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Floral richness drives pollinator diversity after fire in upland forests and meadows of the Sierra Nevada, California

Gina L. Tarbill[1,2] | Angela M. White[1] | Rahel Sollmann[2,3]

[1]Pacific Southwest Research Station, USDA Forest Service, Placerville, California, USA

[2]Department of Wildlife, Fish, & Conservation Biology, University of California, Davis, California, USA

[3]Department of Ecological Dynamics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany

Correspondence
Gina L. Tarbill, 1731 Research Park Dr, Davis, CA 95618, USA.
Email: gina.tarbill@usda.gov

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Abstract

1. There are concerns over the effects of increasingly large and high-severity fires that burn outside the local natural range of variation on ecosystem services and biodiversity.
2. Pollinators provide important ecosystem services in the dry forests of the western United States where they depend on open habitat created or maintained by frequent, low- to moderate-severity fire.
3. We investigated the impact of burn severity on pollinator diversity in upland forest and meadow habitat at local (i.e., at the plot scale) and regional (burn severity class) spatial scales in the Sierra Nevada of California.
4. In meadows, pollinator richness declined with increasing burn severity, but in uplands, there was no significant effect of burn severity on pollinator richness. Absence of pollinators was more likely to occur in unburned or high-severity uplands.
5. At the regional scale, we found that α was similar among burn classes in both habitats, although communities in burned uplands tended to be less even than unburned uplands. β was significantly higher in moderately burned than unburned upland habitat, but there were no significant differences in β for meadow habitats.
6. Because meadows tend to be both more diverse and more sensitive to the negative impacts of high-severity fire than uplands, conservation measures for pollinators could prioritise the removal of encroaching conifer species that may increase fire severity in these systems.

KEYWORDS
alpha, bees, beta, community composition, insects

INTRODUCTION

Fire controls the composition and structure of many terrestrial ecosystems, and repeated fires that vary in extent, severity (here, the amount vegetative mortality they cause) and frequency over geologic time scales result in pyrodiverse landscapes. These landscapes are characterised by heterogeneity of successional stages, resulting from interactions among fire regime characteristics and species traits, climate, topography and human intervention (Steel et al., 2021). The "pyrodiversity begets biodiversity" hypothesis suggests that regions with temporally and spatially varying fire histories support higher biodiversity by creating more niche space at multiple scales, allowing

more species to coexist (Jones & Tingley, 2021; Martin & Sapsis, 1992; Ponisio et al., 2016). Moreover, disturbance-prone systems may rely upon perturbations to maintain biodiversity by continuously shifting the competitive landscape, such that no one (set of) species can become dominant (Burkle et al., 2015; Grime, 1977; Tilman, 1994). As such, fire may not only increase species richness but also increase species evenness by disrupting the dominance of highly competitive species (Cadotte, 2007; Connell, 1978). Pyrodiversity is maintained by feedbacks in fuel, climate and biotic factors that reinforce a particular fire regime, resulting in habitat heterogeneity (Bowman et al., 2016; Hempson et al., 2018). When fires in historically pyrodiverse regions are regularly suppressed, the diversity of fire effects declines (Steel et al., 2018; Stevens et al., 2017), potentially reducing not only species richness and evenness at local scales, that is, alpha diversity (α) but also the diversity of sub-communities within the larger region, that is, beta diversity (β).

In the mixed-conifer forest of the central Sierra Nevada, frequent and variable intensity fire created a pyrodiverse landscape that shaped community structure and composition for hundreds of years (Skinner & Chang, 1996). Historically, fires in the mid-elevation, mixed coniferous forests burned at low-moderate severity every 5–25 years, with limited high-severity effects (Beaty & Taylor, 2008; Collins & Stephens, 2010). In contrast, mid-elevation meadows burned at low severity every 40 years, with high-severity fire occurring every 200 years (Caprio & Lineback, 1997; Ratliff, 1985). Fires, ignited by both lightning and Indigenous Nisenan, Maidu, Washoe and Me-wuk peoples (Anderson & Moratto, 1996; Klimaszewski-Patterson et al., 2018; Lake et al., 2017), consumed surface fuels (Parks et al., 2015; Ritter et al., 2020), created a heterogeneous patchwork of variable age and stand densities (Bowman et al., 2016; Perry et al., 2011) and prevented conifer encroachment of meadows (Boisramé, Thompson, Kelly, et al., 2017; Lepofsky et al., 2003; Norman & Taylor, 2005). Climate change, land use shifts and fire suppression have increased the extent and severity of fires in this region in recent years, with 10 of the largest and nine of the most destructive wildfires in California's recorded history occurring in the last 10 years (California Department of Forestry and Fire Protection, 2018). These fires burn outside the historic range of variation in size, severity and frequency (Stephens et al., 2014; Williams, 2013) and are expected to have major ecosystem consequences (Bond & Keeley, 2005; Keeley et al., 2011; Pausas & Parr, 2018). In the Sierra Nevada, high-severity fire is associated with lower α of carnivores (Furnas et al., 2022), small mammals (Culhane et al., 2022), plants (Richter et al., 2019) and lichens (Miller et al., 2018) and changes to β of flora (Deak, 2022; Richter et al., 2019; Weeks et al., 2023). Declines in diversity may have larger ecosystem impacts, for example, pollinator diversity loss is associated with decreased pollination services, which may impact both crops and wild plant communities (Albrecht et al., 2012; Martins et al., 2015; Ollerton et al., 2011, Ollerton, 2017).

Pollination is an ecosystem process that is likely affected by pollinator diversity and mediated by fire (Brittain et al., 2013; LoPresti et al., 2018; Peralta et al., 2017). Habitat heterogeneity produced by pyrodiversity may increase pollinator diversity (Brown et al., 2017; Ponisio et al., 2016; Rodríguez & Kouki, 2017), but homogeneous high-severity fire may limit pollinator diversity if the local source populations are destroyed (Brown et al., 2017; Cane & Neff, 2011), floral resources are slow to recover (Potts et al., 2003) or colonisation is limited to disturbance-tolerant species (Brown et al., 2017; Pausas, 2019). In forest habitat, fire creates and maintains gaps in the canopy where understory species dominate, providing ephemeral, but important, pollinator habitat (Matonis & Binkley, 2018). Indeed, several studies have found positive response of bees to high- or moderate-severity fire in these systems (Galbraith et al., 2019, 2023; LaManna et al., 2021; Ponisio et al., 2016). The effects of fire on pollinator diversity in meadows are less clear: both burned and unburned meadows tend to have dense and diverse floral resources (Tarbill, 2022); furthermore, meadows recover relatively quickly from disturbance (DeBenedetti & Parsons, 1979) although community composition may shift (Deak, 2022), thus, pollinator diversity may not be impacted by fire except under the most extreme conditions (Brown et al., 2017; Cane & Neff, 2011).

