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Mortality and Flowering of Great Basin Perennial Forbs After Experimental Burning: Implications for Wild Bees☆

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A B S T R A C T

The fates of native bee communities in the Great Basin sagebrush steppe are linked with the susceptibilities of their floral hosts to increasingly frequent wildfires. Postfire survival and subsequent flowering of six prevalent perennial wildflowers representing five families were quantified across a range of realistic fire severities created using a calibrated propane burn barrel. Five burn prescriptions of varying intensity and duration were applied to cultivated rows of basalt milkvetch (Astragalus filipes Torr. ex A. Gray), Blue Mountain prairie clover (Dalea ornata Eaton & J. Wright), sulphur-flower buckwheat (Eriogonum umbellatum Torr.), fernleaf biscuitroot (Lomatium dissectum Nutt.), blue penstemon (Penstemon cyanus Pennell), and gooseberryleaf globemallow (Sphaeralcea grossularifolia Hook. & Arn.). Overall differences in their fire sensitivities were maximal at peak fire severity, ranging from 80% survival (L. dissectum) to complete mortality (E. umbellatum and P. cyanus). Although A. filipes survived well (85%), half of the 95 burn survivors then failed to flower the year after burning. The postfire fate of plant-pollinator interactions is a function of the bees’ nesting habits, their floral host’s sensitivity to a given burn intensity (both in terms of survival and flowering), and the reproductive interdependence of bee and floral host (taxonomic specialists vs. generalists).

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Introduction

Great Basin sagebrush steppe is among the most imperiled large terrestrial ecosystems in the United States (Noss et al., 1995; Stein et al., 2000; Davies et al., 2011; Miller et al., 2011). Once covering over 60 million ha in western North America (West, 2000; Beck et al., 2009), sagebrush-dominated communities have been substantially diminished; much that remains is fragmented and degraded (Walker and Shaw, 2005; Chambers et al., 2009; Chambers and Wisdom, 2009; Hanna and Fulgham, 2015). Their fire regimes have changed dramatically, owing to an accelerated fire cycle fueled by the invasion of aggressive and highly flammable annual Eurasian grasses, primarily cheatgrass (Bromus tectorum L.) and medusahead (Taeniatherum caput-medusae [L.] Nevski) (D’Antonio and Vitousek, 1992; Brooks and Pyke, 2001; Chambers et al., 2007). Wildfires return not only more frequently—with return intervals measured in years rather than decades (Whisenant, 1990)—but are also larger in size and more severe (Chambers and Pellant, 2008; Keane et al., 2008), sometimes removing all aboveground vegetation over tens of thousands of hectares (e.g., Love and Cane, 2016).

The sagebrush ecosystem in the US Intermountain West still hosts a diverse, albeit poorly known, bee fauna that relies on and also pollinates many of the native perennial wildflowers common to this region (Cane, 2008; Cane et al., 2012). Most bees of this and other temperate-zone regions excavate nests deep enough in soil that their progeny should escape lethal soil heating by rangeland fire to emerge as adults the next year (Cane and Neff, 2011). Our work in the Great Basin sagebrush steppe (Love and Cane, 2016; Love and Cane, unpublished) corroborates this prediction, finding diverse bee communities active in the weeks and years following a wildfire. To retain this persistent bee fauna, their floral hosts must not only survive fire but also produce timely and sufficient bloom the next growing season. Most bees have an annual lifecycle, similar to annual plants, but without the insurance of a seedbank to endure unfavorable periods (such as after a fire). Disrupted or diminished pollen and nectar supplies during the first growing season after a fire would constrain reproduction by the local surviving bee community, thereby limiting pollination during their recovery years.

Much is known about the general effects of fire on Great Basin plant communities and ensuing vegetation changes (e.g., West and Yorks,
Experimental Design

We chose 6 of the 17 available herbaceous perennial forb species representing a range in taxonomy (5 families), morphologic characteristics, season of bloom, and importance to bees and other wildlife (Table 1). A randomized block design with four replicates was used to evaluate the survival and reproductive responses of burned plants to five incrementing intensities of simulated wildfire per species, plus an unburned control. Burn trials took place at the end of the natural fire season (Knapp et al., 2009) over a 10–d period, from 21 to 30 August, 2012. Combustion took place during daylight hours under mostly sunny conditions, with air temperatures ranging between 18°C and 36°C. The plants tested were well into autumnal senescence (e.g., aboveground tissues had all—mostly—died back). Before treatment application, 1-m² plots were demarked and live mature plants counted (see Table 1). Plants were trimmed to 10 cm in height, and loose dead vegetation was cleared from around the burn area for safety and to standardize minimal fuel loads.

