Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers

JOHN M. MOLA iD † AND NEAL M. WILLIAMS

Graduate Group in Ecology and Department of Entomology and Nematology, University of California, 1 Shields Avenue, Davis, California 95616 USA

Abstract. Fire is a dominant, and well-studied, structuring force in many temperate and semi-arid communities; yet, few studies have investigated the effects of fire on multi-trophic interactions. Here, we ask how fire-induced changes in flowering affect the abundance of bumble bee foragers (*Bombus vosnesenskii*) and whether differences in floral resource availability are due to changes in plant species composition or lengthened bloom of a consistent set of species within burned and unburned grasslands. Following fire, burned and unburned sites had similar early spring bee and floral abundances. However, after the early bloom, forager activity remained high only in burned sites, where floral abundance persisted for longer. Importantly, the increased floral abundance following fire was due to a lengthening of within-species flowering phenology, as burned areas later in the season retained floral abundance and composition similar to that of unburned areas early in the season. Furthermore, density of flower patches chosen by bumble bee foragers was significantly higher at burned sites, suggesting an increase in patch quality for foragers in post-fire communities. Our results suggest positive effects of fire for bumble bee foragers and forb communities in California grassland ecosystems in the year following disturbance, namely through differences in plant phenology and floral density. We conclude that fire-induced changes in flowering phenology can alter interspecific interactions and benefit pollinators.

Key words: bumble bees; disturbance; fire; flowering; interspecific interactions; phenology; pollinators; seasonality.

† **E-mail:** jmmola@ucdavis.edu

INTRODUCTION

Fire is a dominant ecological disturbance affecting plant communities worldwide (Bond and Van Wilgen 1996). Fire-induced changes in soil nutrient availability (Henry et al. 2006), hydrologic regimes (Daubenmire 1968), and reduced competitive pressure (Naveh 1975) influence the resultant post-fire plant community, particularly for fire-adapted species common to fire-prone ecosystems (Keeley et al. 2011, Lamont and Downes 2011). Post-fire changes to plant communities also will likely impact floral visitors, particularly bees, which rely exclusively on flowers for food resources. Given the large-scale impact of fire on plant communities,

increases in wildfire due to changes in climate and land use (Jolly et al. 2015), and the reliance of most angiosperms on insect pollinators for successful reproduction (Ollerton et al. 2011), understanding the direct and indirect ways fire alters flower use by bees and other pollinators will be important for the maintenance of ecosystem services in many fire-prone regions.

Recent studies have found a range of positive to negative effects of fire on pollinator communities using space-for-time substitutions (Ne'eman et al. 2000, Potts et al. 2001, 2003, Moretti et al. 2009, Grundel et al. 2010), prescribed burn history (Campbell et al. 2007, Nuland et al. 2013), or experimental burning (Tunes et al. 2016). Overall,

heterogeneous fire regimes appear to increase pollinator diversity (Ponisio et al. 2016), but explanations for why some bee species respond positively to fire are largely undeveloped. Here, we test whether fire-induced changes in flowering phenology and floral density can be exploited by bumble bees, resulting in a potentially beneficial impact for individuals capable of surviving fire or recolonizing burned areas.

Fire has been found to increase nectar concentrations (Potts et al. 2003) and can prolong flowering for some individual plants (Wrobleski and Kauffman 2003). For generalist flower visitors such as bumble bees, population- or community-level floral abundance is also critical and will determine resource availability throughout the flight season. A prolonged flowering season, often sustained by diverse and abundant flower species, is especially important for bumble bees, whose flight seasons are long relative to many other bee taxa (Williams et al. 2012). Bumble bees are often ecologically and economically important pollinators (Free 1970, Goulson 2009, Kleijn et al. 2015), so understanding whether and how fires create conditions favorable to their populations is of great importance for wild and managed plants that depend on them for pollination.

We asked how floral abundance, density, and phenology of the plant community changed within the flowering season for grasslands following fire and how those changes altered bumble bee foraging activity and patch use within burned and unburned meadows. We hypothesized that (1) floral abundance and forager activity would be higher in burned compared to unburned areas in the year following fire, (2) burned areas would have high floral abundance for a longer duration, and (3) floral density would be higher in burned areas compared to unburned both within and across year. If bumble bee foragers are able to fly to and exploit flower patches in burned areas, fire may have a beneficial impact beyond simple increases in plant abundance, by inducing a prolonged flowering season with dense flower patches that afford greater resource availability for pollinators.

