, including those that are primarily wind-pollinated (e.g.,

**Fig. 5.** Bee feeding on willow. (Photograph courtesy of S. Mitchell.)

some species of willows, Fig. 5), are important pollen and nectar sources for foraging insect pollinators (Pendleton et al. 2011; Ostaff et al. 2015). Flowering diversity in riparian or other wooded areas embedded in grasslands may be bolstered by an increase in forbs that are either adapted to shaded and/or moist conditions or may persist later in the season than in surrounding grasslands because of cooler, moister conditions (Gonzalez et al. 2013). Given the rarity of wood in most Great Plains environments, wooded riparian areas provide nesting resources for some pollinators, including many species of orchard and mason bees (Roof and DeBano 2016). Woody vegetation also aids some pollinator species in mate location; for example, males of some bumble bee species locate females by scent-marking landmarks, such as trees or hedgerows.

Riparian areas in the Great Plains have been adversely affected by a variety of human activities, including conversion to agriculture and other land uses and degradation by altered hydrology, timber harvest, exotic species invasion, and overuse by native ungulates and livestock (Hoover et al. 2001; Ripple and Beschta 2007). Restoration of riparian areas is a high priority throughout the nation, including in the Great Plains. Various forms of assistance are available to private landowners to enhance riparian buffers on agricultural lands. Restoration efforts can employ a range of methods, from fencing to exclude ungulates and livestock, including use of downed trees to reduce access, to active vegetation management. For example, shrub species (e.g., willows, *Salix* spp.; snowberry, *Symphoricarpos* spp.; currants, *Ribes* spp.) can be planted by land managers in riparian restoration projects to benefit stream health and wildlife.

Riparian restoration may involve both removal of non-native invasive species and the active planting of desired species. Some work suggests that native plants benefit pollinators (Fargione and Tilman 2005; Maron and Marler 2007; Morandin and Kremen 2013; Palladini 2013). For example, Fiedler et al. (2012) found bee and butterfly abundance and diversity in restored plots were similar to reference plots and distinct from invaded plots during the first growing season following removal of invasive glossy buckthorn (*Frangula alnus* L.) from a prairie fen wetland in Michigan. Pendleton et al. (2011) found that willows harbored more species of bees and Lepidoptera compared to non-native shrubs (e.g., tamarisk, *Tamarix*, Russian olive, *Eleagnus angustifoloia*), and Haunla and Horn (2011a, b) showed that removing non-native shrubs can improve habitat for pollinators. However, a lack of consensus persists about the overall effects of non-native plants in riparian areas (Salisbury et al. 2015; Albrecht et al. 2016), with some studies suggesting that introduced plants are equally or more attractive to many bees and may have a neutral or even positive effect on native bee abundance and diversity (Tepedino et al. 2008; Roof et al. 2018). Introduced plant species may extend the flowering season and provide more foraging options for late-season bees (Salisbury et al. 2015). Thus, managers must carefully balance the risks associated with planting, or failing to remove, non-native plants in riparian areas with any potential benefits provided to pollinators in the form of increased food, nesting habitat, or mating areas.

Few studies have evaluated the success of riparian restoration efforts on pollinators. One Great Plains study (Nelson and Wydoski 2008) found that non-native shrub removal alone was ineffective in restoring habitat in ways that benefit pollinators; specifically, *Tamarix* removal efforts did not improve riparian habitat for butterflies, possibly because restoration also must enhance herbaceous plant richness, nectar resources, and larval host plants to be successful for butterflies. Work outside of the Great Plains suggests that successfully restoring riparian areas for pollinators should take into account not only flowering plant abundance, species richness, and composition but also the physical structure of plants and soil cover, which may influence microclimate and the availability of nesting sites (Fleishman et al. 1999; Williams 2011; Trathnigg and Phillips 2015).