Heat Treatment

A number of techniques have been used to simulate natural or prescribed fire. The better ones control time-temperature exposures to allow for relatively consistent, repeatable, and contained treatments. Most use portable metal fire enclosures to safely contain the fire fueled either by straw (Korfischer et al., 2003), shredded paper (Wright and Klemmedson, 1965), or propane (Wright et al., 1976; Britton and Wright, 1979). Variations include fire rings (horizontal fuel jets) (Rohrberecht and Defosse, 1995) or hand-held propane torches (e.g.,
These methods offer experimental control and flexibility over spatial, temporal, and environmental factors associated with fire studies. We chose to use the portable propane burner method using Wright et al. (1976) as a guide. A ring of mild steel sheeting 1 m tall × 1 m diameter contained 5 equally spaced internal gas jets model (Red Dragon–Engineering Inc. LaCrosse, KS) positioned 20 cm above the soil surface, leaving only the upper portion of the thermocouple tip exposed to direct contact with the soil. Two pairs of thermocouples were placed in the direct path of the burner jets (left and right of center). A larger thermocouple (6.35 mm diameter) was buried 2 cm below the soil surface directly under the larger thermocouple. Figure S1 (available online at https://doi.org/10.1016/j.rama.2018.11.001) illustrates the variation in measured soil temperature exhibited during the heating trials for Medium and Very High intensity burn treatments. After each combustion period, the plots were sprayed with a liter of water to safely extinguish any embers during the burn treatments.

Temperature data were collected using type K thermocouple probes (Omega TJ36-CAXL) recorded at 2-sec intervals (Omega RDXL4SD). Two pairs of thermocouples were placed in the direct path of the burner jets (left and right of center). A larger thermocouple (6.35 mm diameter) was pressed into the soil surface, leaving only the upper portion of the thermocouple tip exposed to direct contact with the flame. We found that this placement reduced otherwise extreme temperature fluctuations recorded when the thermocouple was simply laid on top of the soil (due presumably to slight ever-present variations in surface microrelief, which altered the amount of thermocouple surface area exposed to the flame). The second, smaller thermocouple (3.18 mm diameter) was buried 2 cm below the soil surface directly under the larger thermocouple. Figure S1 illustrates the variation in measured soil temperature exhibited during the heating trials for Medium and Very High intensity burn treatments. After each combustion period, the plots were sprayed with a liter of water to safely extinguish any embers during the burn treatments.

**Table 1**

<table>
<thead>
<tr>
<th>Species common name (code)</th>
<th>Family</th>
<th>Bee fauna</th>
<th>Dormant appearance</th>
<th>Average number plants (std dev)</th>
<th>Yr planted</th>
</tr>
</thead>
<tbody>
<tr>
<td>Astragalus filipes (ASFI)</td>
<td>Fabaceae</td>
<td>Gen</td>
<td>Stout taproot, shallowly buried rootcrown</td>
<td>c = 4.3 (1.0)</td>
<td>2009</td>
</tr>
<tr>
<td>Eriogonum umbellatum (ERUM)</td>
<td>Polygonaceae</td>
<td>Gen</td>
<td>Spreading woody caudex, dormant buds above surface</td>
<td>c = 6.8 (2.2)</td>
<td>2005</td>
</tr>
<tr>
<td>Lomatium dissectum (LODI)</td>
<td>Apiaceae</td>
<td>Gen/Oligo</td>
<td>Massive taproot, buried rootcrown</td>
<td>c = 6.0 (2.6)</td>
<td>2005</td>
</tr>
<tr>
<td>Penstemon cyaneus (PECY)</td>
<td>Scrophulariaceae</td>
<td>Gen/Oligo</td>
<td>Thick taproot, branched caudex, buds at surface</td>
<td>c = 3.5 (1.0)</td>
<td>2009</td>
</tr>
<tr>
<td>Sphaeralcea grossulariifolia (SPGR)</td>
<td>Malvaceae</td>
<td>Gen/Oligo</td>
<td>Thick taproot, short-branched caudex</td>
<td>c = 6.5 (1.0)</td>
<td>2006</td>
</tr>
</tbody>
</table>

