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Short-Term Response of Two Beneficial Invertebrate Groups to Wildfire in an Arid Grassland System, United States☆

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ABSTRACT

Rangeland invertebrates contribute greatly to biodiversity and provide important services including pollination, pest control, and nutrient cycling. As wildfire frequency increases across these areas of the United States, it is imperative to understand how these disturbances affect beneficial invertebrate communities. We examined bee (Hymenoptera), spider (Araneae), and vegetative communities 1 yr before and 1 yr after a large wildfire swept across an intact grassland in eastern Oregon. Several sites were left unburned after the fire, and a before-after-control-impact study design was used to assess changes within the communities. Fire had no effect on bee or spider abundance, or spider diversity or richness; however, fire significantly increased native bee diversity and richness. In addition, composition of both native bee and spider communities differed significantly between burned and unburned areas 1 yr after the fire. Sheet web spiders (Linyphiidae) and several bee species (primarily large, generalist species) were associated with burned sites. Invasive annual grass and biological soil crust cover decreased significantly in burned sites, but maximum vegetation height and litter cover did not differ significantly among treatments. Forb abundance increased in burned sites; however, species richness of forbs in burned and unburned sites did not differ significantly 1 yr after the fire. Several forbs were indicative of burned areas including non-native species, such as Douglas' knotweed *(Polygonum douglasii)* and Russian thistle *(Salsola tragus)*, and native species such as Canadian horseweed *(Conyza canadensis)*, hoary tansyaster *(Machaeranthera canescens)*, and tall willowherb *(Epilobium brachycarpum)*. This study demonstrates that both invertebrate and plant communities show strong short-term responses to wildfire, and our results can be used to inform management of rare habitat and biodiversity in rangelands impacted by wildfire in arid grasslands.

Introduction

Grassland invertebrates are integral components of rangeland biodiversity and provide important ecosystem services, such as pollination, nutrient cycling, food for vertebrates, and pest control (Weisser and Siemann, 2004; DeBano, 2006; Kennedy et al., 2009; Black et al., 2011; Kimoto et al., 2012, 2012; Tubbesing et al., 2014). Currently these beneficial invertebrate communities are at risk as large portions of North American rangelands, including sagebrush steppe and arid-grassland habitat, have been lost to land conversion or ecologically degraded (Sampson and Knopf, 1994; West, 2000). One major contributor to this degradation is the invasion of non-native annual grasses, which alters disturbance regimes, especially fire frequency and intensity (Pyke, 1999; Davies et al., 2012). The potential effects of these invasive grasses on fire regimes is predicted to be exacerbated by climate change and, in fact, during the past 3 decades wildfire frequency and size have increased across western North America (Schoennagel et al., 2017). As wildfire increases across the northwestern United States, understanding its effects on beneficial invertebrates and their associated ecosystem services becomes imperative, especially to inform management of these ecosystems after fire.

Here, we focus on two beneficial invertebrate groups, native bees, which provide pollination to many important rangeland plants and adjacent crops (Kremen et al., 2002), and spiders, which are generalist predators that enhance pest control and play an important role in rangeland food webs (Sunderland, 1999; Malumbres-Olarte et al.,

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2013). Bees are one of the most diverse groups of insects, with an estimated 20,000 species occurring globally (Michener, 2007). Given that 35% of crops and 80% of native plants rely on animal pollination (Klein et al., 2007; Winfree et al., 2007; Potts et al., 2010), declines in honey bees and some native bee species have resulted in an increased interest in pollinator conservation. Although less is known about trends in spider diversity, they are the seventh most diverse taxon in the world with approximately 40,000 species globally (Mirshamski Kakhki, 2005; Zamani and Rafinejad, 2014). Fire can affect both groups through mortality, injury, and displacement; however, both can survive if they have the ability to disperse (easier for larger, highly mobile bees) or find shelter underground (Bell et al., 2001; Love and Cane, 2016). Bees that build shallow nests in the ground, such as cavity-nesting Apidae, or aboveground nests, such as some species of leafcutting and mason bees (*Megachile* and *Osmia*), are at a higher risk of mortality than species that nest deep in the soil (Cane and Neff, 2011). In addition, timing of the fire in relation to the invertebrate's location (e.g., foraging, in a nest), fire intensity, and developmental stage of the invertebrate (e.g., less mobile bee larvae vs. mobile adults) can also influence the impact of fire on invertebrate communities (Swengel, 2001).

Previous studies have found variable responses of bee and spider communities to fire; however, several have found the greatest differences in diversity, richness, and community occur within the first year after the fire (Buddle et al., 2000; Moretti et al., 2002; Potts et al., 2003; Pryke and Samways, 2012). Multiple studies have shown that bees respond positively to fire, with initial increases in abundance, richness, and diversity at burned sites due to additional access to nesting resources such as charred wood cavities and more bare ground and floral resources (e.g., increased herbaceous plant growth, richness, and diversity) (Moretti et al., 2002; Grundel et al., 2010; Bogusch et al., 2015). However, Potts et al. (2001) found that bee abundance and diversity decreased in response to wildfire, most likely due to fire reducing herbaceous growth and lowering nectar standing crop. Likewise, some studies have found that spider communities change drastically with increased species richness and diversity at burned sites due to quick colonization of open habitat specialists (Buddle et al., 2000; Bell et al., 2001; Koponen, 2005; Langlands et al., 2012), while others have found no change in abundance or richness due to rapid vegetation recovery (Samu et al., 2010). These ambiguous results may be due to variation relative to a number of study factors, including bee and spider community composition, the duration and intensity of fire, and postfire duration. In addition, geographic area and habitat type may explain much of this variation.