METHODS

Study design

The study was conducted at the University of California's McLaughlin Reserve (38°52′25.74″ N, 122°25′56.25″ W) in 2016. Study sites were in grasslands with spring-flowering forb communities typically adjacent to chaparral, oak woodlands, and spring-fed seeps. The forb species bloom over a short period in the spring (typically April–May) and are quickly overgrown by a mix of native and invasive grasses that dominate for the summer. The region has a relatively infrequent fire return interval (ca. 15–75 yr), with short-term positive effects on forb species richness and abundance in grasslands documented after a 1999 fire at the reserve (Safford and Harrison 2004).

Two wildfires burned through the focal grasslands and surrounding areas in August of 2015 (Fig. 1), after most, if not all, bumble bee colonies had completed reproduction and queens had begun overwinter diapause underground (Koch et al. 2012; Appendix S1: Fig. S1). Fires created a set of burned and unburned areas within the region. We capitalized on the natural experiment to compare the impacts of wildfires on floral abundance, phenology, and patch density as well as the resulting impacts on bumble bee use of floral resources. In spring of 2016 (post-fire), we established replicated sites in burned and unburned areas (four in the burned area and five in unburned areas). Sites range from 1.39 to 6.04 ha (mean 2.95 ha), with site boundaries defined by natural barriers such as water, woodland, or a large gap in flowering vegetation (mean nearest neighbor site distance 862.24 m, SD = 593.81 m). There was no correlation between site area and capture rate (Pearson's product-moment correlation = 0.0448, df = 7, P = 0.9089).

Bumble bee captures

In late spring 2016, *Bombus vosnesenskii* were collected at sites during two-hour sampling periods, or until 24 individuals were captured, whichever occurred first. We chose to focus on *B. vosnesenskii* since it was known to be present at all sites prior to fire. Although three bumble bee species are present at the reserve, in previous spring surveys at the field station *B. vosnesenskii* accounted for over 95% of the bumble bee captures, with the other two species (*B. melanopygus* and *B. californicus*) being patchily distributed and rare (J. M. Mola, *unpublished data*). We collected individuals from all areas at the site with flowers, on days with full or partial sun and
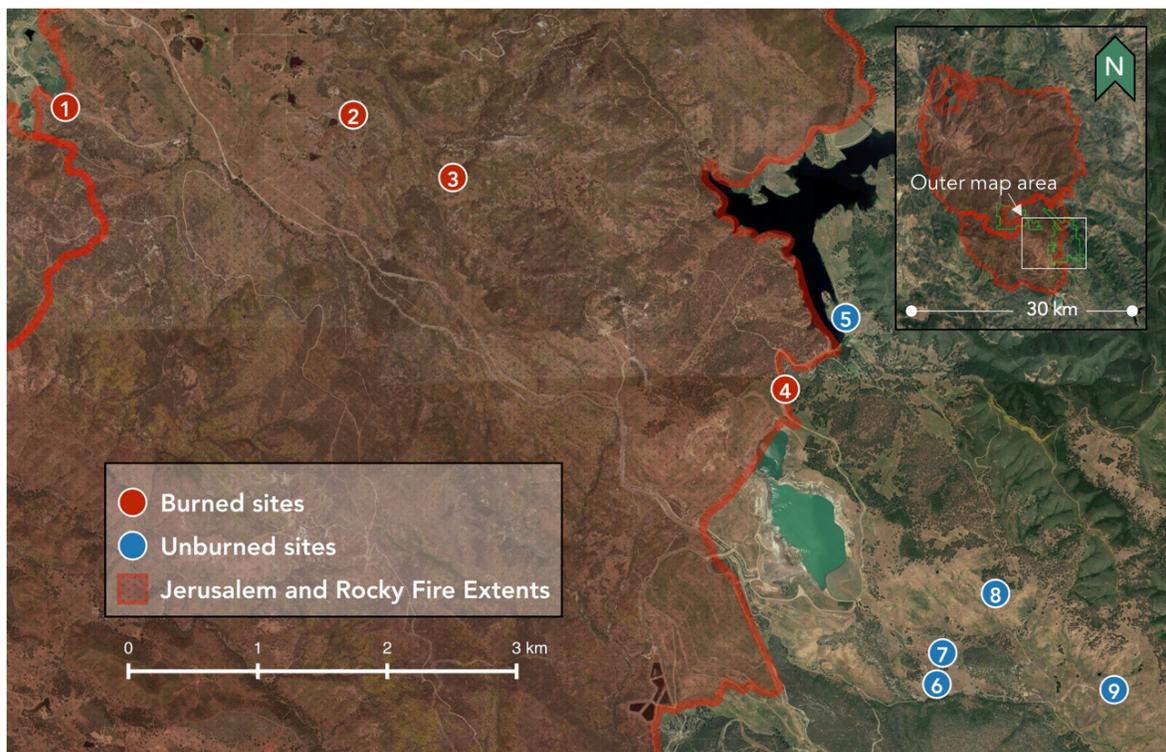
Fig. 1. Map of the study area showing the extent of the Rocky and Jerusalem fires. Red and blue points represent burned and unburned study sites, respectively. Sites 2, 3, 7, 8, and 9 were part of previous surveys on bumble bee floral use. Inset map shows full extent of fire with study area outlined within.