1 Penstemon pollen is collected by pollen wasps in the genus Pseudomasaris.

**Table 2**

<table>
<thead>
<tr>
<th>Treatment (code)</th>
<th>Prescription</th>
<th>Peak temp (°C) at surface</th>
<th>Peak temp (°C) 2 cm below surface</th>
<th>No. of trials</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control (C)</td>
<td>No fuel applied</td>
<td>Ambient</td>
<td>Ambient</td>
<td>na</td>
</tr>
<tr>
<td>Very Low (VL)</td>
<td>52 kPa (7.5 psi), 25 sec</td>
<td>132 ± 37</td>
<td>49 ± 4</td>
<td>5</td>
</tr>
<tr>
<td>Low (L)</td>
<td>52 kPa (7.5 psi), 50 sec</td>
<td>241 ± 60</td>
<td>57 ± 4</td>
<td>15</td>
</tr>
<tr>
<td>Medium (M)</td>
<td>103 kPa (15 psi), 65 sec</td>
<td>353 ± 31</td>
<td>66 ± 6</td>
<td>5</td>
</tr>
<tr>
<td>High (H)</td>
<td>103 kPa (15 psi), 175 sec</td>
<td>500 ± 78</td>
<td>102 ± 23</td>
<td>8</td>
</tr>
<tr>
<td>Very High (VH)</td>
<td>103 kPa (15 psi), 240 sec</td>
<td>629 ± 52</td>
<td>129 ± 15</td>
<td>5</td>
</tr>
</tbody>
</table>
this dry part of the season. Before moving the portable burner, post-
treatment temperature monitoring continued for about 15 minutes,
until subsurface temperatures had peaked.

Analysis

Plant data were collected the next growing season during April and
May 2013, counting again live plants in the strip of uniform heating
across each plot. The relationship between fire intensity and individual
mortality was tested using logistic regression. For all significant models,
treatment effects were compared against control groups with a Dunnett
post hoc multiple comparison test. Survival data were transformed by
adding one to all counts when the control group value was zero (no
mortality). All analyses used R Core Team (R version 2.14.1, Vienna,
Austria) (R-Team, 2012) and an alpha of 0.05.

The relationship between fire intensity and several flowering parame-
ters relevant to bees were also tested, specifically whether fire in-
tensity suppressed all bloom (plants survived but did not bloom) or
changed flower abundance. Not all parameters could be measured for
all species. Bloom suppression was evaluated for Astragalus filipes
using logistic regression described earlier. All other bloom parameters
were tested using analysis of variance and pairwise multiple compari-
sions with Bonferroni adjustment for significant models. Data were log
transformed to meet normality assumptions. Differences in bloom
abundance were tested on all species, with the exception of Sphaeralcea
grossulariifolia, because its resprouting confounded counts of survivors.
A. filipes bloom abundance was estimated by counting the number of
seed pods per plant, a conservative measure of earlier flower abundance
(Watrous and Cane, 2011). For the remaining plant species, average
numbers of flowering spikes (Dalea ornata), racemes (Penstemon
cyanus), or umbels (Eriogonum umbellatum and L. dissectum) per trial
were used to calculate averages per surviving plant. Before burning,
treatment groups had similar numbers of spikes, racemes, or umbels
(P > 0.3). For D. ornata, we found that the flower number was highly cor-
related with spike length (n = 35, r² = 0.9) over a range of spike
lengths, allowing use of summed spike lengths per plant as a proxy for
total production of its tiny crowded flowers (Pavlovic et al., 2011).
Data are presented as the mean ± one standard deviation unless other-
wise stated.