Another limitation of past research on wildfire is a lack of studies with prefire data. Because of the unpredictable nature of wildfire, collecting data before wildfire is rare and the majority of fire-impact studies only compare burned sites with control sites post fire (e.g., Buddle et al., 2000; Moretti et al., 2002; Koponen, 2005; Grundel et al., 2010; Bogusch et al., 2015; Love and Cane, 2016). We found only one study that was able to collect invertebrate data before a wildfire (Bess et al., 2002) and no studies that were able to use a before-after-control-impact (BACI) design (no areas were left unburnt in the Bess et al., 2002 study). Having prefire data, in addition to controls, offers the rare opportunity to better understand initial conditions and better quantify wildfire impacts on beneficial invertebrate communities and identify habitat factors associated with observed responses.

The occurrence of a wildfire during the course of a multiyear study of beneficial invertebrates in a Pacific Northwest grassland allowed us to address limitations of previous work on wildfire effects on invertebrates. Because of the nature of the fire, we were able to collect bee, spider, and habitat data before and after wildfire in both burned and unburned sites. Thus, our objectives were twofold: 1) determine how wildfire affects native bee and spider communities including abundance, composition, species richness, and diversity 1 yr after the burn and 2) investigate which habitat factors are strongly associated with observed patterns for each invertebrate group. On the basis of prior studies, we expected bee communities to respond strongly to fire-induced changes in floral resources (e.g., plant richness and abundance) (Grundel et al., 2010; Mola and Williams, 2018) and spider communities to respond to fire-induced changes in vegetation structure (e.g., invasive species cover, plant litter) (Bell et al., 2001; Samu et al., 2010; Smith et al., in review).

Methods

Study Site

The study took place at The Nature Conservancy Boardman Grasslands Preserve (the Preserve) in Morrow County, Oregon (45.636738°N, −119.860457°W). The Preserve occupies 9 163 ha of arid grassland and shrub-steppe from 120- to 295-m elevation (Fig. 1). Common invasive grasses include cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* [L.] Nevski), while native grasses include bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), Sandberg bluegrass (*Poa secunda* J. Prsel), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey ssp. *brevifolius* [J. G. Sm.] Barkworth), and needle-and-thread grass (*Heterostipa comata* [Trin. & Rupr.] Barkworth). The average precipitation is 22 cm with the majority of the precipitation falling from November to February, and annual average temperatures range from 5°C to 18°C with temperatures frequently reaching 32°C in the summer (30-yr average, US Climate Data 2017).

Site Selection

We established 18 sites across the Preserve in 2014 as part of a long-term study examining the effects of grassland restoration on beneficial invertebrates (Smith DiCarlo and DeBano, 2018). All sites were accessible by old farm roads on relatively flat slopes and were separated on average by 623 m, a distance judged to be sufficient to ensure independence of sites, given typical bee and spider movement patterns (see Fig. 1). Many spiders do not move more than a few meters a day (depending on their hunting strategy), and bee foraging distances are largely dependent on body size, with most smaller bees (the majority of species in this study) probably traveling no more than a few hundred meters at most (Greenleaf et al., 2007). On 1 June, 2015 a large wildfire started from a haystack that spontaneously combusted just outside of the Preserve. In 2 d the fire burned over 16 000 ha (Plaven, 2015), leaving large areas of moderate to severe surface burns on the Preserve (Fig. 2) (Keeley, 2009). In 2016, one yr after the fire, we resumed sampling at the original 18 sites, 5 of which had burned—resulting in 5 burned replicates and 13 control, or nonburned, replicates.

Spider Sampling

At each site, eight pitfall traps were placed in a 10-m radius circle (Fig. S1; available online at: https://doi.org/10.1016/j.rama.2018.11.011). Pitfall traps, 470-mL plastic cups filled with wildlife-friendly propylene glycol and placed flush with the soil, are well suited for collecting ground-active spiders (Kelton, 1978). Spiders were collected at all sites three times each year during June-July, July-August, and August-September by opening traps for 1 wk each time period to collect invertebrates. After 1 wk, traps from each site were collected, combined, and transported to the laboratory. Samples were then washed over a 250-μm sieve, and spiders were sorted from other invertebrates and debris and preserved in 70% ethanol. All juvenile spiders were identified to family, and all mature spiders were identified to species, if possible.

Bee Sampling

Bees were sampled using pan traps, 236-mL plastic cups painted fluorescent blue, yellow, and white to attract different pollinators. Using plant stakes, all pan traps were elevated approximately 1 m aboveground to be at a similar height as the vegetation and filled with

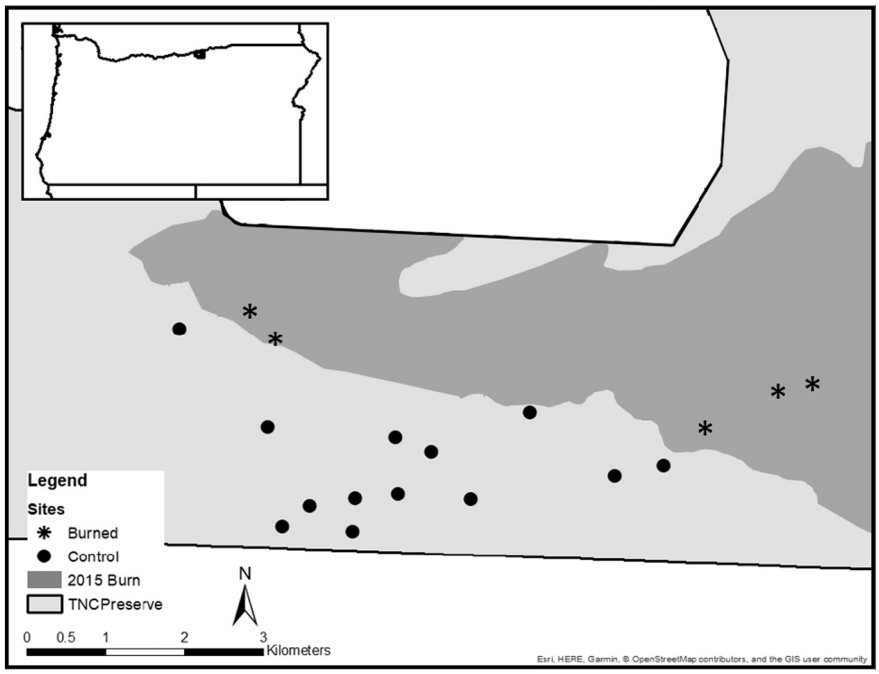

Figure 1. Map of Nature Conservancy Boardman Grasslands Preserve with inset of location in Oregon, United States. *Stars* represent burned sites, and *circles* represent control sites.

a solution of water and detergent. Nine pan traps were placed at each site in a 10-m radius circle, with one in the center (see Fig. S1). Bees were collected during the same periods as spiders, except that bee sampling was not conducted during the June-July sampling bout, and pan traps were collected in the field after 2 d. All traps from each site were combined and transported to the laboratory, where bees were washed, dried, pinned, and identified. All specimens were identified to species, if possible.