Here, we investigated how fire affects pollinator diversity and how that response may be moderated by burn severity and habitat (upland forest vs. meadow). To do so, we sampled pollinators in and around the 2014 King fire (lat: 38.805437, long: −120.629714) in the Sierra Nevada, California. This region had not burned in nearly a century; thus, the fire history of the study area was characterised by suppression. We sampled the area 3 years post-fire in upland and meadow habitats that experienced different burn severities. We predicted that fire effects on pollinator diversity would depend on burn severity and habitat type. In upland habitats, we expected pollinator α and β diversity to peak at moderate burn severities due to higher habitat heterogeneity. In contrast, we expected these diversity metrics to be lower in both fire-suppressed unburned and high-severity burned upland habitats that may lack structural and compositional diversity. We expected differences in composition to be greater among unburned and high-severity burned habitat, with moderate-severity habitat sharing species with the other burn categories. In comparison, we expected that burn severity would not be associated with pollinator α and β diversity and composition in meadows because of the high heterogeneity and floral richness in this habitat regardless of burn status. In both habitats, we expected floral richness to positively influence pollinator diversity.

METHODS

Study area

The study area was located in upland and meadow habitats in and around the King fire, which burned in September of 2014 in the Eldorado National Forest, California (Figure 1). Over the two-week period of fire activity, over 39,000 hectares burned, and about half of this area burned at high severity (greater than 75% basal area mortality, USDA Forest Service, 2014). The climate of the study region is Mediterranean, with wet, cool winters and

dry, warm summers. Before the King fire, the forest was largely composed of dense stands of relatively young white fir (Pinales: Pinaceae *Abies concolor* Lindl. ex Hildebr.), ponderosa pine (*Pinus ponderosa* Lawson), sugar pine (*Pi. lambertiana* Douglas), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and incense cedar (Cupressales: Cupressaceae *Calocedrus decurrens* Florin). Pre-fire meadows were dominated by grasses (Poaceae, Juncaceae and Cyperaceae), forbs and small shrubs, with some conifer encroachment. Pollinator taxa found in the area include moths and butterflies (Lepidoptera), bees, wasps and sawflies (Hymenoptera), flies (Diptera), beetles (Coleoptera) and hummingbirds (Trochilidae). We considered any species interacting with the reproductive parts of the flower as a potential pollinator, with the caveat that the influence of species on pollination will vary along the mutualism–parasitism continuum. Furthermore, including all species provides much needed information on the response of non-hymenopterans to changing fire regimes.

Sampling design

Sites were located in roughly homogenous areas (~200 m^2) of a given burn class determined using the United States Department of Agriculture (USDA) Forest Service King fire Rapid Assessment of Vegetation Condition after Wildfire (RAVG, USDA Forest Service, 2014) composite burn index (hence, burn class). The burn class is categorised as unburned (unchanged), low (surface fire with little mortality of dominant vegetation), moderate (mix of surface fire with little mortality and more severe fire with some mortality of the dominant vegetation) and high-severity fire (dominant vegetation has high to complete mortality; Figure 1). Low- and moderate-severity fire was limited, so these categories were grouped into a single category (hence, moderate-severity) to increase sampling area. To minimise differences in pollinator communities due to elevation, we restricted our sampling sites to lower montane forest and meadow communities (between ~1300 and 1800 m above sea level). We excluded private lands, areas slated

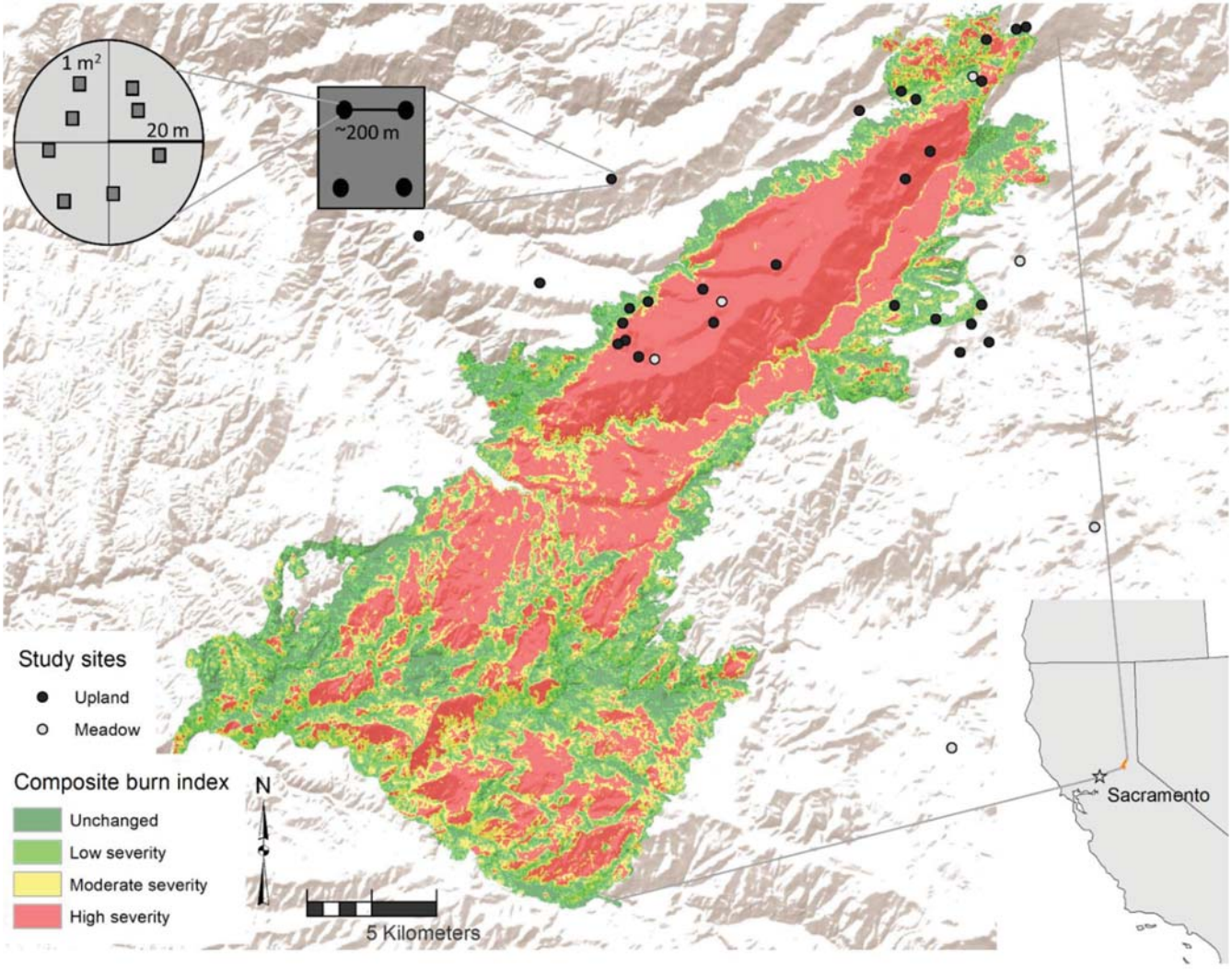

FIGURE 1 Map of study area showing the region of the Sierra Nevada, California, where the King fire burned in 2014 (bottom inset). Points on map indicate study sites within each burn-habitat class, with top insets showing how plots were organised within sites. Pollinators were surveyed within each 20-m radius circular plot, plants with open flowers were surveyed in eight randomly located 1-m^2 quadrats within each plot.

for post-fire management (logging and other site preparation for tree planting) and areas that were inaccessible due to slope (>30%) or distance (>1 km from road). Sites were selected from the remaining area to maximise sample size using ArcGIS 10.6 (Environmental Systems Reasearch Institute, Inc, Redlands, California, USA) in unburned, moderate- and high-severity upland sites and unburned and burned meadow sites in 2017. Ground-truthing ensured that sites were assigned the appropriate burn severity category and habitat type (Supplementary Appendix C).