Results

The six species in this study, represented by 915 individual plants
(see Table 1), exhibited species-specific responses to increasing intensi-
ties of experimental burning treatments. Mortality results are addressed
first for all species, and then individual reproductive responses are re-
ported in separate subsections.

Mortality

Incremental increases of fire intensities differentially influenced
overall mortality for all species tested in this study except L. dissectum
(Table 3). The six species can be sorted out into two response groups
—“fire-tolerant” and “fire-intolerant” (refer to Miller et al., 2015) (Fig.
2). The two most intense heating treatments killed 41–100% of individ-
ual plants of three of the six species (E. umbellatum, P. cyanus, and S.
grossulariifolia) (Dunnett P < 0.02) (see Fig. 2a). Plants of the tolerant
group—L. dissectum, A. filipes, and D. ornata—largely survived burning
at even the most extreme fire intensities (prolonged burns with surface
temperatures ≥300°C), rarely exceeding 30% mortality (see Fig. 2b).
Conversely, even the mildest fire intensity treatment killed > 30% of E.
umbellatum and P. cyanus. Together with S. grossulariifolia, intense
heating killed 60–100% of plants representing these three fire-intolerant
species (see Fig. 2a).

Reproductive Responses

Lomatium dissectum

Of the 125 individual plants in this group, 23 control plants persisted
through the year (96%), as did 94 of the burned (treated) plants (93%
survival) and all plants flowered. Their average number of umbels per
plant was unaffected by burn intensity (F = 1.1; P = 0.42). Before

Table 3

<table>
<thead>
<tr>
<th>Plant code</th>
<th>Deviance (d.f.)</th>
<th>Fisher value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ASFI</td>
<td>2.22</td>
<td>84 (111)</td>
</tr>
<tr>
<td>DAOR</td>
<td>2.95</td>
<td>90 (195)</td>
</tr>
<tr>
<td>ERUM</td>
<td>7.26</td>
<td>252 (187)</td>
</tr>
<tr>
<td>LODI</td>
<td>-0.56</td>
<td>59 (124)</td>
</tr>
<tr>
<td>PECP</td>
<td>4.71</td>
<td>116 (83)</td>
</tr>
<tr>
<td>SPGR</td>
<td>5.02</td>
<td>158 (172)</td>
</tr>
</tbody>
</table>

AIC indicates Akaike information criteria.
burning, plants averaged two umbels each across all control and treatment plots. A year later, after burning, umbel counts doubled or tripled (ranging from 4 to 6).

*Astragalus filipes*

Of the 112 plants in this group, all 17 controls persisted through the year, as did 81 of the burned plants (85% survival). Burn intensity was a significant factor for predicting bloom among surviving *A. filipes* individuals the year after burning ($z = 2.41$, $P = 0.02$). Half as many surviving plants bloomed after high-intensity burning compared with unburned controls (40% vs. 87%) (Dunnett test, $z = -2.55$, $P = 0.04$) (Fig. 3). However, among openly pollinated survivors that did bloom, seed pod production was similar across fire intensities (average 46–272 pods per plant) ($F = 1.81$, $P = 0.16$).

*Dalea ornata*

Of the 196 plants in this group, all 20 control plants survived, as did 164 burned plants (93% survival). All but one survivor flowered the following summer. Fire intensity did somewhat affect the cumulative number of flowering racemes per plant ($F = 4.99$, $P = 0.005$) except for the mildest fire intensity (Very Low) (pairwise multiple comparison test with Bonferroni adjustment, $P = 0.053$) (Fig. 4). In the year after burning, plants in the Control and Very Low fire treatment produced an average of 9–11 racemes each, which was about two racemes fewer than the year before. In contrast, per plant in each treatment (as a surrogate for flower counts) did not change with increasing fire intensity ($P = 0.08$).