## Habitat restoration to benefit pollinators

Habitat loss and degradation, including replacement of native plants with non-native species, have affected pollinator abundance and richness in the Great Plains (Kwaiser and Hendrix 2008; Farhat et al. 2014; Otto et al. 2017; Kral-O'Brien et al. 2019) and globally (Stout and Morales 2009). Restoration can help reverse this loss and degradation by recreating heterogeneous and diverse plant communities in Great Plains grasslands that support a variety of taxa, including pollinators, and accommodate a broad set of insect needs and life histories, including food plants, nesting substrates, and landscape context and connectivity (Fuhlendorf and Engle 2001; Harmon-Threatt and Chin 2016; Denning and Foster 2018; Tonietto and Larkin 2018). Restoration practices often involve short-term but intense disturbance (e.g., fire, flash grazing, herbicides, solarization) that removes existing vegetation, thereby creating openings that provide opportunities for seedling establishment (Black et al. 2011; Harmon-Threatt and Chin 2016). Immediate, short-term negative impacts of intensive vegetation-clearing practices on pollinators can be mitigated by treating only a portion (e.g., one-third) of a site in any given year, thereby giving invertebrate pollinators a refuge (McKnight et al. 2018). Active replanting with preferred native species is recommended to prevent a cycle of treatment followed by reestablishment of the same undesired species. Slower amendments such as carbon addition in the form of wood chips or biochar may help improve restoration success (Blumenthal et al. 2003; Adams et al. 2013).

Herbicides can be effective as a restoration treatment for killing unwanted vegetation in rangelands. However, herbicide application reduces food supplies and nesting resources (McKnight et al. 2018). Although effects are generally short-lived, herbicides differ substantially in their longevity in the environment, especially in the soil. For example, certain chemicals persisting in the soil can negatively affect ground-nesting bee populations (Kopit and Pitts-Singer 2018), and even nonlethal doses of glyphosate can interfere with the ability of honey bees to navigate (Balbuena et al. 2015).

Mechanical disturbances, such as mowing, haying, or tilling, are often applied for habitat restoration in rangelands. Short-term negative impacts include direct mortality of egg and larval stages and reduction of flower abundance and diversity, but longer-term benefits include suppression of woody growth and thus promotion of open habitats suitable for pollinators (Black et al. 2011). Like fire, effects of mechanical disturbance on pollinators will vary with frequency and timing, location, ecosystem, and the taxa of pollinators in question (Smart et al. 2013; Prevéy et al. 2014; Harmon-Threatt and Chin 2016). However, a meta-analysis on habitat restoration effects on wild bees found that mowing had an overall positive effect on wild bee abundance (Tonietto and Larkin 2018).

Removing vegetation to create openings for preferred plant establishment may be insufficient to prevent establishment of unwanted species in degraded grasslands with a high percentage of non-native species. For habitat restoration to be effective for pollinators, native plants may need to be reintroduced to occupy openings, consequently resisting invasive species encroachment. In grassland systems with limited species richness, seeding or planting plugs may also be necessary to increase plant diversity (Stanley et al. 2011). Flowering plants ideally should be available during the full active period of pollinators, with overlapping bloom times. A diverse range of plants supplies continuous blooms and will better match pollinator shape, size, and color preferences, compared with mass-flowering of one flower type by single, dominant plant species (McKnight et al. 2018). Seed mixes for restoration often include the most common commercially available species, but better options are composed of a high diversity of species to increase long-term suitability of the restored habitat for flower visitors and include host plants that support imperiled or specialist butterflies (e.g., *Viola* and *Asclepias;* Havens and Vitt 2016). Recent research by Harmon-Threatt and Hendrix (2015) showed that commercially available seed mixes in the Great Plains can restore functioning habitat for potential pollinator communities, but diversity of bee species supported at restored sites will likely be lower than in remnant sites because plant diversity in these mixes is about half that typically present in prairie remnants.

Adding plant species that are especially attractive to bees can substantially increase the number of bees a restored site is likely to support, and incorporating plants that support specialist pollinators will increase pollinator richness. Diverse seed mixes typically will attract a greater number and abundance of wild bee species and can be economical, but only three species—*Monarda fistulosa, Sonchus arvensis,* and *Zizia aurea*—represented 24% of all bee visitations in a study in eastern North Dakota (Otto et al. 2017). Harmon-Threatt and Hendrix (2015) demonstrated that four plants, *Amorpha canescens, Dalea purpurea, Ratibida pinnata,* and *Zizia aurea,* represent potential keystone species for bee communities in many parts of the tallgrass prairie ecoregion, in part because of their high flower number per plant, high pollen to ovule ratios, wide and overlapping flowering periods, and broad geographic ranges.

