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The birds and the bees, flowers and burnt trees: plant-pollinator communities after fire in the Sierra Nevada of California

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The birds and the bees, flowers and burnt trees: plant-pollinator communities after fire in the  
Sierra Nevada of California

By

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DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

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DAVIS

Approved:

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## **Abstract**

Fire is the dominant source of disturbance that impacts the distribution of species, but in many regions of the world, fire regimes are changing in response to global change, with cascading impacts on ecosystem diversity and function. In the coniferous forests of the western United States, incidences of extremely large and high-severity fires (i.e., megafires) are increasing due to a century of fire suppression combined with a warming, drying climate. Loss or degradation of ecosystem processes, such as pollination, may be especially detrimental after large-scale, high-severity fire removes biomass and fragments habitat. I studied the response of pollinator communities and floral resources to the King Fire, a large-scale, high-severity fire which burned in 2014 in the mid-elevation coniferous forest and meadows of the Sierra Nevada, California.

In chapter 1, I investigated how burn severity in upland and meadow habitat interacted with floral phenology to impact the pollinator resources available after fire, using flowering plant survey data. I modeled floral abundance and floral richness to evaluate the influence of burn severity, habitat, and time since snowmelt on pollinator resources. I further compared alpha and beta diversity and community composition among burn-habitat classes at three points in time during the flowering season. Meadows tended to have more diverse and abundant flowering resources throughout the season; fire increased floral abundance and diversity in upland habitat. All burn-habitat classes had similar amounts of  $\beta$  diversity, but fire increased habitat heterogeneity temporally, with upland habitats peaking in diversity at different points of the season. Forests that have experienced some fire may be more resilient to climate-induced shifts in flowering if the overall community compensates through this increased temporal heterogeneity.

Chapter 2 investigated the impacts of burn severity, habitat, and floral resources on pollinator abundance, by modeling their effects on count data of floral visitors (bees, wasps, flies, beetles, and true bugs), butterflies, and hummingbirds. Although many relationships were not significant, I found highly consistent positive responses to floral richness, negative responses to burn severity in meadows, and mixed responses to burn severity in uplands for floral visitors. Hummingbirds and two families of butterflies responded positively to burn severity in uplands. Hummingbird abundance was also significantly higher in high-severity meadows. Whereas high-severity fire, particularly in meadows, has the potential to affect most pollinators negatively, moderate-severity fire can improve the quality of previously fire-suppressed upland habitat. Given that much of the Sierra Nevada is predicted to burn at high severity, reducing risk of high-severity fire around meadows may protect sensitive pollinator communities.

In chapter 3, I focused on how pollinator diversity was impacted by burn severity in upland and meadow habitat. I compared alpha and beta diversity and community composition among burn-habitat classes and modeled species richness and beta diversity as functions of burn severity, habitat, and floral resources. Alpha and beta diversity were similar among all burn-habitat classes at the broader scale, but when plot-level metrics were modelled, burn severity had significantly negative impacts on richness in meadow habitat. Community composition differed among green and high-severity meadow, and green and high-severity upland. As expected, floral richness was positively associated with pollinator species richness. Pollinator diversity is more sensitive to the negative impacts of high-severity fire in meadows, and as such this habitat should be the focus of conservation measures given the high diversity and abundance of species it supports.

## **Introduction**

Understanding how deviations from natural disturbance regimes affect biodiversity is a key challenge in the Anthropocene, given the relationship between diversity and ecosystem services and functions (Loreau et al. 2001, Cardinale et al. 2012). Fire is the dominant source of disturbance that impacts the distribution and composition of species, globally (Bond and Keeley 2005, Bond et al. 2005, Burkle et al. 2015). Fires can impact nutrient cycling, soil decomposition rates, microclimates, and primary productivity with the magnitude of effects dependent on local conditions, history, and climate (Raison et al. 2009). In many regions of the world, fire regimes are shifting in response to changes in land use, management, and climate (Flannigan et al. 2009, Pausas and Fernández-Muñoz 2012, Pausas and Keeley 2014). Changes to the historic fire regime of a system may result in feedbacks that disrupt resilience, produce novel ecosystem states and affect ecosystem processes (Bowman et al. 2015, Johnstone et al. 2016, Hughes et al. 2019).