*Penstemon cyaneus*

Of the 84 individual plants in this group, 13 control plants survived (93%), whereas only 27 survived burning (39%). The response of bloom-to-burn intensity was analyzed at the plot level because data had not been collected by individual plant. Instead, we counted the total numbers of flowering racemes per plot in each trial, from which we calculated an average number of racemes per plant. Consequently, we can only report a failure to bloom when the sum of racemes in a plot was zero. We are therefore confident that at a minimum, 11 of the 27 survivors (41%) failed to flower. Of the 16 plants that did bloom, burning reduced the numbers of racemes in all treatments ($F = 4.99$, $P = 0.005$) except for the mildest fire intensity (Very Low) (pairwise multiple comparison test with Bonferroni adjustment, $P = 0.053$) (Fig. 4). In the year after burning, plants in the Control and Very Low fire treatment produced an average of 9–11 racemes each, which was about two racemes fewer than the year before. In contrast,
survivors of Low and Medium fire intensities averaged fewer than two racemes each and the three plants surviving the High intensity burning together produced only two racemes. No plants survived the Very High treatment.

**Eriogonum umbellatum**

Of the 188 individual plants in this group, all 27 control plants were alive the year after treatment, whereas only 48 survived burning (30%). As with PECY, we could not test whether fire suppressed bloom but we can report that at least 22 survivors (46%) failed to flower. Those that did bloom produced significantly fewer umbels than unburned controls ($F = 18.02; P < 0.0001$) (Fig. 5), regardless of fire intensity ($P < 0.0001$). Umbel counts in the control group doubled in the year following burn treatments (from 12 to 28 per plant), whereas survivors of the three milder burn intensities (Very Low, Low, and Medium) produced far fewer umbels after burning (dropping from 10 to 2 per plant). The four plants surviving the hottest fire intensity (Very Hot) failed to flower.

**Discussion**

The reciprocal nature of the plant-pollinator relationship requires the continued and uninterrupted presence of both participants. Landscape-level disturbances like fire can temporarily disrupt this relationship by removing the supplies of pollen and nectar needed by bees and thereby the pollination services that they provide to wildflowers. The outcomes of such disruptions are of interest to land managers tasked with rehabilitation, especially in sagebrush ecosystems, where wildfires are growing in size, frequency, and intensity compared with historical norms (e.g., Chambers and Wisdom, 2009). The results of this study advance the work of others in the Great Basin, showing that fire intensity is a defining—albeit variable—factor influencing survival and reproduction of perennial herbaceous forbs.

The species studied here represent a spectrum of fire sensitivities, underscoring the key role of plant species identity for characterizing fire severity in a wildflower community. On the one hand, species like *L. dissectum* are virtually fireproof, surviving and flowering well across a range of fire intensities. Likewise, both *A. filipes* and *D. ornata* were resistant to a broad range of fire intensities, but some surviving plants then failed to bloom. At the other extreme, both *P. cyaneus* and *E. umbellatum* were vulnerable to even the mildest fire intensities, and those that did survive were less likely to bloom. Insights into the fates of local plant-pollinator relationships can be gained when comparing the species-specific survival and flowering probabilities of wildflowers with natural history traits of the bee species in their floral guilds—specifically nesting habits and breadth of diet. How these bee traits combine with wildflower fire susceptibility to predict the fate of their interaction can be illustrated by the following example combinations of wildflowers and their guilds of bees.

Resource specialization is a trait that can increase a species’ risk of extinction (or local extirpation) (Groom et al., 2005). This type of extinction is exemplified by the pollen wasp *Pseudomasaris vespoidea*, a prevalent pollen specialist (oligolectic) for some Great Basin *Penstemon* species (Torchio, 1974; Gess, 1996). Most wasps feed their young a diet of animal protein, but larval *Pseudomasaris* (Masarinae) wasps receive a pollen diet (Gess, 1996). Adult wasps construct mud nests against aboveground surfaces of rocks and woody stems. The *Penstemon* hosts of *P. vespoidea*, including *P. cyaneus*, seem vulnerable to fire (inferred in Pechanez et al., 1944). We found that half of *P. cyaneus* plants burned in this study died after even mild heating, and high-intensity fire completely eradicated this species. In addition, at least 22% of the surviving plants failed to bloom the year after fire and those that did produced 40–60% fewer flowering racemes. Burn mortality, coupled with curtailed bloom among survivors, will sharply diminish available *Penstemon* bloom the year after fire. Being an oligolectic, *P. vespoidea* cannot exploit other flowering genera. Moreover, the exposed nests of *Pseudomasaris* render them susceptible to lethal heating by fire as well. In this example, the plant and pollinator are both at risk of extirpation from the burned area. Presumably they will eventually reestablish, although the larger fires now common in the Great Basin (Chambers and Pellant, 2008; Keane et al., 2008), will slow recolonization (Love and Cane, 2016).