sustained winds below 10 mph. This approach yielded a capture rate, which served as our estimate of bumble bee foraging activity at the site. New colonies are founded each spring; thus, for the burned sites these capture rates represent the abundance of workers from queens who either survived the fire in 2015 or dispersed into the study area post-fire (2016; Appendix S1: Fig. S1). We visited each site twice in a randomized order. Early and late sampling rounds occurred from 19 April to 4 May and 11 May to 20 May 2016, respectively, the critical period for colony growth in our study region (Crone and Williams 2016).

Site-level floral abundance

We estimated floral abundances for all sites on the same day as bee captures. Estimates of the number of inflorescences for each plant species in bloom were made within 50 m radius of site center, and inflorescence abundance was recorded in $\log_{10}$ bins following Williams et al. (2012). For consistency, one observer (JMM) conducted all estimates. Only plant species visited by *Bombus vosnesenskii* at some point in the study, or in previous surveys in this landscape, were retained for analyses (Appendix S2: Table S1). To measure the difference in floral abundance between early and late sampling rounds, we calculated the proportional change in floral abundance, by burn status. The proportional change for each species was then multiplied by its within-treatment (burned or unburned) abundance and standardized by dividing the total floral abundance of all species across all sites. This yielded proportional change weighted by a species' relative floral abundance, and thus quantified a within-species proportional difference in bloom between sampling rounds.

Floral patch quality following fire

Because bumble bees often selectively forage within dense patches of wildflowers (Sih and Baltus 1987, Goulson 1999), we estimated floral density within foraging patches as the percent cover of conspecific flowers within a 1.5 m

radius of capture point for each bee. Estimates were recorded as ranks from 1 to 6 (1: 0–5%, 2: 5–25%, 3: 25–50%, 4: 50–75%, 5: 75–95% and 6: 95–100%). These locations are not independent of the bees captured and reflect resources at patches chosen by foragers within a site, rather than independent measures of the available resources throughout the site. Regardless, these patch-level densities provide us with a proxy for the quality of floral resources available to foragers.

Pre-burn bumble bee capture rates and floral densities

Although it seems unlikely, it is possible that background abundance of bumble bees and flowers differed between sites independent of fire. Because natural wildfire cannot be predicted, fully replicated, pre-fire testing of these variables was precluded; however, five of our nine sites were part of a previous monitoring effort examining foraging pattern of bumble bees, two of which subsequently burned. In a separate analysis, we compared bumble bee capture rates and floral density among these sites using available pre-fire data. In 2015 (pre-fire), capture rates were not recorded using two sampling rounds with timed observations as in 2016. However, time logs derived from Global Positioning System (GPS) units are well correlated with actual collection effort (Pearson's product-moment correlation = 0.953, df = 3, P = 0.01203; Appendix S3), allowing us to use the GPS-derived capture rates as a proxy for pre-fire forager abundance.