Habitat Survey

To determine which habitat characteristics were related to spider and bee abundance, richness, and species composition, each site was surveyed for environmental variables once in 2014 and three times in 2016, coinciding with invertebrate sampling. Variables were estimated to the nearest 5% cover in sixteen 63 × 63 cm subplots located in a 50 × 50 m square around the pitfall and pan traps (see Fig. S1). Variables estimated included the percent cover of invasive annual grasses (cheatgrass *[B. tectorum]* and medusahead *[T. caput-medusae]*), biological soil crusts, and litter. We also estimated maximum vegetation height by measuring the tallest stem in each subplot. During bee sampling we also counted and identified every blooming plant and shrub within the 50 × 50 m square to determine forb abundance and species richness.

Analyses

Spider and bee abundance at each site was characterized by the average number of individuals per trap as not all traps were present during collection due to weather or animal tampering. Prefire and postfire abundance, diversity, and species richness data were averaged over the three sampling bouts for spiders and two sampling bouts for bees in both 2014 and 2016. The Shannon-Weiner index was used to estimate spider and bee diversity of each site. Habitat variables for each site were calculated by first averaging subplots by site and then averaging over the number of sampling bouts per year (one in 2014, three in 2016). Floral abundance and richness data were averaged over two sampling bouts in both 2014 and 2016.

To determine if the wildfire had an impact on spider or bee abundance, diversity, richness, and habitat variables, a BACI design was used with 5 impact (burned) sites and 13 control (unburned) sites with data from 1 yr before and 1 yr after. Because having more control sites than impact sites enhances the power to detect differences (Underwood, 1994), we used all control sites in analyses. We used a

Figure 2. A, Photograph of a burned site in 2014, 1 yr before fire. **B,** Photograph of a burned site in 2015 showing moderate to severe surface burn, 7 d postfire. **C,** Photograph of vegetation regrowth in 2016 at a site 1 yr postfire.

two-factor analysis of variance to analyze raw data. Both factors were fixed and included period (before/after) and treatment (burned/control). In addition to examining the main effects, we also examined the interaction between period and treatment (Smith, 2002, Table 3; Schwarz, 2015). Analyses resulting in significant *P* values (alpha < 0.05) were considered to have had a significant stepwise change over time compared with the control, an effect that can be attributed to the wildfire (Schwarz, 2015). We also calculated the estimated BACI contrast (the differential change between the before and after periods, Schwarz, 2015; Meroni et al., 2017, equation 1). The BACI contrast is expressed in the same units of the variable of interest (in our case, abundance, Shannon-Wiener diversity, species richness, or vegetative cover or height) and can result in either a negative or positive contrast (Meroni et al., 2017). A negative contrast value indicates that the variable has increased more (or decreased less) in the burned sites compared with the control sites (Meroni et al., 2017). All BACI analyses were completed in RStudio 1.0.153 (R Development Core Team, 2015).

PC-ORD Software version 7.287 (McCune and Mefford, 2015) was used for all community analyses. Family-level abundance was used in all multivariate analyses for spiders instead of genus or species abundance to allow for use of juvenile spiders in the analysis (juvenile spiders cannot be positively identified to genus or species without introducing error); however, species-level abundance was used for bees and flowering forbs. The spider family dataset contained average spiders per pitfall trap (18 sites for each year [36 total] × 10 families), the bee species dataset contained average bees per pan trap (18 sites for each year [36 total] × 46 species), and the forb species dataset contained total stem (1 plant = 1 stem) counts (18 sites for each year [36 total] × 21 species). The environmental dataset contained habitat variables (18 sites each year [36 total] × 6 variables) including average maximum vegetation height, forb abundance, forb richness, and average percent cover of invasive annual grasses, litter, and biological soil crust.

Nonmetric multidimensional scaling (NMS) with Sorensen distances was used to ordinate sites in the spider family space matrix, the bee and forb species space matrices, and the environmental matrix. NMS does not assume linearity between family or species response and environmental gradients and exposes relationships between the family matrix and environmental matrix (McCune and Grace, 2002). NMS was performed with 250 random starts, and ties were not penalized. A randomization procedure was included to test if solutions were stronger than those obtained by chance, resulting in *P* values. R^2 values were calculated to represent the percent variance explained by each axis, and relationships of each axis with spider families and habitat variables were quantified with Pearson correlation coefficients.

Multiresponse permutation procedures (MRPPs) were used with Sorensen distances to test for differences in family and species composition across sites among groups, with four groups: control prefire, control postfire, burned prefire, and burned postfire. Pairwise comparisons resulted in A-statistics, the chance-corrected within-group agreement, and *P* values.

Indicator Species Analysis was performed to assess family-specific (spiders) and species-specific associations across groups (bees and flowering plants). Resulting indicator values ranged from 0 to 100, with higher scores indicating stronger associations between taxa and treatments. A randomization test was used to test for statistical significance of the indicator values by using 4 999 random permutations, resulting in a *P* value for each indicator value. Families or species with high indicator values and significant *P* values (alpha < 0.05) were considered indicative of that treatment.