By itself, such taxonomic specialization is not a factor that always exacerbates vulnerability to fire. Other natural history traits—of both the pollinator and plant—must be considered. For instance, across the Great Basin, a group of small solitary bees (*Andrena*, esp. subgenus *Micranda*) (Ribble, 1968) seem to be consistently reliant on species of *Lomatium* for pollen to provision their nests (Cane and Love, 2016 and personal observation). Adults of these oligolecic *Andrena* bees are active only in the early spring, well before the fire season. Like all *Andrena*, their soil nests are excavated deeply enough that their progeny escape lethal temperatures (Cane and Neff, 2011). Thus, all life stages of these *Lomatium* pollinators are safe from fire. As others have earlier reported (Kaye et al., 2001; Miller et al., 2015; Wrobleski and Kaufman, 2003), we regularly found populations of *Lomatium* to be present in the years after fire (Cane and Love unpublished). Our experiments showed that these plants are likely survivors, as mature *L. dissectum* grew and bloomed the year after even after the most intense burning treatment. As with *Micranda* nests, we expect that *Lomatium* taproots benefit from the sharp attenuation of surface heating with soil depth (DeBano, 2000). We measured taproot crown depths in one population of mature *L. dissectum* growing naturally near Logan, Utah, finding them buried 6 cm beneath the soil surface ($n = 20$, range $3.5–8$ cm), deep enough to realize a dramatic reduction in surface heating. For *L. dissectum* and *Micranda*, their mutually specialized plant-pollinator relationship is nearly fireproof, owing to the early spring bloom and robust fire protection of the buried taproot of *Lomatium*, coupled with the soil nesting habit and spring flight season of their oligolecic *Micranda* bees. If both are present before a fire, we can be confident they will be present after, regardless of fire intensity.

This stark contrast in postfire survival between *P. cyaneus* and *L. dissectum* likely results from the exact positions of basal buds relative to the soil surface and the proportions of plants thus exposed, rather than any innate differences in thermal tolerance. For our hottest burn treatment, a thermocouple tip buried just 2 cm below the soil surface was 500°C cooler than one placed at the soil surface (see Table 2). Given this insight for the thermal insulation of buried dormant buds, we can reasonably extend our results to some other groups of

![Figure 5. Burn intensity sharply reduced umbel counts on *E. umbellatum* survivors; asterisks indicate significant difference compared with control using pairwise multiple comparison test with Bonferroni adjustment (± standard deviation).](image-url)
herbaceous perennial wildflowers that are common in sagebrush steppe. Species like *L. dissectum* (and its congeneric) that grow from a taproot or bulb often have their dormant basal buds well below the soil surface. In the Great Basin flora, these would include bulb-forming species in the Liliaceae (e.g., *Allium, Camassia* and *Toxicoscordion*) and many tap-rooted Asteraceae (e.g., *Balsamorhiza* and *Crepis*) and Fabaceae (e.g., *Astroagalus* and *Dalea*). Like *L. dissectum* and *A. filipes*, we expect plants of these taxa to survive many Great Basin fires. Conversely, the woody twigs of *E. umbellatum* and surface rosettes of *P. cyanus* bear the basal dormant bud(s) where they experience the direct surface heat of flames during fires. Most of the hundreds of other species of *Eriogonum* and *Penstemon* have similar dormant forms and so should also be vulnerable to wildfire. For other wildfire taxa, we were not satisfied with our ability to measure the precise placement of a plant’s basal buds relative to the soil surface, particularly away from our controlled agricultural setting.