Although we cannot directly compare capture rates before and after fire due to limited data, all bees captured before the fire had floral density estimates recorded in the same manner as for post-fire (described above in *Floral patch quality following fire*). These pre-fire density measures thus allow us to test whether patch-level floral density differed among sites before fire, as well as to test for changes in floral density following fire. The latter comparison is critical, as it allows us to determine whether any changes in floral density are fire-induced, or simply preexisting differences among sites.

Statistical analyses

Statistical analyses for all post-fire (2016) data were performed using linear mixed-effects models in R (version 3.3.2) with the *lme4* package (Bates et al. 2014). To test whether fire affected bumble bee foraging activity through its impact on floral abundance following fire, we analyzed differences in bumble bee capture rate with sampling round (early, late), burn status (burned, unburned), log inflorescence abundance, and the interaction between sampling round and burn status, as fixed effects. We used a similar model to test for effects of fire on floral abundance, with log inflorescence abundance as a function of the fixed-effects sampling round, burn status, and their interaction. Similarly, we used the *ordinal* package in R (Christensen 2015) to test for differences in the floral density of patches used by foragers by fitting cumulative-link mixed models with floral percent cover at the capture point as the response variable and sampling round, burn status, and their interaction as fixed effects. Site was treated as a random effect in all models. All presented estimates and analyses of floral abundance are performed on log10 values of inflorescence number. P-values were obtained by likelihood ratio tests of a model with the focal effect against a null model with the focal effect removed.

To test for pre-fire differences in bumble bee abundance among the five sites sampled in 2015, we fit a linear model of GPS-derived capture rates as a function of their future burn status and tested for significance using a one-way ANOVA. We conducted an additional test of floral density between year and burn status using cumulative-link mixed models with floral percent cover as the response variable and year, burn status, and their interactions as fixed effects. This between-year comparison is not possible for bumble bee captures due to differences in collection methods before wildfire; however, the comparison of floral density before and after fire is a critical link between the pre- and post-fire floral community.

RESULTS

Bumble bee captures

Burn status positively affected capture rate, but that effect depended on sampling round (Burn status × Sampling round P < 0.05; Table 1). Capture rates did not differ between burned and unburned areas during the early sampling round but were significantly higher at burned sites during the late sampling round (Fig. 2A). Log inflorescence abundance positively affected bumble bee capture rate (Fig. 2B, Table 1).

Table 1. Results of likelihood ratio tests for linear mixed-effects models and cumulative-link mixed models with site as a random effect.

Response variable	Fixed effects	χ^2	P
(A) Capture rate†	Log inflorescence abundance	13.036	<0.001***
	Burn status	3.106	0.077
	Sampling round	0.056	0.813
	Burn status × sampling round	6.173	0.013*
(B) Log inflorescence abundance†	Burn status	6.993	0.008**
	Sampling round	3.724	0.054
	Burn status × sampling round	9.088	0.002**
(C) Floral density (2016 post-fire only)‡	Burn status	4.335	0.037*
	Sampling round	28.412	<0.001***
	Burn status × sampling round	32.684	<0.001***

Notes: Each test was a comparison of a model with the fixed effect, or interaction, against a null model omitting the fixed effect of interest. Level of statistical significance indicated by *, **, *** for *P*-values <0.05, <0.01, <0.001, respectively.
† Linear mixed-effects model.
‡ Cumulative-link mixed model.

Site-level floral abundance

Burn status significantly increased floral abundance (Fig. 2C; Table 1). Like for bumble bee captures, the increase depended on sampling round (Burn status × Sampling round $P < 0.05$; Table 1), with the overall effect driven by a strong decrease in floral abundance in the late sample round only at unburned sites (Fig. 2D). By contrast, floral abundance at the burned sites remained high and did not significantly differ between the early and late sample rounds (Fig. 2D). The overall species-weighted abundance of blooms declined more steeply in unburned areas, compared to burned sites (-4.91 and -13.26; weighted log abundance for burned and unburned sites, respectively). Declines were not driven by differences in plant species, either between sites of different burn status or from early to late sample rounds (Table 2; Appendix S4). Plant species unique to the burned sites (*Thermopsis californica*, *Wyethia angustifolia*) accounted for <4% of floral abundance within burned sites, and no foragers were captured from these species in 2016 (Appendix S2).