We used a hierarchical sampling design, with multiple plots nested within sites (Figure 1). We sampled unburned sites to characterise pre-fire conditions and burned sites to compare pollinator communities under severe (high-severity) and more historic (low to moderate-severity) fire conditions. Sites were at least 500 m apart, with three to five plots within a site, depending on the amount of available habitat of interest within a relatively homogenous burn patch. Circular plots (20-m radius) were separated by at least 100 m in either a linear or a circular orientation that best characterised the habitat of interest (Figure 1). Twenty-seven upland sites were divided among unburned forest ($n = 9$), moderate-severity ($n = 9$) and high-severity burns ($n = 9$), with each upland site containing four 20-m circular sampling plots, for a total of 108 unique upland plots (Figure 1). Each upland site was visited twice per season. Meadow habitat was limited within the fire footprint; however, due to their outsized importance to pollinators, we included as many sites as we could within ($n = 3$) and balanced this with sites outside the fire footprint ($n = 3$). Each meadow site was visited three times per season and had three or four plots per site for a total of 22 meadow plots. Plot size and layout followed Loffland et al. (2017) to allow comparison with other studies on bumblebee (*Bombus* spp., Hymenoptera: Apidae) populations in the Sierra Nevada.

Flower-visitor surveys

At each plot during each visit, two observers used a 381-mm (15-in) sized insect net to capture all *Bombus* species in two consecutive 16-min fixed area surveys and all other flower-visiting insects (including Hymenoptera, Diptera, Coleoptera, Hemiptera and Lepidoptera) in one separate 16-min fixed area survey. Although visitation does not necessarily correspond to pollination, the two are highly correlated (Alarcón, 2010) and we refer to flower visitors as pollinators for simplicity. Upon capture, each individual was placed in a vial and held in a cooler until the end of the flower-visitor sampling period, then either identified to species and released or collected for later identification to species or morphospecies using published keys or expert opinion (Triplehorn & Johnson, 2005, University of California, Davis Bohart Museum). Surveys were completed from June to September 2017, during daylight hours (between 8 AM to 5 PM local time) when weather conditions supported insect activity (Supplementary Appendix Figure A1 and A2). For each plot, pollinator abundance of each species or morphospecies was summed across all visits. All specimens were vouchered at the University of California, Davis Bohart Museum.

Floral abundance and richness

We sampled floral abundance and richness to quantify the importance of floral resources to pollinator diversity. We evaluated floral abundance and richness in eight 1-m^2 quadrats in each plot (Figure 1). Plots were divided into quarters and two quadrats were randomly placed in each quarter plot. In each quadrat, we identified every plant in flower to species or morphospecies following the Jepson manual (Baldwin et al., 2012) and counted all inflorescences with open flowers. We chose to only include plants with open inflorescences because they best represent the food resources of nectar and pollen available to pollinators at the time of the visit. Floral abundance was defined as the number of inflorescences with open flowers. Floral richness was the number of unique species with open flowers.

Burn severity metrics

Although sites were selected using coarse categorical assessments of burn severity, we also extracted a point estimate of continuous burn severity for each plot, using the Relative Differenced Normalised Burn Ratio (RdNBR), from the 30-m resolution US Forest Service RAVG data (USDA Forest Service, 2014). RdNBR is considered highly accurate in high-severity, heterogeneous landscapes and is derived from the Normalised Burn Ratio vegetation index that detects differences in pre- and post-fire imagery (Miller & Thode, 2007), with higher RdNBR values indicating more severe burn severity (USDA Forest Service, 2014).

Analysis

All analyses were performed using R statistical program (version 4.1.0, R Development Core Team 2021).

Sampling effort

For diverse taxa, such as insects, species richness tends to increase with sampling and thus differences in sampling effort can introduce bias when comparing communities. To combat this bias, we attempted to equalise effort when collecting data through the use of timed surveys. Despite this, we found large differences in the number of individuals and species detected in upland and meadow habitats. Thus, we decided to model habitats separately to compare the effects of burn severity and floral resources within rather than among habitats (e.g., we do not compare unburned meadow with unburned upland). Within each habitat, we evaluated sampling coverage with the *iNEXT* function in the *iNEXT* package (version 3.0.0, Hsieh et al., 2020) and

TABLE 1 Number of plots sampled (with number of plots that had zero pollinator observations given in parentheses), plot-visits (with the number of plot-visits that had zero pollinator observations given in parentheses), total abundance, total pollinator richness, plot-level mean and standard deviation (SD) of pollinator richness, and sampling coverage (SC, Hsieh et al., 2020) for unburned, moderate-and high-severity uplands and unburned and high-severity meadows in the Sierra Nevada, California, 3 years after the 2014 King fire.

Burn-habitat class	Plots ($n = 0$)	Visits	Total abundance	Total richness	Mean richness	SD	SC
Unburned upland	36 (22)	2	54	28	1.03	1.73	0.69
Moderate-severity upland	36 (12)	2	149	48	2.36	2.52	0.81
High-severity upland	36 (18)	2	113	35	1.75	2.56	0.79
Unburned meadow	11 (2)	3	186	57	8.46	7.20	0.81
High-severity meadow	11 (1)	3	178	58	8.73	7.07	0.80

found coverage was high and fairly similar among burn severity classes (Table 1).

Drivers of pollinator richness

We considered floral resources and continuous burn severity as drivers of pollinator richness. Floral richness and abundance were highly correlated in meadow habitats ($R = 0.82$; Supplementary Appendix Table A1) and somewhat correlated in upland habitats ($R = 0.48$). Floral richness is an important driver of pollinator richness (Kral-O'Brien et al., 2021), with stronger effects on pollinator communities than floral abundance (Blaauw & Isaacs, 2014; Potts et al., 2003; Tarbill et al., 2023); therefore, we chose to only include this metric of floral resources in our models. All continuous explanatory variables were scaled and centred.