Results

We collected 811 spiders in 2014 (prefire) and 895 spiders in 2016 (postfire) and identified 30 species in 10 families (20 species in 2014 and 15 species in 2016). In 2014, approximately 15% of spiders were mature, and in 2016 approximately 12% were mature. We collected 4 109 bees in 2014 and 3 392 bees in 2016. We identified 46 bee species in five families, with 37 species in 2014 and 31 species in 2016. Over the 2 yr we counted 14 737 blooming plant stems and identified 11 species in 2014 and 19 species in 2016 (21 species in total).

Spiders

Spider abundance, diversity, and richness did not change significantly in response to the fire (F [1, 1] = 0.11, $P = 0.73$; F [1, 1] = 1.78, $P = 0.20$; F [1, 1] = 2.32, $P = 0.14$, respectively) (Fig. 3). Community composition of spiders differed among sites (Fig. 4a); the NMS randomization procedure resulted in a stable three-dimensional solution (final stress = 8.98, final instability = 0.00, $P = 0.02$) with a cumulative R^2 of 93.6 for spiders. Axis 1 accounted for 55.8% of the variation in spider family space, axis 2 accounted for 28.5%, and axis 3 accounted for 9.3%. Pearson correlations between the three axes and spider taxa and environmental variables are listed in Table S1 (available online at https://doi.org/10.1016/j.rama.2018.11.011). Separation among treatment types occurred on both Axes 1 and 2 (Fig. 4a), and centroids for each of the four treatments are shown in Figure 4b. MRPP showed that spider community composition differed significantly among treatments (A = 0.15, $P < 0.00001$). While pairwise comparisons showed that prefire spider communities differed significantly from postfire communities for both control and burned sites (A = 0.03, $P = 0.04$; A = 0.18, $P = 0.002$, respectively), the distance between centroids of prefire and postfire burned sites was much greater than the distance between centroids of prefire and control sites (see Fig. 4b), indicating that spider communities at burned sites changed more than those at unburned sites. In general, all spider communities became less dominated by jumping spiders (Salticidae) and more dominated by wolf spiders, (Lycosidae), cobweb spiders (Theridiidae), and crab spiders (Thomisidae) from 2014 to 2016; however, sites that burned showed more of an increase in cobweb spiders and sites that did not burn showed more of an increase in wolf and crab spiders (see Fig. 4).

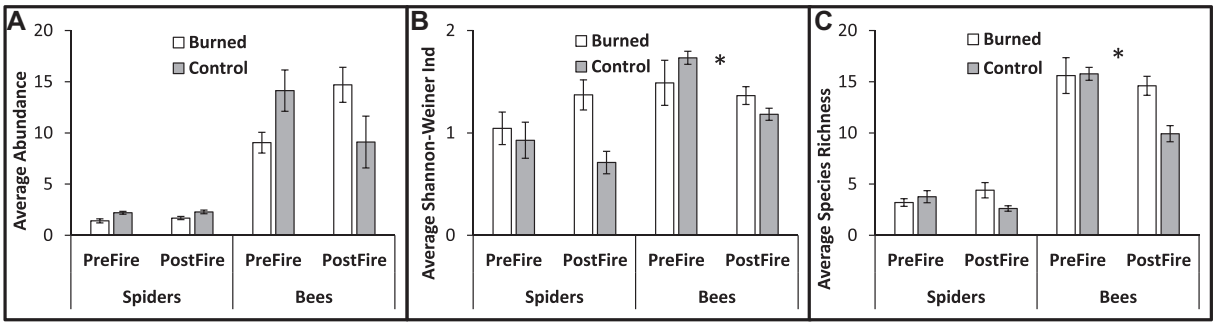

Figure 3. A, Average individuals per trap prefire and postfire for both spiders and bees. **B,** Average Shannon-Weiner Index prefire and postfire for both spiders and bees. **C,** Average species richness prefire and postfire for both spiders and bees. *Stars* above each grouping denote significant before-after-control-impact results. $N = 5$ burned sites; $N = 13$ control sites; *bars* indicate standard errors.