We encountered several serendipitous field opportunities the year after a wildfire to ground-truth these predictions of fire tolerance among Great Basin forbs. At several locations (near Hanford, Washington and King Hill, Idaho), we found large scattered plants of *D. ornata* persisting in dense stands of unchared grass. Recent wildfires had facilitated cheatgrass’s dominance at this site (Chambers et al., 2007). The persistence of mature blooming *D. ornata* plants after these fires is consistent with results from our experiments. In 2013, we surveyed wildflowers and bees the spring after a wildfire in northern Elko County, Nevada. Large mature sagebrush had been burned down to charred stumps. Despite the apparent severity of the fire and in accord with our experimental results, we found several hundred robust *A. filipes* plants blooming the year after burning. The bases of these plants were visibly charred (Fig. S2; available online at https://doi.org/10.1016/j.rama.2018.11.001) showing that the fire had burned over them without killing them or deterring bloom. Their numerous flowers were being visited by ground-nesting *Eucera* and *Osmia* bees. In contrast, the year after a wildfire west of Grouse Creek, Utah, we found that *A. filipes* beyond the fire perimeter was similarly robust and laden with bloom (and bees), but those inside the fire perimeter were far shorter and lacked bloom. This fire burned through juniper woodland and so may have been hotter. Each of these forb responses is consistent with the results of our burning experiments.

Fire-tolerant forbs can differ in their value to the broader Great Basin bee community. At one extreme, *L. dissectum* attracts a small guild of ground-nesting solitary bees, mostly *Andrena*, and in particular, two oligolectic *Micrandrena* (Cane and Love, 2016). These species are shared with other *Lomatium* (e.g., *L. ambiguum, L. rudiacaule, L. triternatum*) but no other forbs that we have surveyed (Cane and Love, 2016). After fire, these bees will continue to faithfully pollinate various *Lomatium*, but little else. In contrast, *A. filipes* attracts a taxonomically rich guild of native bees, primarily solitary species of *Anthidium, Eucera,* and *Osmia* plus social bumble bees (*Bombus*) (Cane and Love, 2016). None appear to be oligolectic. Of the 85 bee species collected at *A. filipes*, 32 are *Osmia*, representing one-fourth of the entire named U.S. *Osmia* fauna (Cane and Love, 2016). We have collected *A. filipes* bees visiting both other Great Basin legumes (e.g., *Dalea, Hedysarum, Lupinus,* and other *Astragalus*) and genera of other families (e.g., *Allium, Camassia,* and *Phacelia*). After fire, surviving *A. filipes* can thus feed its diverse guild of bees that in turn visit and likely pollinate a diverse mix of other forbs in the Great Basin. Conversely, where *A. filipes* is reintroduced by seeding after fire, it is likely to have at least one of its necessary pollinators (*Watrous and Cane, 2011*) already available in all but the most degraded plant communities. Like *A. filipes*, species of *Balsamorhiza* also have diverse guilds of bees (76 species for *B. sagittata*) that are shared with other flower genera (Cane and Love, 2016). Like *L. dissectum*, species of *Balsamorhiza* are likely rendered fireproof by their deep taproots and vernal flowering (Pechanec et al., 1944). By integrating knowledge of the common forbs in their local communities with insights into their likely fire susceptibilities and guilds of bees, local land managers can strategically choose forbs for reseeding mixes that best benefit desired native bees that will pollinate additional forbs and/or have ready-made pollinators at hand after a wildfire.

**Implications**

The fates of native bees after fire in sagebrush habitats are inextricably linked with the fates of their native floral hosts and vice versa. Where fire eliminates fire-intolerant forbs, their surviving pollinators would suffer diminished reproduction, switch to fire-tolerant local hosts (unless oligolectic), or be forced to try dispersing beyond the burn perimeter. In turn, a vacated local bee fauna jeopardizes sexual reproduction of their recovering floral hosts in later years, particularly in the Great Basin, where the common perennial forbs typically benefit from, or require, pollinating bees (Cane, 2008). Identifying vulnerable plant-pollinator relationships is an important conservation goal, as in the case of the mutual fire intolerance of *Penstemon* and *Pseudomasaris*. However, as the *Lomatium*/*Andrena* relationship illustrates, other specialized plant-pollinator relationships endure fire. Rangeland managers wanting to leverage scarce restoration resources can take advantage of forbs that attract diverse generalist bees. Fostering fire-tolerant *A. filipes* and *D. ornata*, for instance, would support dozens of generalist bee species. These bees can use and pollinate many additional floral hosts in the flora of the sagebrush steppe.

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