To determine the factors that influence pollinator richness at local scales, we used the *GLMMadaptive* package (version 0.8–2, Rizopoulos, 2020) to build generalised linear mixed models (GLMM) of species richness (observed unique number of species per plot) with site as a random effect to account for multiple plots nested within a site. The meadow data were modelled with a negative binomial distribution to account for overdispersion and included floral richness, continuous burn severity and elevation, because of relatively high variation in elevation in meadows. We did not include a quadratic burn severity term in meadow habitat because values were largely bimodal indicating that meadows were either unburned or burned at high severity. The upland data were modelled with a hurdle model, a two-part model that handles count data with excess zeros and overdispersion. In this case, we first model the binomial probability that no pollinators occur at a plot and then apply a GLMM with the zero-truncated Poisson distribution to describe the positive counts of pollinator species. This structure was necessary to account for the large number of upland plots without any pollinator observations. Both components modelled their respective response variables as a function of floral richness (averaged over all visits) and burn severity (linear and quadratic continuous burn severity), to account for peaks in richness at moderate severity that have been observed for understory plants (Richter et al., 2019) and pollinator abundance (Tarbill et al., 2023). Estimates of coefficients for the non-zero submodel relate to a Poisson mean adjusted to include zero data to account for the fact that a Poisson random variable can take on zero values (Rizopoulos, 2020). Hence, we interpret the coefficients qualitatively as significantly positive or negative, rather than as absolute values of change in richness. Model fit was evaluated with the *Dharma* package (version 0.4.6, Hartig, 2021, Supplementary Appendix Figures A3 and A4).

Alpha diversity (α)

Because species diversity is linked to both the number of unique species and their relative abundance, we used Hill's diversity (D) to provide a measure of α for each habitat in each burn class. Hill's numbers are a family of α measures that differ only by the value of an exponent q, which represents sensitivity of diversity to common species: as q increases, species abundance is weighed more heavily such that abundant species contribute more to D, and rare species are discounted. The family of Hill's numbers for a given community may be defined as a diversity profile, a function for Hill's diversity that varies in sensitivity to abundance (q):

$$D = \left(\sum_{i=1}^{S} p_i^q\right)^{(1/1-q)},$$

where S is the number of species, p_i is the relative abundance of species i and q is the sensitivity parameter ($q \geq 0$; Chao et al., 2014). When $q = 0$, species abundance is not considered, and D is equal to species richness. For $q = 1$, the function is undefined, but as q approaches 1, D is equivalent to the Shannon diversity (exponential of Shannon index) and at $q = 2$, D is equivalent to the Simpson diversity (inverse Simpson concentration). Thus, Hill's numbers are scaled to represent the number of equally abundant species needed to give the same value of diversity in a community, and as such, communities that differ in richness and evenness may be intuitively compared (Chao et al., 2014; Jost, 2006, 2007). When D is plotted against q, the result is a profile or curve with an intercept indicating species richness and a slope that reflects the influence of evenness in that particular community (Chao et al., 2014). We generated diversity profiles for each habitat in each burn class at 80% sampling coverage for estimates of richness and Shannon and Simpson diversity with the *estimated* function in the *iNEXT* package (Hsieh et al., 2020). This

function uses coverage-based interpolation and extrapolation of sampling curves to allow for comparison of diversity metrics across assemblages that differ in community size (Chao et al., 2014; Chao & Jost, 2015). We considered estimates significantly different if the 95% bootstrapped confidence intervals were non-overlapping.

Beta diversity

Beta diversity describes the variation in composition among subunits within a larger community and in the simplest definition is the ratio of the α (local) to γ (regional) diversities (Jost, 2007; Whittaker, 1960). High β values indicate that a subunit shares few species with other subunits, making it unique within the larger community. Low β indicates that most species are shared among subunits and may be a sign of homogenisation. The variation in species composition may be represented by plotting the dissimilarities among subunits in multivariate space. The community composition is represented as the spatial median, the point in multidimensional space that minimises the sum of the distances of all of the subunits of a community (Anderson et al., 2006; Legendre & De Cáceres, 2013; Qian, 2009). Then β is the average distance of all subunits to their spatial median, that is, the average variation of the local composition from the regional pool, with greater distances indicating fewer shared species. To estimate β, we summed species abundances within sites and treated each site as a sampling unit and each visit as a repeated measure of that site. We created site by species matrices of abundance for each habitat in each burn class and added a dummy species to each site-visit to include visits where no pollinators were detected, reduce the underestimation of similarities among communities and increase precision (Hardersen & La Porta, 2023). We square root transformed the matrices to reduce the influence of the most common species, which are likely to be generalist and shared among communities and thus less informative when attempting to differentiate communities (Cao et al., 2001; Melo, 2021). The *vegdist* function in the *vegan* package (version 2.5–7, Oksanen et al., 2020) transformed community matrixes into Bray–Curtis dissimilarities, an index that tends to be robust to differences in sample sizes (Beck et al., 2013; Bray & Curtis, 1957). We then calculated β as the average distance of each site-visit subcommunity from the overall burn-habitat community with the *betadisper* function in *vegan*. We used the *permutest* function in the *vegan* package to statistically compare β among burn classes in meadow and upland habitats with restricted permutation testing. We ran 999 permutations, where observations were exchangeable between, not within, sites to account for the repeated visits to each site.

We tested if burn classes within each habitat type differed significantly in their composition by comparing the locations of their spatial medians with permutational multivariate analysis of variance (PERMANOVA, Anderson, 2017) using the *adonis2* function in *vegan*. We included burn classes and floral richness (unique species observed on a site per visit) in both upland and meadow models. In addition, we included elevation in meadow models to account for relatively higher variation. Again, permutations were restricted such that observations were only exchangeable only between sites, to account for the repeated visits. PERMANOVA assumes that variances within burn severity classes (i.e., mean distance to spatial medians) are homogeneous, which we tested with the *betadisper* function as described above (Table 2). Variances were homogenous among burn classes in meadows and uplands, indicating that any significant differences found by PERMANOVA are due to variation among (not within) subcommunities. Permutations were run 999 times for upland habitat and 719 (the maximum number of permutations) for meadow habitat.

TABLE 2 Pollinator β diversity unburned, moderate- and high-severity upland and unburned and high-severity meadows of the Sierra Nevada, California, in 2017, following the 2014 King fire. β is the mean distance of all sampling plots in a class to the spatial median of the Bray–Curtis dissimilarity matrix. The permutation test assesses whether there are significant differences in the dispersion around the median between burn severity classes for each habitat type.

		Permutation test	
Upland	β	$F_{2,51}$	*p* value
Unburned	0.52		
Moderate severity	0.60	0.84	0.60
High severity	0.53		
Meadow		$F_{1,16}$	*p* value
Unburned	0.60		
High severity	0.59	0.47	0.70

RESULTS

We observed 680 individuals of 130 pollinator species or morphospecies comprising 74 bees and wasps ($n = 539$), 28 flies ($n = 67$), 16 beetles ($n = 48$), 9 true bugs ($n = 20$), 2 butterflies ($n = 5$) and 1 neuropteran morphospecies ($n = 1$; full list in Supplementary Appendix B). Observed species richness and abundance were similar in meadow habitat with 178 observations of 58 species in high-severity meadow and 186 observations of 57 species in unburned meadow (Table 1). For upland habitat, the moderate-severity burn class had the most species and individuals observed (48 species, $n = 149$), followed by the high-severity burn class (35 species, $n = 113$), and the unburned burn class (28 species, $n = 54$). Fifty-two out of 130 plots did not have any pollinator species detected. When data were summed among plots, one visit to an unburned meadow site, six visits unburned sites, three visits to moderate-severity sites and six visits to high-severity burned sites resulted in no pollinator observations.