While pollen and nectar from flowers may be the primary direct factor influencing pollinator abundances, availability of nesting habitat and materials also can limit abundance of pollinators in prairies (Anderson and Harmon-Threatt 2016; Buckles and Harmon-Threatt 2019). Thus, enhancing nesting opportunities for multiple insect groups by ensuring the presence of bare soil, cavities, wood, and plants with pithy stems may be considered when planning habitat restoration in rangelands (Winfree 2010; Buckles and Harmon-Threatt 2019). For example, creating or maintaining bare ground can benefit ground-nesting species (Potts et al. 2005), and many native social bees (bumble bees in particular) use cavities such as vacant rodent burrows, which should be protected whenever possible.

One of the greatest challenges of habitat restoration is identifying the desired endpoint, which is often selected on the basis of the conditions believed to have existed before widespread European settlement. However, historical conditions of plant and pollinator communities in the Great Plains generally are largely unknown, and conditions certainly varied from region to region (Currier and Davis 2000; Johnson and Boettcher 2000). In some situations, patches of remnant prairie provide reference conditions with which existing conditions can be compared. For example, Tonietto et al. (2017) found that bee communities in restored tallgrass prairie sites became more similar to bee communities in remnant patches as time since restoration increased. In other situations, however, the environment today may be so altered that restoration to conditions resembling those existing historically may be impossible. Tools such as Floristic Quality Assessments (FQA) and visits to sites with relatively intact vegetation provide guidance on floristic quality and species mixes (e.g., Buckles and Harmon-Threatt 2019). Restoration also may focus on restoring ecological functions believed to have existed in the past, including enhancing connectivity that historically may have linked remnant areas and facilitated movement of pollinators and plants (DeBano et al. 2003).

Future research should focus on identifying plant species and limiting resources that are critical for supporting pollinators. Such efforts will help managers know which plants in their systems are most useful in supporting pollinator populations and may increase the success of restoration efforts (Menz et al. 2011; Roof et al. 2018). Some threatened Great Plains plants rely on a small number of pollinator species (Travers et al. 2011) and determining how common grassland management practices impact those pollinators will be key for their conservation.

## The road ahead: Management and research needs for pollinators of the Great Plains

Despite development of management plans for pollinators, management actions at any scale aimed specifically at protecting pollinator communities are uncommon in the Great Plains and elsewhere (Otto et al. 2017). Most habitat restoration efforts in the Great Plains and other regions are driven by concern over other taxa (e.g., wildlife, fish) or broader objectives of improving vegetation conditions, rather than pollinators (Tonietto et al. 2017), and only 11% of grassland managers considered native bees in their restoration planning (Harmon-Threatt and Chin 2016). However, most Great Plains states, from Texas to North Dakota, have developed pollinator protection plans for pesticide use and management recommendations. These strategies outline resources, partnerships, educational outreach, citizen involvement, and habitat conservation (e.g., North Dakota Department of Agriculture 2016; Texas Parks and Wildlife Department 2016a; Texas Parks and Wildlife Department 2016b; North Dakota Game and Fish Department 2018).

Federal pollinator initiatives include strategies to provide educational outreach, develop partnerships, enhance pollinator habitat, incorporate pollinator habitat into restoration projects and rights-of-way, and reduce pollinator exposure to pesticides (Pollinator Health Task Force 2015). Federal solutions to address pollinator health and declines include expanding commercial availability and use of pollinator-friendly native seed mixes and plant material, which governmental agencies are well positioned to accomplish (Pollinator Health Task Force 2015). Best management practices for federal land managers in conservation and management of pollinators and pollinator habitat on federal lands include (1) identifying quality and quantity of habitat and pollinator species of concern and associated plants, (2) replacing invasive species with native species, (3) adaptive management to improve pollinator habitat, and (4) guidelines for pesticide use, burning, grazing, and mowing (US Department of Agriculture and US Department of Interior 2015).