Floral patch quality following fire

Total floral densities of all plant species in 2016 were significantly different between sampling rounds, but the magnitude also depended on burn status ($P < 0.05$; Table 1C), with burned areas having higher floral densities across the season (mean ± SD: 4.43 ± 1.24 and 3.79 ± 1.09 in burned and unburned areas, respectively).

Pre-burn bumble bee capture rates and floral densities

Sites did not significantly differ in their pre-fire bumble bee capture rates when grouped by their future burn status (ANOVA: df = 1, $F = 0.657$, $P = 0.477$). Using 271 pre-fire estimates, sites did not differ in their floral density before fire (cumulative-link mixed model: $\chi^2 = 0.474$, $P = 0.491$). Comparisons of all pre- and post-fire floral densities showed that between-year floral density did not differ for burn status (cumulative-link mixed model: $\chi^2 = 1.129$, $P = 0.288$) or year (cumulative-link mixed model: $\chi^2 = 1.104$, $P = 0.293$) alone, but the interaction between burn status and year was highly significant (cumulative-link mixed model: $\chi^2 = 13.860$, $P = 0.003$), with floral density increasing in burned sites following fire.

DISCUSSION

Burned grasslands sustained abundant floral resources longer into the season than did unburned areas, resulting in prolonged habitat use by bumble bees. These results provide potential mechanisms behind previously reported positive effects of fire on bees (Potts et al. 2003, Ponisio et al. 2016). We demonstrate how bumble bees capitalize on the abundant and prolonged flowering season following fire, highlighting an important within-season difference in the effect of disturbance. More generally, our findings reinforce previous theories of how disturbance can mediate the timing of interspecific interactions (Thompson 1988).
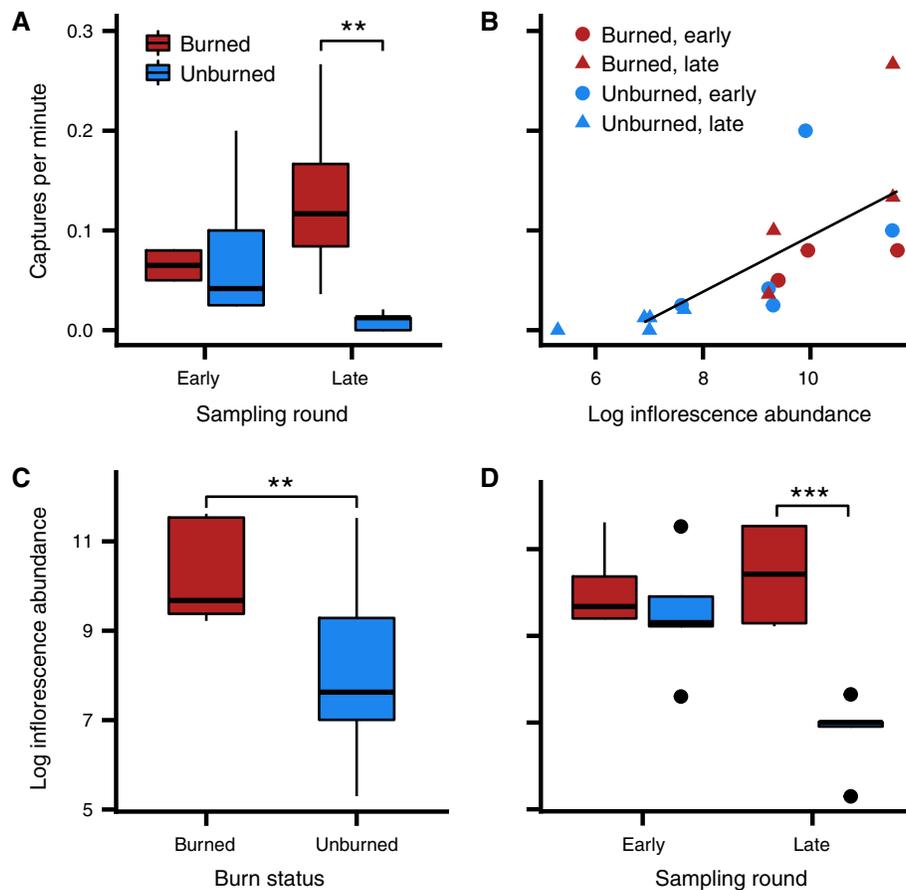
Fig. 2. Bumble bee capture rates and floral abundance in burned (red) and unburned (blue) sites. (A) Captures per minute as a function of burn status and sampling round. (B) Regression of captures per minute and log inflorescence abundance ($R_c^2 = 0.52956$). Early and late sampling periods are represented by circles and triangles, respectively. (C) Floral abundance as a function of burn status. (D) Floral abundance grouped by both sampling round and burn status. Error bars extend to the highest or lowest value within $1.5 \times$ interquartile range from the 3rd or 1st quartile, respectively. Outliers are shown by points outside of this range. Significant pairwise comparisons are shown with brackets (**$P < 0.01$, ***$P < 0.001$).