Drivers of pollinator richness

At the plot scale, we found that floral richness was an important driver of pollinator richness and habitat mediated the response of pollinators to burn severity (Figure 2, Table 3). In meadow habitat, pollinator

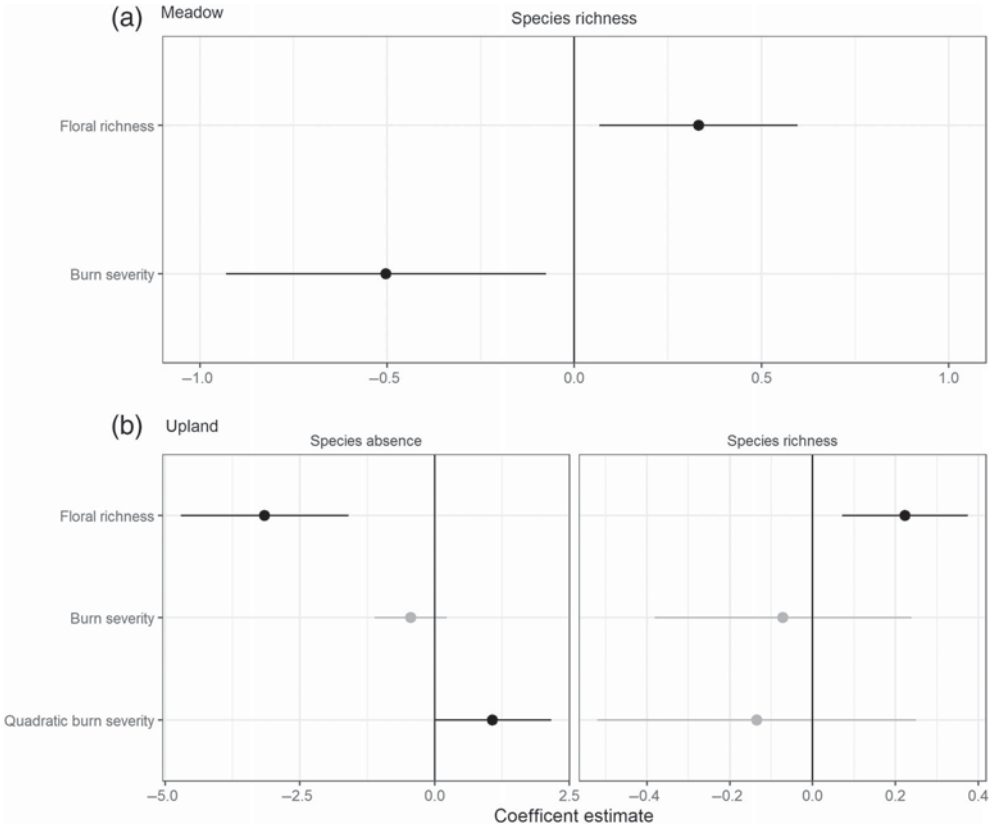

FIGURE 2 Factors influencing pollinator richness in (a) meadow and (b) upland habitat of the Sierra Nevada, 3 years after the 2014 King fire, from generalised linear mixed models. In meadow habitat, species richness was modelled as a function of floral diversity, burn severity and elevation with a negative binomial distribution. In upland habitat, we used a hurdle model to first consider the factors influencing species absence (i.e., when no species where detected) using the binomial distribution, then factors influencing species richness (when at least one species was detected) using the Poisson distribution. Both response variables were modelled as functions of floral richness, burn severity and quadratic burn severity. The effect was significant at $\alpha = 0.05$, noted in black.

richness was negatively associated with burn severity and positively associated with floral richness (Figure 2 and Table 3). There was no significant effect of elevation in meadows. In upland habitat, the probability of observing zero pollinator species decreased significantly as floral richness increased. There was a significant effect of the quadratic burn severity term on pollinator absence, suggesting that upland habitat at the extremes of the burn severity gradient were more likely to have zero species, whereas moderately burned plots were more likely to have at least one species detected. Pollinator richness was not significantly impacted by burn severity but was positively associated with floral richness.

Alpha diversity

At the class level, pollinator species richness did not differ significantly across burn classes within each habitat. As predicted, species richness (i.e., D at $q = 0$) was slightly higher in meadow habitat than in upland habitat and slightly higher in unburned meadows compared with high-severity meadows. Burned upland habitat tended to have higher richness than unburned upland habitat, although these differences were not significant (Figure 3).

We expected moderate-severity fire to reduce dominance and increase evenness, resulting in diversity profiles with shallower slopes and higher Shannon and Simpson diversity indices, with unburned and high-severity burned habitat being similar in evenness with unburned areas dominated by competitive species and high-severity areas dominated by ruderal species. In upland habitats, however, fire resulted in less even communities. Differences in diversity indices were significant when comparing unburned upland habitat to both moderate and high-severity burn classes (Simpson diversity), indicating that communities in unburned upland habitats were more even. In meadows, high-severity and unburned burn classes did not differ significantly, although burned meadows tended to be more even (Figure 3).

Beta diversity

Contrary to our expectations, we did not find significant differences in β among burn classes in upland habitat (Table 2 and Figure 4). Heterogeneity was highest in moderate-severity ($\beta = 0.60$), followed by high-severity ($\beta = 0.53$) and unburned ($\beta = 0.52$) upland burn classes. As expected, β did not differ significantly among unburned ($\beta = 0.60$) and high-severity meadow ($\beta = 0.59$) burn classes.

TABLE 3 Drivers of pollinator diversity in unburned, moderate and high-severity upland and unburned and high-severity meadows of the Sierra Nevada of California, 3 years after the 2014 King fire. Results for generalised linear mixed models for pollinator richness (Poisson–binomial hurdle) where meadow is the reference category.

a. Meadow model				
Negative binomial model of species richness			**Random effect SD = 0.81**	
Explanatory variables	**Estimate**	**SE**	***z* value**	***p* value**
Intercept	1.80	0.35	5.12	
Floral richness	**0.33**	**0.14**	**2.56**	**0.01**
Elevation	−0.45	0.38	−1.20	0.23
Burn severity	**−0.50**	**0.22**	**−2.31**	**0.02**
b. Upland hurdle model				
Binomial submodel of species absence				
Explanatory variables	**Estimate**	**SE**	***z* value**	***p* value**
Intercept	−2.04	0.71	−2.88	
Floral richness	**−3.16**	**0.79**	**−3.98**	**< 0.01**
Burn severity	−0.45	0.34	−1.30	0.19
Burn severity^2	**1.08**	**0.56**	**1.94**	**0.05**
Poisson submodel of species richness			**Random effect SD = 0.35**	
Explanatory variables	**Estimate**	**SE**	***z* value**	***p* value**
Intercept	1.01	0.23	4.48	
Floral richness	**0.22**	**0.08**	**2.88**	**<0.01**
Burn severity	−0.07	0.16	−0.45	0.65
Burn severity^2	−0.14	0.20	−0.69	0.49

Note: Bold values are significant at $\alpha = 0.05$.
Abbreviations: SD, standard deviation; SE, standard error.