Pollination is an ecosystem process that may be impacted by fires that burn with higher severity, frequency, or at larger extents than those under which the system evolved (Miller and Safford 2019, White et al. 2019, Steel et al. 2021). Fire may affect the availability of floral resources by changing the abundance, diversity, or composition of plant communities or by altering the phenological cues that stimulate flowering, which in turn will affect the higher trophic levels that depend on them (Forrest and Miller-Rushing 2010, Miller-Rushing et al. 2010, Yang and Rudolf 2010). Pollinators are highly dependent on floral resources; many synchronize reproduction to coincide with peak bloom times, and they often rely on multiple plant species that flower asynchronously to meet their needs over the course of the season (Aldridge et al. 2011). A decline in pollinator diversity or abundance may impact pollination, and by extension,



plant regeneration after fire. The tightly interdependent nature of plant-pollinator communities indicates that loss or decline of one trophic level may have cascading and far reaching impacts on the other (Biesmeijer et al. 2006, Kaiser-Bunbury et al. 2010, Potts et al. 2010).

Despite this, the effects of changing fire regimes on pollinators and floral resources are not well-understood. We used the mid-elevation, coniferous forests of the Sierra Nevada (California, USA) as a model system in which to study these effects. This region historically experienced high-frequency, low-moderate severity fire that created ephemeral floral patches within forest, and maintained more permanent floral habitat in meadows. In this region, plant-pollinator communities tend to be more diverse in areas with high pyrodiversity (i.e., a diversity of fire histories in terms of severity, extent and timing), similar to the historic disturbance regime (Burkle et al. 2015, Ponisio et al. 2016, Richter et al. 2019). A century of fire suppression and intense logging, combined with a warming and drying climate, have led to an increasing incidence of high-severity and large-scale fires in this system (Westerling et al. 2006, Abatzoglou and Williams 2016, Lydersen et al. 2017), with unknown impacts on the pollinator community. I investigate these impacts in and around the King fire, which burned 39,000 ha in the Eldorado National Forest (California, USA) in 2014. I collected field data on pollinators and their floral resources two (2016) and three (2017) years following fire in upland (dry, forested) and meadow habitat in the Eldorado National Forest. In general, I expect fire to increase pollinator and floral resource abundance and diversity in upland habitat, which are typically limited under fire suppression. I expect moderate-severity fire to be more beneficial than high-severity fire, as it more closely resembles historic fire regimes. Meadows historically experienced less frequent fire, and I expect a decrease in diversity and abundance of floral

resources and pollinators after high-severity fire in meadows due to damage to soils, seedbanks, and source populations of pollinators.

In chapter 1, I test these predictions for pollinator resources, by investigating how abundance and diversity of flowering plants are distributed in space and time after fire in green and burned meadows and upland habitat. In chapter 2, I model the effects of burn severity and habitat, as well as flowering resources, on pollinator abundance for bees and wasps, butterflies, flies, beetles, and hummingbirds. In chapter 3, I investigate how patterns of pollinator alpha diversity, beta diversity, and community composition differed by burn severity and habitat. The research improves our understanding of how changes in disturbance regimes may impact communities that provide important ecosystem services. Given that much of the Sierra Nevada mountains (and similar biomes) are dominated by fire-suppressed forest that is predicted to burn outside the range of natural variation in terms of size and severity (Mallek et al. 2013, Dennison et al. 2014, Lydersen et al. 2017), this research informs the conservation and management of pollinator communities under a changing disturbance regime.

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## **Chapter 1. The effect of burn severity depends on habitat: floral abundance, diversity, and phenology following a megafire in uplands and meadows of the Sierra Nevada, California**