Importantly, we found that the longer flowering season was not due to differences in plant species composition in burned and unburned sites, whereby additional species that flower sequentially might be promoted as a result of competitive release, nutrient pulses, or other post-fire mechanisms (Bond and Van Wilgen 1996, Keeley et al. 2011). Instead, fire lengthened the flowering season of species common to both burned and unburned sites and thus maintained ample flowering resources for bees. The increase in bloom in burned areas seemed to have caused floral abundance to be sustained at high levels in burned areas in both sampling rounds, which is reflected

in the similarity of burned sites in the late sampling round to unburned sites in the first sampling round (Table 2; Appendix S4). Previous studies have demonstrated that many plants only flower following fire, or have found increased diversity of forb communities following fire (Naveh 1975, Lamont and Downes 2011). Our results add to a growing list of examples showing how fire alters the within-species phenology of flowers (Platt et al. 1988, Wrobleski and Kauffman 2003). However, we are unable to determine whether the prolonged flowering observed here is due to larger plant populations (Miller-Rushing et al. 2008), prolonged individual flowering (Wrobleski and

Table 2. Total log floral abundance at burned and unburned sites for 2016.

| | Burned | | | | Unburned | | | |
| | Sampling round | | | | Sampling round | | | |
Plant species	Early	Late	Proportional change	Weighted abundance	Early	Late	Proportional change	Weighted abundance
Trifolium fucatum	32.20	0.00	−1.00	−8.70	2.30	0.00	−1.00	−0.62
Vicia villosa	29.90	41.40	0.39	7.41	36.80	32.20	−0.13	−2.33
Lupinus succulentus	25.30	11.50	−0.55	−5.42	4.60	0.00	−1.00	−1.24
Lupinus microcarpus	16.10	11.50	−0.29	−2.13	25.30	6.90	−0.73	−6.32
Mimulus guttatus	9.20	13.80	0.50	3.11	9.20	11.50	0.25	1.40
Trifolium hirtum	6.90	11.50	0.67	3.31	6.90	0.00	−1.00	−1.86
Thermopsis californica	4.60	0.00	−1.00	−1.24	0.00	0.00	0.00	0.00
Wyethia angustifolia	4.60	0.00	−1.00	−1.24	0.00	0.00	0.00	0.00
Collinsia heterophylla	0.00	0.00	0.00	0.00	4.60	0.00	−1.00	−1.24
Phacelia tanacetifolia	0.00	0.00	0.00	0.00	6.90	4.60	−0.33	−1.04
Sum (Mean)	128.80	89.70	(−0.23)	-4.91	96.60	55.20	(−0.49)	−13.26

Note: Weighted abundances are adjusted by the proportional change of the plant species and the magnitude of change.

Kauffman 2003), or some combination of the two, but the resulting impact on floral visitors resources remains. Future studies should seek to disentangle the causes of lengthened post-fire flowering. Regardless, this phenological impact has important implications for studies of fire effects on plant and animal communities, because the effect may be missed in studies sampling only a single time in the season.