Burn class did not significantly affect community composition in either meadows or uplands; however, the effect of floral richness on community composition was significant in uplands and marginally significant in meadows (Table 4 and Figure 4). Elevation did not have a significant effect on community composition in meadow habitat (Table 4).

DISCUSSION

We found that the response of pollinator communities to fire in mid-elevation coniferous forest depended on habitat type and varied among different aspects of diversity. The greatest impacts of fire on pollinator communities occurred at smaller scales on species richness. At the local scale, there was a negative relationship between burn severity and pollinator richness in meadow habitat. The relationship between local pollinator richness and burn severity was less clear in upland habitat, where high-severity fire was associated with the absence of any pollinator species but not with pollinator richness. High-severity fire may negatively affect pollinators directly by reducing populations or indirectly via habitat changes to floral or nesting resources (Abella et al., 2009; Esque et al., 2010; Lipoma et al., 2018). Whether fire acted directly or indirectly, the impacts of the King fire were highly localised and the negative effects were not observed at larger spatial scales.

The local, negative effects of fire in meadows are of particular concern as these habitats comprise about 2% of the area in the Sierra Nevada, yet they support high levels of biodiversity, perform important ecosystem functions and provide consistent and diverse pollinator resources. Historically, meadows were maintained by a balance of hydrogeomorphic and disturbance processes that excluded woody species (Allen-Diaz, 1991; Loheide & Gorelick, 2007; Norman & Taylor, 2005); however, interactions among fire suppression, draining, grazing and conifer encroachment have degraded the function and shifted the composition of many meadows (Norman & Taylor, 2005; Ratliff, 1985). Furthermore, at the time of the King fire, the Sierra Nevada was in one of the most severe multiyear droughts in recorded history (Griffin & Anchukaitis, 2014), which desiccated fuels in and around meadows and may have increased encroachment by woody species. Thus, when the King fire reached these meadows, the fuel loads were both higher and drier, resulting in high-severity fire that could smoulder deeper into the soil with longer residence time than typical meadow fires, which may have killed pollinators sheltering underground (Cane & Neff, 2011). Pollinator abundance also tended to be lower in burned meadows, further indicating that high-severity fire in these systems may hinder survival or re-colonisation of

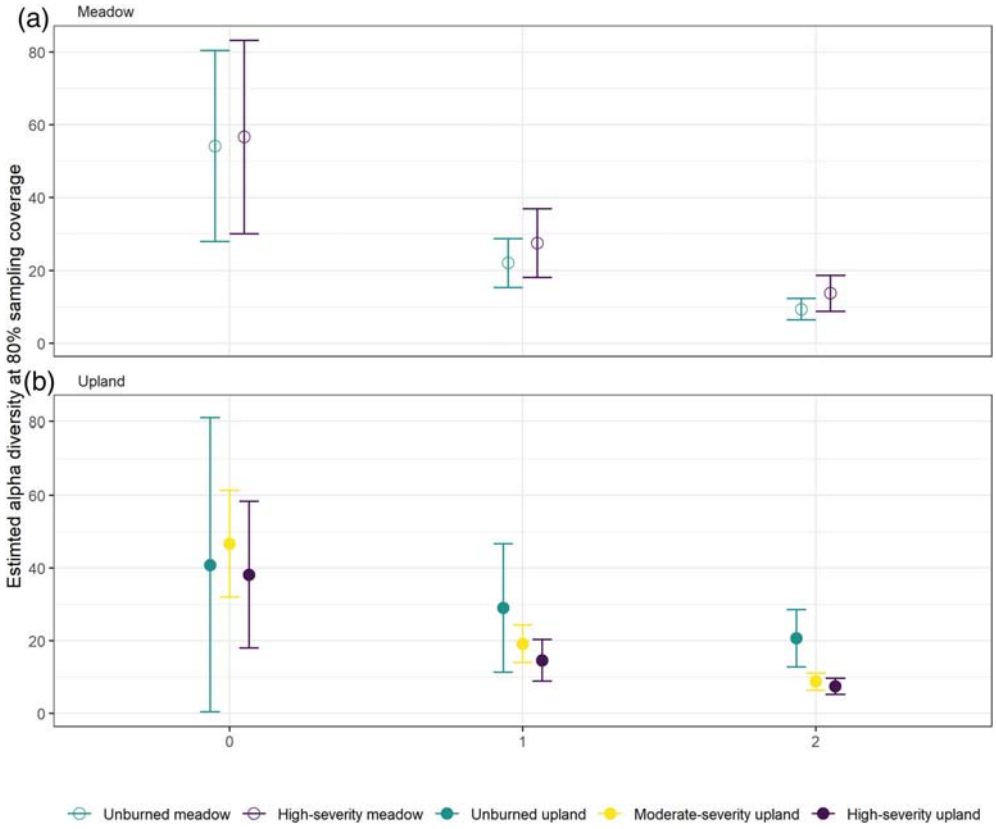

FIGURE 3 Alpha diversity of pollinators in different burn-habitat classes in a post-fire forest in the Sierra Nevada, California, 3 years after the 2014 King fire. Estimates of species richness ($q = 0$), Shannon diversity ($q \rightarrow 1$) and Simpson diversity ($q = 2$), in increasing importance of evenness for each burn-habitat class in (a) meadow and (c) upland habitats with bootstrapped 95% confidence intervals. Estimates with non-overlapping confidence intervals are considered significantly different.

pollinators (Tarbill et al., 2023). This negative impact on α appears to be compensated for by high heterogeneity among pollinator communities in burned meadows, as differences in α were not significant in the regional analysis. It is important to note that because meadows recover from fire so quickly, we were unable to ground truth the burn severities assigned by remote sensing. To remedy this, we only selected plots in locations that burned at high severity but acknowledge that actual burn severity in meadows was mixed. However, we would expect the juxtaposition of less severely burned habitat to dampen the negative response to fire we observed, suggesting our results may be conservative.

We expected fire to increase pollinator richness in upland habitat, with a peak at intermediate burn severities. The only significant evidence supporting this hypothesis was the positive influence of the quadratic burn severity term on species absence, suggesting that the probability of observing at least one species of pollinator was highest in upland habitats that burned at moderate severity (Figure 2b, species absence binomial sub-model). Upland habitat that burns at high-severity may be less likely to host any pollinator species if it is in the interior of the burn due to dispersal or connectivity limitations, whereas unburned habitat may lack any floral resources due to the nature of closed-canopy forest. In contrast, richness at upland sites was not significantly impacted by burn severity, suggesting fine-scale heterogeneity within habitats and variability in species-level responses.

Contrary to our expectations, we found that pollinator communities in uplands tended to be more even in the unburned class than the burned classes. Pollinator evenness may decrease in response to disturbance due to changes in the abundance of one or few species (Coulin et al., 2019). In this study, we found higher evenness in the unburned upland class, but this appeared to be an artefact of a sparse pollinator community (i.e., many sites had a few species, each with one individual detected), whereas sites in burned upland classes had many more species represented by variable numbers of individuals. Fire in upland habitat may reset plant successional dynamics favouring the establishment of disturbance-affiliated species, increasing floral diversity that supports more pollinators (Yeboah et al., 2016). As the canopy closes, and understory species decline over time since fire, both the number and diversity of pollinators may decline as they move to better habitat in meadows or more recent burns with abundant floral resources.