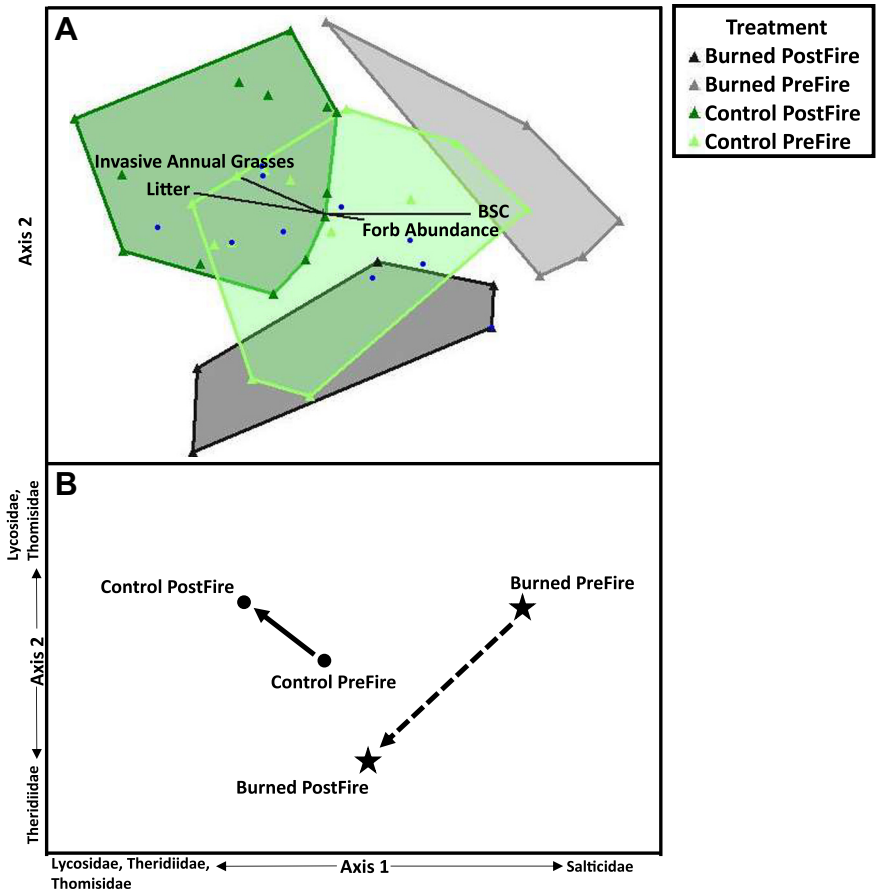

Figure 4. A, Nonmetric multidimensional scaling ordination of sites in spider family space along with weighted average positions for spider families for axes 1 versus 2. Each triangle represents a site, and each circle represents a spider family. A joint-plot from the environmental matrix is overlaid with variables of $r^2 > 0.15$ being displayed with vector lengths corresponding to the correlation strength along the axes (shown in *thick black lines*). Convex hulls connect each group of treatments. Sites that are closer together are more similar than sites farther away from each other. **B,** *Arrows* from each treatment's centroid in spider family space indicate community changes prefire to postfire along axes 1 and 2. Spider families that have significant positive and negative correlations with each axis are indicated. See Table S1 for correlations of each axis with habitat variables and spider families.

Indicator analysis revealed that sheet web spiders (Linyphiidae) were strongly associated with the postfire burned sites, while wolf and crab spiders were strongly associated with postfire control sites (Table 1).

Bees

Bee abundance did not differ significantly between burned and unburned sites ($F[1, 1] = 3.63$, $P = 0.07$), but bee diversity increased in burned sites ($F[1, 1] = 5.1$, $P = 0.04$, BACI $= -0.35 \pm 0.15$) and richness showed a similar trend ($F[1, 1] = 4.27$, $P = 0.06$, BACI $= -3.71 \pm 1.79$) (see Fig. 3). The NMS randomization procedure resulted in a stable three-dimensional solution (final stress = 8.36, final instability = 0.00, $P = 0.004$) with a cumulative R^2 of 92.6. Axis 1 accounted for 41.4% of the variation in bee species space, axis 2 accounted for 40.7%, and axis 3 accounted for 10.5%. Pearson correlations between the three axes and bee taxa and environmental variables are listed in Table S2 (available online at https://doi.org/10.1016/j.rama.2018.11.011). Separation among treatment types occurred on both Axes 1 and 2 (Fig. 5a), and centroids for each of the four treatments are shown in Figure 5b. MRPP showed that bee community composition differed significantly among treatments ($A = 0.18$, $P < 0.00001$). Pairwise comparisons showed that prefire bee communities differed significantly from postfire communities for both control and burned sites ($A = 0.15$, $P < 0.0001$; $A = 0.11$, $P = 0.01$); however, unlike spiders, the distance between centroids of prefire and postfire control sites was much greater than the distance between centroids of prefire and postfire burned sites (see Fig. 5b), indicating that bee communities at control sites changed more than those at burned sites. In general, bee communities at burned and unburned sites were similar before the burn, but after the fire, unburned communities were dominated by sweat bees (*Halictus* and *Lasioglossum*) and burned communities were dominated by a number of other species in six different genera (see Fig. 5b). Indicator species analysis revealed significant indicator species for all four treatments (see Table 1). Species indicative of prefire burned sites were small mining bees *(Perdita)*. In contrast, indicator species for postfire burned sites included large bees, many of which are known generalists (e.g., *Apis mellifera*) (see Table 1). Indicator species for control sites, both prefire and postfire, were primarily species of long-horned bees *(Melissodes)*.

Habitat Variables

Invasive annual grass cover and biological soil crust cover decreased significantly in burned sites ($F[1, 1] = 34.53$, $P < 0.0001$, BACI $= 38.30 \pm 6.52$; $F[1, 1] = 18.92$, $P = 0.0005$, BACI $= 28.73 \pm 6.60$), but there was no change in litter cover or maximum vegetation height ($F[1, 1] = 0.01$, $P = 0.93$; $F[1, 1] = 0.09$, $P = 0.77$, respectively) (Fig. 6). There was also a significant effect of the fire on forb abundance ($F[1, 1] = 4.99$, $P = 0.04$, BACI $= 331.42 + 148$), but the wildfire did not significantly affect forb richness ($F[1, 1] = 0.22$, $P = 0.64$) (Fig. 7). A NMS randomization procedure for forbs did not result in a stable solution. Indicator analysis resulted in eight blooming plant species for all treatments except for control prefire (see Table 1). Burned postfire indicator species included

Table 1
Indicator values (IV) and *P* values for spider families, bee species, and forb species. Only significant families or species are reported. See Table S3 (available online at https://doi.org/10.1016/j.rama.2018.11.011) for nonsignificant families and species.

		IV	*P*		IV	*P*
Spider families	**Burned prefire**			**Burned postfire**		
	None			Linyphiidae	49	0.01
	Control prefire			**Control postfire**		
	None			Thomisidae	46	0.002
				Lycosidae	41	0.03
Bee species	**Burned prefire**			**Burned postfire**		
	Perdita aridella	69	0.0004	*Anthophora urbana*	77	0.003
	Tripeolus paenepectoralis	49	0.005	*Apis mellifera*	73	0.0006
	Perdita dubia	39	0.0008	*Agapostemon femoratus*	68	0.0002
				Nomada spp. 4	40	0.03
				Halictus tripartitus	38	0.04
				Nomada spp. 5	36	0.03
				Megachile coquilletti	31	0.04
	Control prefire			**Control postfire**		
	Melissodes subagilis	80	0.0002	*Melissodes rivalis*	48	0.02
	Melissodes semilupinus	65	0.0002			
	Melissodes bimatris	48	0.01			
	Triepeolus grindeliae	44	0.03			
Forb species	**Burned prefire**			**Burned postfire**		
	Chrysothamnus viscidiflorus	69	0.02	*Polygonum douglasii*	100	0.0002
				Conyza canadensis	77	0.0004
				Epilobium brachycarpum	76	0.0004
				Salsola tragus	60	0.002
				Machaeranthera canescens	46	0.05
	Control prefire			**Control postfire**		
	None			*Ericameria nauseosa*	91	0.0002
				Centaurea solstitialis	52	0.02

Canadian horseweed (*Conyza canadensis* [L.] Cronquist), tall willowherb (*Epilobium brachycarpum* C. Presl), hoary tansyaster (*Machaeranthera canescens* [Pursh] A. Gray), Douglas' knotweed (*Polygonum douglasii* Greene), and Russian thistle (*Salsola tragus* L.).