Bumble bees in burned areas were captured from patches with higher floral density in both sampling periods (Table 1C), suggesting the presence of dense aggregations of flowers for pollinators following fire. Furthermore, the comparison of pre- and post-burn samples from several of the study sites is consistent with the idea that differences in floral density are fire-induced, and not simply due to preexisting site-level differences. Dense floral patches are known to be attractive to workers and result in faster resource return to colonies (Goulson 1999). Increased nectar concentrations following fire, as shown by others (Potts et al. 2003), make it possible that floral quantity and quality both increased following fire. Thus, there is a benefit of fire for bees not only because of longer duration of resource availability, but likely also because of increased efficiency of resource acquisition that can improve colony fitness (Westphal et al. 2006).

The duration of our study is relatively short; however, bumble bee colonies only store enough pollen and nectar for a few days (Heinrich 1979) and colony growth is sensitive to resource dynamics over very short time periods (Crone and Williams 2016), so even a short pulse of resources can positively affect colonies and populations. The grasslands in our study system provide some of the earliest resources to colonies in their development and may be critical for colony establishment. In laboratory-reared and field colonies, a pulse of early-season resources increased the body size and survivorship of workers and ultimately increases reproductive output (R. L. Malfi, N. M. Williams, and E. E. Crone, *unpublished manuscript*). Additionally, the flowering season within our study area in 2016 was lengthened in the adjacent drainages and ephemeral streams (Eric LoPresti, *personal communication*), where we have observed bumble bees foraging after the grasslands completed flowering. Fire therefore likely provides a more sustained spatio-temporal mosaic of floral resources that bridges gaps in the floral community between spring-flowering grasslands and the summer-flowering riparian areas.

In our study, we use capture rate as a proxy for bumble bee abundance. Although these measurements are an activity-based metric and do not assess abundance independent of the presence of flowers, this methodology is standard for assessing relative abundance of pollinator populations (Westphal et al. 2008, Garibaldi et al. 2013) and correlates strongly with colony density (Geib et al. 2015). Because we removed individuals as we sampled, we can be confident we were not simply resampling individual foragers with fidelity for these sites (Ogilvie and Thomson

2016). We conclude that the fire benefitted bumble bee colonies within the foraging range of the burned area and potentially served as a major resource pulse within the landscape.

Fire had a strong positive effect on bumble bee foraging activity through increased floral abundance throughout the burned area, increased floral density in foraging patches, and a prolonged flowering season. The effects of fire on bumble bees were only fully revealed through examining fire's indirect effect operating through changes on floral abundance and by resampling. The main effect of fire on bumble bee captures was only marginally significant, but it is clear that the difference is driven by prolonged floral abundance in burned areas, resulting in a significant interaction between burning and sample round (Table 1; Fig. 2). As such, our results highlight the need to include a phenological component in studies of interspecific interactions and resource use following fire. The decoupling of plant–pollinator phenology due to climate change has been of particular interest to ecologists (Yang and Rudolf 2010), and changes in fire regimes (Jolly et al. 2015) make it likely that plant and pollinator populations will be impacted by both of these processes simultaneously. Including other factors that alter species phenology can help to explain the temporal availability of interaction partners, such as fire, and will be important for understanding of interaction decoupling.

Literature Cited

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Bond, W. J., and B. W. Van Wilgen. 1996. Fire and plants – population and community biology series, 14. Chapman and Hall, London, UK.

Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the blue ridge province in North Carolina. Biological Conservation 134:393–404.

Christensen, R. H. B. 2015. ordinal – regression models for ordinal data. R package version 2015.6-28.

Crone, E. E., and N. M. Williams. 2016. Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production. Ecology Letters 19:460–468.

Daubenmire, R. 1968. Ecology of fire in grasslands. Pages 209–266 in J. B. Cragg, editor. Advances in ecological research. Academic Press, Cambridge, Massachusetts, USA.

Free, J. B. 1970. Insect pollination of crops. Academic Press, Cambridge, Massachusetts, USA.

Garibaldi, L. A., et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611.