Both fire suppression and high-severity fire may have homogenising effects on habitats and communities (Cassell et al., 2019; Hessburg et al., 2005; Merschel et al., 2014); however, we did not find a significant relationship between burn class and β. Recent studies in similar habitats also did not find significant relationships among

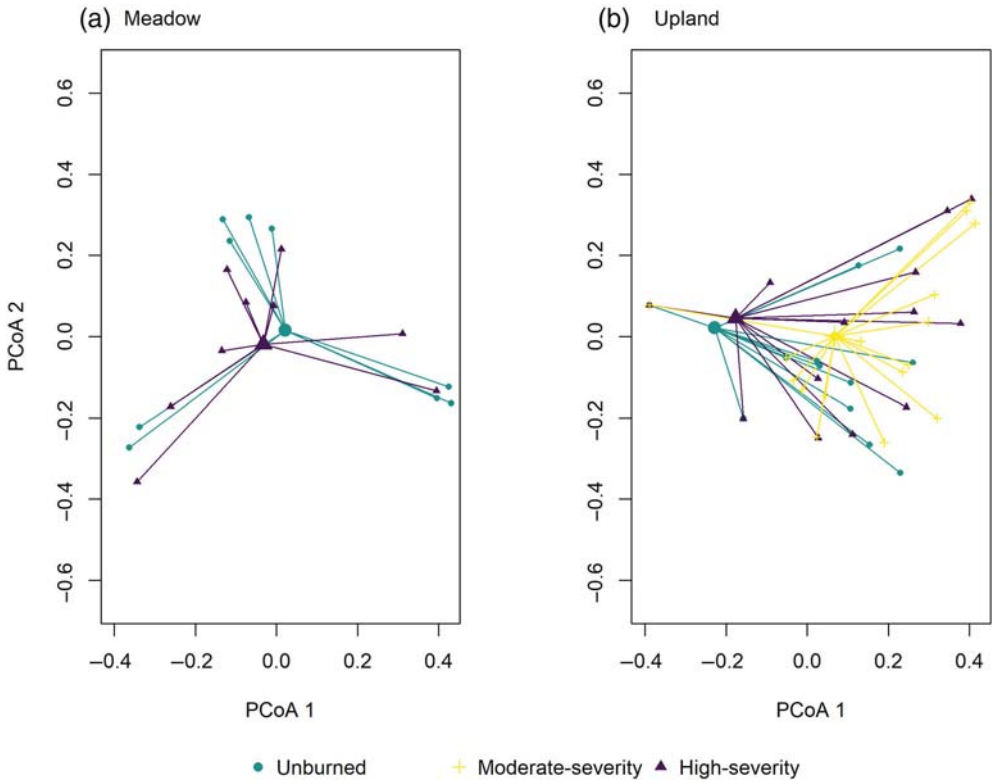

FIGURE 4 Beta diversity (β) of pollinators in (a) meadow and (b) upland habitat in the Sierra Nevada, California, 3 years after the 2014 King fire. The community of each site on a particular visit (smaller symbol) is located in space based on the abundance-based matrix. The spatial median for each burn severity class (larger symbol) is the point in multidimensional space where the sum of the distances from all the sites of a burn-habitat class is minimised. The location of the spatial median represents the community composition for each burn severity class, whereas the mean distance of all sites to their respective median represents the β or heterogeneity in composition. A dummy species was added to every site to reduce the influence of the most common species and allow us to include sites where no pollinators were detected. The Principal Coordinate Analysis (PCoA) axes best preserve the distances from the Bray-Curtis matrix.

TABLE 4 Comparing community composition of unburned, moderate- and high-severity upland and unburned and high-severity meadows of the Sierra Nevada, California, in 2017, following the 2014 King fire. Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) compares the Bray–Curtis dissimilarity matrices between burn severity classes within each habitat. We restricted permutations in the models to account for repeated visits to each site.

Meadow	**df**	R^2	F	p **value**
Burn severity class	1, 17	0.06	1.14	0.67
Floral richness	*1, 17*	*0.07*	*1.34*	*0.08*
Elevation	1, 17	0.09	1.80	0.24
Upland	**df**	R^2	F	p **value**
Burn severity class	2, 53	0.04	1.23	0.30
Floral richness	**1, 53**	**0.10**	**5.70**	**<0.01**

Note: Bold indicates significance at $\alpha = 0.05$; italics indicate significance at $\alpha = 0.10$.

pollinator β and burn severity (Ponisio et al., 2016) or found that pollinator β was highest in unburned habitat but suggest that this relationship was driven by higher abundance and species richness not homogenisation (LaManna et al., 2021). Beta diversity may differ across communities due to random sampling effects, for example, when higher beta is observed where there are fewer individuals or species (Myers et al., 2015). However, this is unlikely to be the case in this study as communities in the moderate-severity class for uplands were both larger and more speciose and had higher β than pollinator communities in either unburned or high-severity classes. Moderate-severity fire may be more heterogeneous due to the patchiness inherent in this disturbance type, with some areas that may act as fire refuges and others that may burn at higher severity due to fuels or topography, supporting a diverse suite of pollinator species. However, the study area was fire-suppressed, with all areas sharing a common fire history, suggesting that much of the temporal pyrodiversity (i.e., variability in time since last fire and number of fires burned) has been lost from the system. This may explain in part why β did not differ significantly across burn classes. It is also important to note the effect of including the high number of unburned and high-severity sites that had zero pollinator detections. These sites shared a single species, the dummy species, which heavily influenced the location of the spatial median (i.e., the community composition) and reduced the heterogeneity among unburned and high-severity sites. We included these sites to better understand the similarities among these sites and how burn class may contribute to the lack of diversity observed.

We found that the community composition was not significantly impacted by burn class. Community composition may in fact be driven by many other variables, at both local and regional scales. For example, we found (as expected) that upland habitat in the moderate-severity burn class tended to share species with both upland habitat in unburned and high-severity classes. These similarities in composition may be driven by patchiness inherent in this burn class, the high mobility of many pollinator species or the tendency of moderate-severity patches to be located near the perimeter of the fire. Patchiness may allow for coexistence of species that differ in their ability to colonise or compete, whereas high-severity habitat may be dominated by disturbance-tolerant colonisers and unburned upland may be dominated by good competitors (Cadotte, 2007; Grime, 1977; Tilman, 1994). Teasing apart the effects of distance to unburned habitat and burn severity was not possible with this fire (and many contemporary fires that burn in similar patterns; Steel et al., 2021) but is critical to improving our understanding of the drivers of diversity after large, severe disturbances.