Discussion

Wildfire affected both spider and bee communities 1 yr after the burn. For spiders, responses were strongest relative to community composition, with dominant families differing between burned and control sites. Bee communities, on the other hand, responded to wildfire with not only compositional changes but also increases in diversity and richness. Although direct mortality associated with fire can affect invertebrate communities, changes are more commonly tied to indirect effects of wildfire on habitat characteristics that can both positively and negatively affect certain taxa.

In our system, habitat responses associated with wildfire included decreases in invasive annual grass and biological soil crust cover. Biological soil crusts are known to burn in high-intensity fires and can be lost if fire intervals are shorter than their recovery period, which can range from 14 to 250 yr (Greene et al., 1990; Whisenant, 1990; Johansen, 1993; Belnap, 2000; Belnap and Eldridge, 2000). However, the decrease in invasive annual grass cover observed in our system differs from other studies that have found increases in cheatgrass within the first year after burn, especially at low-elevation sites (West and Hassan, 1985; Davies et al., 2012). Invasive annual grass cover may have decreased in our system due to the early season timing of the fire (Meyer et al., 2000) or because of the relatively low coverage of invasive grasses before the burn. Several other habitat variables did not show significant responses to wildfire, including maximum vegetation height. Vegetation height may not have been strongly affected because of the potentially rapid regeneration of bunchgrasses (Uresk et al., 1980; West and Hassan, 1985) or because of the presence of pockets of unburned tall bunchgrasses within burned sites. While perennial bunchgrasses can reestablish cover at preburn levels (West and Hassan, 1985), some studies have found that the grass layer may be reduced and not completely recover until 2.5 yr after the fire (Britton et al., 1990; Samu et al., 2010). Litter cover also did not respond to wildfire, a result also found by Niwa and Peck (2002) in a forested system. This was somewhat surprising because the fire burned with moderate severity at our study site, and both litter and the majority of grasses in burned areas combusted completely (see Fig. 2). Thus, we would have expected to find a decrease in litter 1 yr after the fire, given the destruction of the existing litter layer and the removal of grasses that would have contributed to a new layer. One explanation is that litter may have blown into the area from surrounding intact habitats (the area is known for its strong wind gusts and dust storms). In addition, we did not measure changes in litter biomass or complexity, which were most likely reduced after the fire and are known to have large impacts on the spider communities (Uetz, 1979; Bell et al., 2001).

Observed changes in habitat variables to wildfire did not translate to responses in spider abundance, diversity, and richness, a result that differs from other studies that found significant responses in one or more of these variables (Bell et al., 2001; Bess et al., 2002; Larrivee et al., 2005; Koponen, 2005; Langlands et al., 2012; Pryke and Samways, 2012). The lack of response may be due to the fire having no detectable effects on litter, considering previous work in this system showed that spider abundance is closely tied to litter cover (Smith DiCarlo and DeBano, 2018; Smith et al., in review). In addition, we found that all families except for funnel weavers (Agelenidae) were present at burned sites, indicating that many spider species may have survived underground or in unburned patches and then quickly recolonized after the fire. While we did see some early colonizers, they were not particularly abundant or diverse. Similar to our results, Samu et al. (2010) found no responses in spider abundance or richness to wildfire and suggested that this was due to a relatively quick recovery of vegetation and a lack of pioneer species. Declines in spider abundance after wildfire found in other studies may be due to direct mortality or abrupt changes in plant communities and litter (Bess et al., 2002; Moretti et al., 2002; Richardson and Hanks, 2009). In contrast to trends in abundance, both spider richness and diversity have been found to increase over time after wildfire (Merrett, 1976; Haskins and Shaddy, 1986; Buddle et al.,