However, much work remains to be done. Generally, insect populations are not well monitored or researched, and indeed, most species remain unnamed, unrecorded, and undescribed, resulting in inadequate knowledge to identify key reasons for decline and develop management strategies tailored for focal taxa (Winfree 2010). For example, pollinator distributions and response to temperature and precipitation gradients at different scales are largely unknown. Although bees generally may use drier environments than flies, species within a pollinator group may respond differently to the same factor. Pollinators may more directly respond to floral characteristics than environmental conditions, which may be influenced by both environmental gradients and pollinators (Robson et al. 2019). Knowledge about distributions, abundances, and trends at several scales within and among regions remains elusive, and citizen participation may help gather data over greater geographic scales for long time intervals. An emphasis of understudied groups (e.g., moths, flies, beetles, wasps) is warranted, as some of these species may be particularly important to specific plants, including species of conservation concern (e.g., Travers et al. 2011). Another option is to focus on pollinator species of conservation concern or those known to be sensitive to management or restoration activities (Nelson 2007; Nelson and Wydoski 2008).

Pollinator conservation efforts need not be limited to managers of large landscapes. Any individual can make a difference through small-scale actions because pollinators generally respond at smaller scales than do larger animals. One of the most cost-effective strategies to initiate pollinator conservation is outreach to increase public participation in providing pollinator resources, reducing stressors, and surveying to determine pollinator community composition. Private citizens who live in rangelands can act as land managers of their own property to provide resources for pollinators. At community scales in rangelands, as cities and towns expand into rangelands and fragment pollinator habitat, maintaining connectivity by establishing a series of high-quality greenspaces and converting manicured lawns to diverse native plant gardens will support both human and pollinator health and well-being (Kuo 2015; New 2018).

## Conclusions

Pollinators are crucial components of healthy ecosystems, including rangelands (Black et al. 2011); therefore, concerns about pollinator decreases in the Great Plains and throughout the world continue to grow. The fates of pollinators and flowering plants are fundamentally linked, and decreases in the abundance and diversity of pollinators and pollination services may ultimately lead to pollen limitations, reductions in seed production, and subsequent declines in flowering plants (Winfree et al. 2009; Larson et al. 2018). While the forces driving declines of managed and wild pollinator species in the Great Plains and elsewhere are diverse and complex, efforts to reduce impacts of stressors and increase the quantity and quality of floral resources and nesting habitat should benefit pollinators. However, lack of adequate data about pollinator communities and how these taxa respond to stressors hinders specific actions for targeted management in many areas. Our knowledge about pollinators and their habitat is limited, which presents management challenges in goal setting, designing adequate monitoring programs, and determining trends in pollinator populations.

Given existing knowledge gaps, we offer the following basic guidelines and practices for pollinators in grasslands of the Great Plains:

- Best management practices can reduce stressors and enhance floral and nesting resources (McKnight et al. 2018). Habitat heterogeneity is an important consideration in enhancing pollinator diversity.
- Prescribed fire, grazing, and other disturbances can be useful management tools for enhancing pollinator habitat (https://xerces.org/publications/fact-sheets/rangeland-management-and-pollinators). How altered grasslands are and the specific causal agent (e.g., degradation by non-native species, fragmentation, shifts from bison herbivory to cattle, or from fire to mechanical and chemical treatments), however, will guide the incorporation of disturbance into management plans while considering ecological context. The intensity and temporal/spatial extent of treatment should be tailored to the local pollinator species of conservation concern whenever feasible, particularly when using fire in small, isolated preserves that support sensitive pollinator species.
- Restoration of native plants may require herbicide control to remove non-native species, in which case herbicide application should follow guidelines similar to other pesticides to avoid pollinator exposure (e.g., McKnight et al. 2018). Following up with native plant restoration to prevent reestablishment by non-native plants can prevent additional herbicide applications.
- Management guidance for pollinators should be based on monitoring pollinator populations in addition to their habitats. The most effective way to understand and manage pollinator responses to disturbance and stressors in the Great Plains is to focus on species and mechanisms driving their response to disturbance (see Fig. 2).

Even with limited information, targeted pollinator management is critical to support declining populations by providing resources to withstand a variety of interacting stressors and, concurrently, support functioning rangeland ecosystems.

## Declaration of Competing Interest

None.

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