In this study, we were only able to investigate the effects of one fire, limiting our ability to make inferences about the response of pollinators to fire in general. Furthermore, our study area was characterised by a fire history of suppression; it had not burned in nearly 100 years. This may explain why the response we observed differed from some other studies. For example, Ponisio et al. (2016) created a pyrodiversity metric (diversity of historical burn severities) and compared richness of bees in areas that most recently burned at low, moderate and high severity. They found no significant effect of pyrodiversity on bee richness in areas that burned at high severity but that pyrodiversity had a positive effect in areas that burned at moderate severity. Bee richness tended to increase with burn severity, a finding that has been observed in other studies as well and is attributed to availability of floral resources and nest sites (Galbraith et al., 2019; LaManna et al., 2021), although negative effects have been observed under the most severe conditions (Galbraith et al., 2023; Lazarina et al., 2019). However, differences in our results may also be due to the inclusion of other pollinator taxa, including flies, beetles and true bugs that are less studied than bees and may differ in their ability to survive and recolonize post-fire landscapes (Lazarina et al., 2019). For example, they may live in the litter layer, predisposing them to mortality from high-severity fire (Wikars & Schimmel, 2001) or they may rely on non-floral food sources or other resources that are destroyed by fire (Bieber et al., 2023; Fettig et al., 2022; Koltz et al., 2018). Further complicating matters, two recent meta-analyses on a broader array of pollinators had opposing results, with diversity declining with fire in one (Bieber et al., 2023) and richness increasing with fire in the other (Carbone et al., 2019), although neither incorporated burn severity. These conflicting results may reflect that community response is highly dependent on burn severity and the groups that are included (Huntzinger, 2003; Lazarina et al., 2019; Mason Jr et al., 2021).

Finally, floral richness appears important to pollinator diversity and was positively associated with pollinator species richness, a pattern observed in many other studies (Lazarina et al., 2019; Ponisio et al., 2016; Rodríguez & Kouki, 2017). In fact, the relationship between pollinator richness and plant richness has been described for most insect pollinators across many landscapes (Kral-O'Brien et al., 2021). A diverse floral community is likely to support more pollinator species that may differ in their ability to extract nectar or pollen and may be more likely to include plant species that specialists require during different stages of their life history (Cardinale et al., 2012; Loreau et al., 2001; Stang et al., 2009). Shifts in pollinator community composition may also be influenced by the timing of flowering plants over the course of the season. Other local and regional factors, such as history, microclimate, propagule availability (Foster & Dickson, 2004; Ohler et al., 2020; Ricklefs, 1987), factors related to the pollinators themselves, such as life history traits (Williams et al., 2010) dispersal ability (Qian, 2009), or preferences for floral host species (Fründ et al., 2010; Ponisio et al., 2016) may also be important in structuring pollinator communities.

Diverse pollinator communities tend to provide more pollination services, particularly in natural systems, where diversity provides complementarity, redundancy and resilience to disturbance (Loreau et al., 2001; Ricklefs, 1987; Senapathi et al., 2015). As such, these communities support understory plants that provide ecosystems services of erosion control, water filtration and carbon sequestration (Costanza et al., 1997; Zedler, 2003). Climate change is predicted to increase severe fires in dry forests due to hotter, drier and longer fire seasons, less snowpack and more extreme weather (Fernandes et al., 2016; Hessburg et al., 2005; Lydersen et al., 2017; Mote, 2006; Westerling et al., 2006). High-severity fire may have negative impacts on pollinator diversity, particularly in meadows or highly fire-suppressed uplands that lack pyrodiversity. The effects in upland habitat are more context-dependent, particularly when fire increases the diversity and abundance of floral resources, as well the abundance of some pollinator species, as we observed in the King fire (Tarbill et al., 2023). Prescribed and managed fires implemented in upland habitat are unlikely to have negative impacts on pollinator communities. However, meadows are pollinator hotspots that may benefit from management that reduces high-severity fire, such as the removal of encroaching conifer species, restoration of hydrologic processes and application of frequent low-severity fire (Boisramé, Thompson, Collins, & Stephens, 2017; Frenzel, 2012; Hunt et al., 2018).

AUTHOR CONTRIBUTIONS

Gina L. Tarbill: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis. **Angela M. White:** Conceptualization; investigation; funding acquisition; methodology; writing – review and editing; formal analysis; supervision. **Rahel Sollmann:** Conceptualization; investigation; funding acquisition; methodology; writing – review and editing; formal analysis; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Gina L. Tarbill https://orcid.org/0000-0003-2294-2413

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supporting Information.

Figure A1. The effect of (a) mean hourly air temperature, and (b) mean hourly windspeed on the number of insects captured. Air temperature was averaged from readings obtained at the Robb's Saddle and Greek Store weather stations located on the east and west sides of the study area, respectively. Data Source: California Department of Water Resources Data Exchange Center, accessed 10/1/23. Windspeed was averaged from readings obtained at the Emigrant Gap, Blue Canyon Nyack Airport weather station located northwest of the study area. Data Source: NOAA National Centers for Environmental Information.

Figure A2. Maps showing location of weather stations relative to fire perimeter and study area. The California Department of Water resources (CA DWR) weather stations provided hourly temperature data and National Oceanic Atmospheric Administration National Centers (NOAA NCEI) for Environmental Information provided windspeed data.

Table A1. Pearson correlation between floral abundance and floral richness in meadow and upland habitats of the Sierra Nevada, California, 2 and 3 years after the King fire.

Figure A3. Residual plot for generalised linear mixed model (negative binomial distribution) for species richness of pollinators in meadows of the Sierra Nevada, CA three years after the 2014 King fire. In the right panel, deviations from uniformity that may indicate lack of fit are visualised with quantile regression at 0.25, 0.50 and 0.75. The black dotted lines show the 0.25 and 0.75 quantile regression lines, where the data are uniformly distributed along the *y*-axis.

Figure A4. Residual plot for generalised linear mixed model (Poisson–binomial hurdle) for species richness of pollinators in uplands of the Sierra Nevada, CA 3 years after the 2014 King fire. In the right panel, deviations from uniformity that may indicate lack of fit are visualised with quantile regression at 0.25, 0.50 and 0.75. The black dotted lines show the 0.25 and 0.75 quantile regression lines, where the data are uniformly distributed along the *y*-axis.

Figure A5. Beta diversity (β) of pollinators in (a) meadow and (b) upland habitat in the Sierra Nevada, California, three years after the 2014 King fire. Plots without any pollinators detected were excluded. Each sampling plot (smaller point) is located in space based on the abundance-based community matrix, the spatial median (larger point) is the point in multidimensional space where the sum of the distances from all the plots of a burn-habitat class is minimised and the ellipse encompasses one SD. The β is the mean distance from the spatial median of all plots in a given class, whereas the community composition of each class is represented by the location of the spatial median. A dummy species was added to every plot to reduce the influence of the most common species.

Table B1. Summary of pollinator observations by burn-habitat classes in green (GU), moderate (MU) and high-severity (HU) upland and green (GM) and high-severity (HM) meadows in the Sierra Nevada, California, 3 years after the 2014 King fire. Identification followed Triplehorn & Johnson 2005.

Figure C1. Upland site photos showing burn severity differences, with (a) unburned, (b) moderate-severity and (c) high-severity conditions represented.

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