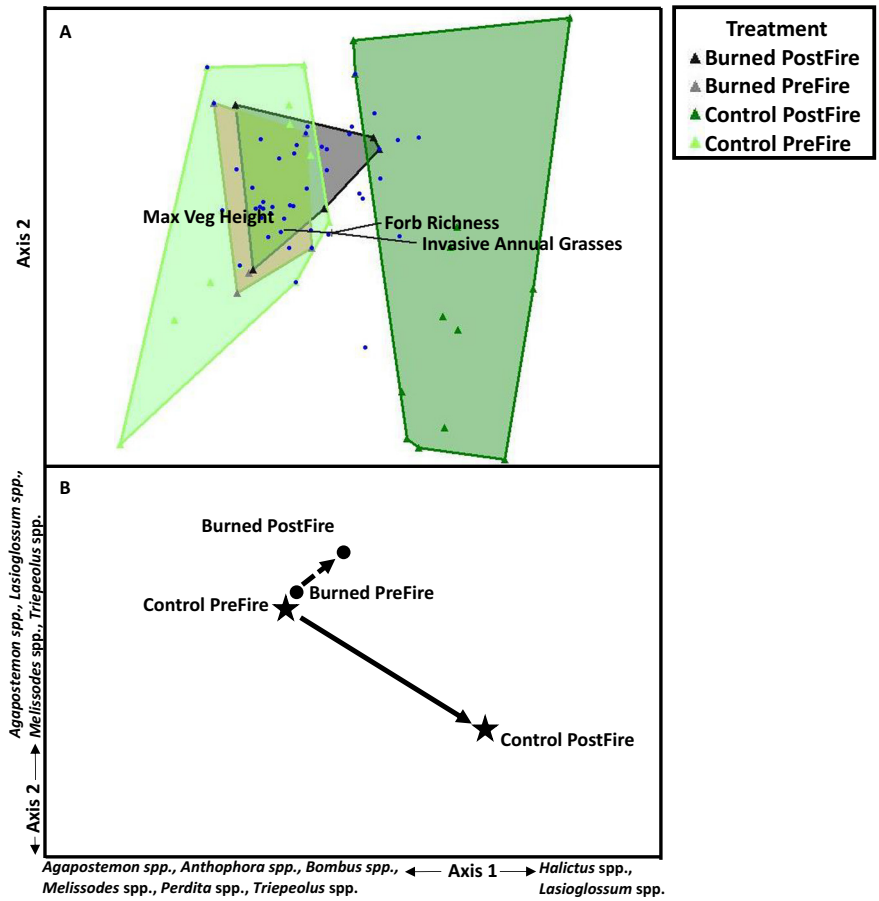

Figure 5. A, Nonmetric multidimensional scaling ordination of sites in bee species space along with weighted average positions for bee species for axes 1 versus 2. Each triangle represents a site, and each circle represents a bee species. A joint-plot from the environmental matrix is overlaid with variables of $r^2 > 0.15$ being displayed with vector lengths corresponding to the correlation strength along the axes (shown in *thick black lines*). Convex hulls connect each group of treatments. Sites that are closer together are more similar than sites farther away from each other. **B,** *Arrows* from each treatment's centroid in bee species space indicate community changes prefire to postfire along axes 1 and 2. Bee genera that have significant positive and negative correlations with each axis are indicated. See Table S2 (available online at https://doi.org/10.1016/j.rama.2018.11.011) for correlations of each axis with habitat variables and bee species.

2000; Koponen, 2005; Langlands et al., 2012), potentially because of the survival of species present before the fire and the addition of colonizing species that specialize in open habitats.

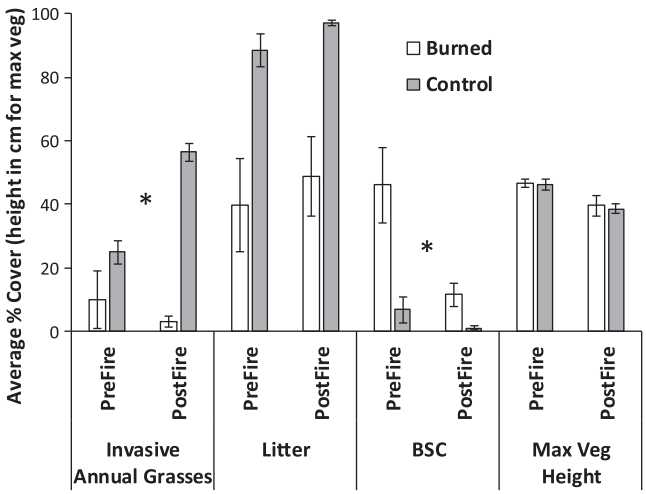

Figure 6. Invasive annual grasses, litter, and biological soil crusts (BSC) are measured by average percent cover, while average maximum vegetation height is expressed in centimeters. *Stars* above each grouping denote significant BACI results, and *bars* indicate standard errors.

Spider community composition did respond to wildfire. Families such as wolf spiders (Lycosidae), cobweb spiders (Theridiidae), and crab spiders (Thomisidae) were abundant at all sites, including burned ones. This may be explained by the fact that successful recolonization is often tied to prior dominance, with more abundant arthropod species more likely to be successful at recolonization after fire (Bess et al., 2002). Individuals in these families may have survived the fire or quickly colonized from adjacent or unburned habitat, especially if the fire did not burn uniformly and left pockets of surviving individuals (Swengel,

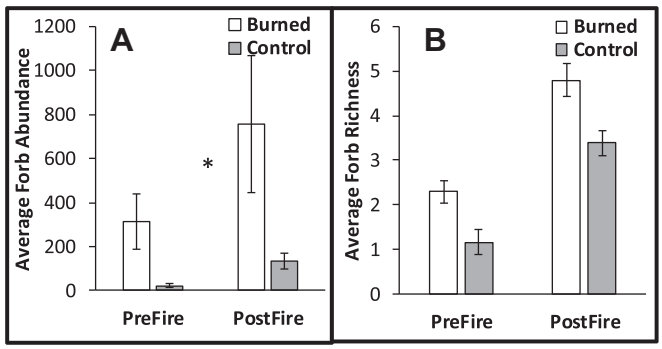

Figure 7. A, Average forb abundance prefire ($N = 5$ burned sites, $N = 13$ control sites) and postfire ($N = 5$ burned sites, $N = 13$ control sites). **B,** Average forb richness prefire ($N = 5$ burned sites, $N = 13$ control sites) and postfire ($N = 5$ burned sites, $N = 13$ control sites). *Stars* above each grouping denote significant BACI results, and *bars* indicate standard errors.

2001; Moretti et al., 2002). However, despite this, community composition at burned and unburned sites diverged. Communities at burned sites became more dominated by cobweb spiders and sheet weavers (Linyphiidae), while control sites were more dominated by wolf spiders and crab spiders. Several studies have found similar results in grasslands, with cobweb and sheet weaver spiders dominating burned areas, most likely due to these families' high tolerance of changes in microclimate (Riechert and Reeder, 1972; Merrett, 1976; Bell et al., 2001). Sheet weavers may also be indicative of burned treatments due to their lack of dependence on vegetative structure and ability to disperse through ballooning throughout their entire lives (Bell et al., 2001). However, other studies have shown different responses in community composition. Koponen (2005) found wolf spiders dominated in burned sites and sheet weavers dominated in nonburned sites in a forested system. These differences may be due to species-specific preferences. The dominant wolf spider found in Koponen's study *(Xerolycosa nemoralis)* is known to colonize open areas, while the species in our study belong to the *Schizocosa* genus. In our study area, both *Schizocosa* and crab spiders are more abundant in heavily vegetated areas dominated by invasive annual grasses (Smith DiCarlo and DeBano, 2018; Smith et al., in review). In addition, *Schizocosa* are also known to respond positively to high soil moisture and full litter cover, which may be reduced in burned areas (Stratton, 1991).