Geib, J. C., J. P. Strange, and C. Galen. 2015. Bumble bee nest abundance, foraging distance, and host–plant reproduction: implications for management and conservation. Ecological Applications 25: 768–778.

Goulson, D. 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. Perspectives in Plant Ecology, Evolution and Systematics 2:185–209.

Goulson, D. 2009. Bumblebees: behaviour, ecology, and conservation. Second edition. Oxford University Press, Oxford, UK.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecological Applications 20:1678–1692.

Heinrich, B. 1979. Bumblebee economics. Harvard University Press, Cambridge, Massachusetts, USA.

Henry, H. A. L., N. R. Chiariello, P. M. Vitousek, H. A. Mooney, and C. B. Field. 2006. Interactive effects of fire, elevated carbon dioxide, nitrogen deposition, and precipitation on a California Annual Grassland. Ecosystems 9:1066–1075.

Jolly, W. M., M. A. Cochrane, P. H. Freeborn, Z. A. Holden, T. J. Brown, G. J. Williamson, and D. M. J. S. Bowman. 2015. Climate-induced variations in global wildfire danger from 1979 to 2013. Nature Communications 6:7537.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. Fire as an evolutionary pressure shaping plant traits. Trends in Plant Science 16:406–411.

Kleijn, D., et al. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nature Communications 6:7414.

Koch, J., J. Strange, and P. Williams. 2012. Bumble bees of the western United States. Publication No. FS-972. USDA Forest Service Research Notes, Fort Collins, Colorado, USA.

Lamont, B. B., and K. S. Downes. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. Plant Ecology 212: 2111–2125.

Miller-Rushing, A. J., D. W. Inouye, and R. B. Primack. 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. Journal of Ecology 96:1289–1296.

Moretti, M., F. de Bello, S. P. M. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. Journal of Animal Ecology 78:98–108.

Naveh, Z. 1975. The evolutionary significance of fire in the mediterranean region. Plant Ecology 29:199–208.

Ne'eman, G., A. Dafni, and S. G. Potss. 2000. The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. Plant Ecology 146:97–104.

Nuland, M. E. V., et al. 2013. Fire promotes pollinator visitation: implications for Ameliorating Declines of Pollination Services. PLoS ONE 8:e79853.

Ogilvie, J. E., and J. D. Thomson. 2016. Site fidelity by bees drives pollination facilitation in sequentially blooming plant species. Ecology 97:1442–1451.

Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Platt, W. J., G. W. Evans, and M. M. Davis. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76:353–363.

Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, T. Griswold, and C. Kremen. 2016. Pyrodiversity begets plant-pollinator community diversity. Global Change Biology 22:1794–1808.

Potts, S. G., A. Dafni, and G.Ne'eman. 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: variation in pollinator diversity, abundance and effectiveness in response to fire. Oikos 92:71–80.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, C. O'Toole, S. Roberts, and P. Willmer. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. Oikos 101:103–112.

Safford, H. D., and S. Harrison. 2004. Fire effects on plant diversity in serpentine vs. sandstone chaparral. Ecology 85:539–548.

Sih, A., and M.-S. Baltus. 1987. Patch size, pollinator behavior, and pollinator limitation in catnip. Ecology 68:1679–1690.

Thompson, J. N. 1988. Variation in interspecific interactions. Annual Review of Ecology and Systematics 19:65–87.

Tunes, P., V. N. Alves, A. Valentin-Silva, M. A. Batalha, and E. Guimarães. 2016. Does fire affect the temporal pattern of trophic resource supply to pollinators and seed-dispersing frugivores in a Brazilian savanna community? Plant Ecology 218:345–357.

Westphal, C., I. Steffan-Dewenter, and T. Tscharntke. 2006. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. Ecological Entomology 31:389–394.

Westphal, C., et al. 2008. Measuring bee diversity in different european habitats and biogeographical regions. Ecological Monographs 78:653–671.

Williams, N. M., J. Regetz, and C. Kremen. 2012. Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93:1049–1058.

Wrobleski, D. W., and J. B. Kauffman. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. Restoration Ecology 11:82–90.

Yang, L. H., and V. H. W. Rudolf. 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. Ecology Letters 12:1–10.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2056/full