In contrast to spiders, bees did show responses in diversity and richness to wildfire, with both variables increasing. Like spiders, however, abundance was unaffected. Other studies found similar results with higher bee species richness and diversity after fires, with both peaking several years after the burn (1 − 3 yr) due to increases in nesting resources, including charred wood, and in floral resources (plant richness and abundance) (Potts et al., 2003; Moretti et al., 2009; Grundel et al., 2010; Bogusch et al., 2015). Like these studies, we found increases in forb abundance, which may have provided additional nectar and pollen resources, although forb richness did not significantly differ due to the burn. After these peaks in richness and diversity, bee richness and diversity can steadily decrease with time as vegetation recovers and pioneering forbs are outcompeted and bare ground available for nesting decreases (Potts et al., 2003; Bogusch et al., 2015). These longer-term responses differ from very short-term responses; for example, Love and Cane (2016) found fewer active species 14 − 21 d after the fire, most likely due to mortality. In our study, higher bee richness and diversity after the fire may have been driven by increased nesting habitat for some species of bees. The fire significantly decreased invasive annual grass cover, potentially providing ground-nesting bees with additional nesting resources. In addition, while the fire intensity was high, a majority of aboveground vegetation was burned, leaving some charred stems from larger sagebrush and juniper plants, potentially providing additional nesting resources for aboveground nesters.

Bee communities diverged in composition in both the burned and control sites, with greater changes in composition seen in the control sites (see Fig. 5). This is not uncommon as bee communities are known to vary strongly both seasonally and annually due to climatic factors and variation in floral phenology (Williams et al., 2001; Kimoto et al., 2012). While both the burned and control sites shifted in community composition, they diverged in two separate directions 1 yr after the fire, resulting in two very different communities (see Fig. 5). Several species were found to be indicative of burned sites that were not collected at the sites prior, including *Halictus tripartitus, Megachile coquilletti,* and two *Nomada* species. One of these species nest in the soil (*H. tripartitus*, Kim et al., 2006) and may benefit from decreased invasive annual grass species cover, potentially opening up additional nesting sites. *M. coquilletti* is the only species that nests aboveground in cavities (Sheffield et al., 2011) and may take advantage of the recently burned woody material. The two unknown *Nomada* species are cuckoo bees that parasitize many other bee species nests including *Agapostemon* species (Eickwort and Abrams, 1980), which were more dominant in sites that burned compared with sites that did not.

Shifts in bee community composition after fire may be due to not only changes in soil and vegetative structural characteristics that affect nesting habitat but also changes in forb diversity and richness (Ne'eman et al., 2000; Moretti et al., 2009; Grundel et al., 2010; Pryke and Samways, 2012; Love and Cane, 2016). Several studies have found that wildfire increases forb abundance and/or richness (Moretti et al., 2009; Grundel et al., 2010; Mola and Williams, 2018). We found that forb abundance increased after the fire and fire influenced species composition. Several forb species were indicative of burned sites, including Douglas' knotweed and Russian thistle (both invasive), and Canadian horseweed, tall willowherb, and hoary tansyaster (all native). Canadian horseweed and hoary tansyaster are both from the Asteraceae family, while Douglas' knotweed, Russian thistle, and tall willowherb are from Polygonaceae, Chenopodiaceae, and Onagraceae, respectively. Unfortunately, bee-floral associations are not well known in this area, but bee species that were indicators for burned sites are known to visit each plant family. *Agapostemon, Anthophora, Apis, Halictus,* and *Megachile* visit members of the Asteraceae family, with *Anthophora urbana* a known pollinator of hoary tansyaster (US National Pollinating Insects Database, 2014). While fewer genera are known to pollinate Chenopodiaceae plants, two genera associated with burned sites (*Agapostemon* and *Halictus*) are pollinators of species within the plant family, with *Agapostemon femoratus* recorded on Russian thistle specifically (US National Pollinating Insects Database, 2014). *Agapostemon, Anthophora, Apis, Halictus,* and *Megachile* are all known pollinators of species in Onagraceae and Polygonaceae (US National Pollinating Insects Database, 2014). Thus, changes in the dominance of these forb species after wildfire may also contribute to observed changes in bee community composition, richness, and diversity.

This study offered a rare opportunity to collect data before and after wildfire in both burned and control sites. Using a BACI design allowed us to partition out effects of the fire from temporal variability and make inferences about fire effects on bee, spider, and forb communities. Power may have limited our ability to detect differences in some responses, especially those that were highly variable (Underwood, 1991; Schwarz, 2015); however, the large number of control sites in our study ($N = 13$) relative to impact sites ($N = 5$) is an optimal design for enhancing the power of BACI analyses (Underwood, 1991). Nevertheless, future studies on fire effects of variables that did not appear responsive to fire in our study (spider abundance, richness, and diversity, bee abundance, forb richness) would be worthwhile.

Implications

Wildfires, especially those that burn large areas with moderate to high intensity, have the potential to alter beneficial invertebrate communities. Changes within the communities can be effected directly through mortality or indirectly through the transformation of the surrounding habitat. Native bee and spider community composition differed 1 yr after wildfire, as did invasive annual grass cover, biological soil crust cover, and forb abundance. Several types of bees, spiders, and forbs appear to be early colonizers of burned areas. As expected, native bee diversity and richness increased, potentially due to additional nesting sites and/or increased floral resources, but no difference was seen in spider abundance, diversity, or richness, most likely due to survival and quick recolonization.

Native bees and spiders play key roles in ecosystem functioning and respond quickly to perturbations in the surrounding environment; these characteristics suggest that they may be ideal monitoring tools for rangelands. Because not all communities respond in the same manner to wildfire due to geographic location, timing of sampling (short-term vs. long-term), and other factors related to the fire, monitoring should be conducted at a broad spatial scale and at both short- and long-term intervals. Furthermore, as little is known about bee-floral associations in arid grasslands, additional observations are needed to inform managers about which wildflowers to plant to assist in bee community recovery after wildfire.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.11.011.

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