### **Abstract**

Fire-prone systems cover much of the land on Earth, with communities that are more variable in vegetative structure than expected by climate by alone. This variability may be lost if land use and climate change cause shifts in the historic fire regime of fire-prone systems, resulting in feedbacks that affect ecosystem processes. Flowering phenology is sensitive to changes in soil conditions, making it vulnerable to increases in fire severity that alter soil temperature, moisture and nutrients. We investigated how burn severity in upland and meadow habitat interacted with floral phenology to impact the pollinator resources available after fire in a mid-elevation, mixed-conifer forest of the Sierra Nevada, California. We used generalized linear mixed models to evaluate the influence of burn severity, habitat, and days since snowmelt on local (i.e., sampling location) floral abundance and richness. We further compared alpha diversity among burn-habitat classes using diversity profiles; beta diversity (species turnover within each burn-habitat class) using Bray-Curtis dissimilarity indices; and community composition with PERMANOVA. The effect of fire on the flowering plant community depended both on burn severity and on habitat type, and both of these factors affected plant community phenology. Under all burn severity categories, meadows tended to have more diverse and abundant flowering resources throughout the season; whereas fire increased floral abundance and diversity in upland habitat. There were no significant differences in class-level beta diversity, indicating that all burn-habitat classes had similar amounts of heterogeneity in floral communities across the flowering season. In upland forest, unburned habitat tended to have higher class-level alpha diversity earlier in the season, and moderate and high severity were more diverse later. Whereas local abundance and diversity of flowering plants generally declined as

the season progressed, the importance of that decline depended on burn-habitat class. In burned upland habitat, the floral resources were available later in the season, suggesting that even high-severity burns create habitat that is complementary to unburned habitat in space and time for both flowering plants and the pollinators they support.

## **Introduction**

Disturbance regimes are rapidly changing around the world, increasing in frequency, severity, or extent due to changes in land use and climate (Turner 2010). Because disturbance has a profound effect on abundance, diversity, and composition of communities, it also tends to drive the spatial patterns of ecosystem functions and processes (Turner 2010, Johnstone et al. 2016, Seidl et al. 2016). Changes to the historic disturbance regime of a system may result in feedbacks that disrupt resilience, affect ecosystem processes, and produce novel ecosystem states (Bowman et al. 2015, Johnstone et al. 2016, Hughes et al. 2019). One ecosystem process that may be affected by disturbance is that of flowering phenology, the timing of angiosperm reproduction. Shifts in flowering phenology triggered by disturbance may impact reproductive success of plant populations and the higher trophic levels that depend on them (Forrest and Miller-Rushing 2010, Miller-Rushing et al. 2010, Yang and Rudolf 2010). Understanding how plant phenology is affected by changing disturbance is crucial given that the reproductive phases of the plant life cycle provide food to a broad array of species that tend to synchronize their own phenology with that of plants (Forrest and Miller-Rushing 2010, Miller-Rushing et al. 2010, Yang and Rudolf 2010). Pollinators in particular are highly dependent on flowers as resources; many synchronize reproduction to coincide with peak bloom times, and they often rely on multiple plant species that flower asynchronously to meet their needs over the course of the season (Aldridge et al. 2011).

Globally, one of most important disturbances that may alter phenology is that of fire (Bond and Keeley 2005, Bond et al. 2005, Bogusch et al. 2015). Fire-prone systems cover nearly 40% of the land on Earth, with communities that are more variable in vegetative structure than expected by temperature and precipitation alone (Bond et al. 2005). Fire regimes are changing due to changes in land use, management and climate, raising concerns that important ecosystem functions may be degraded or lost (Skinner et al. 1996, Pausas and Fernández-Muñoz 2012, Haggmann et al. 2021). Plant phenology may be affected by post-fire conditions that alter the cues that stimulate flowering. Flowering phenology is typically influenced by photoperiod, temperature, and soil moisture and chemistry, allowing plants to take advantage of temporally variable resources to enhance reproduction (Kameyama and Kudo 2009, Wang et al. 2018, Ramirez-Parada et al. 2020). Fire may impact the latter three cues by consuming existing vegetation, which increases solar radiation and alters soil moisture and chemistry (Neary et al. 1999, Paritsis et al. 2006). In addition, many plants only flower after accumulating some threshold of resources, and resource availability may also affect the number of blooms produced or the length of the bloom period (Rathcke 1983, Ramirez-Parada et al. 2020). Fire, through consumption of existing vegetation, impacts nutrient and water availability (Neary et al. 1999), and therefore, may also influence the initiation, duration, or extent of blooming period (Rathcke and Lacey 1985, Paritsis et al. 2006).

The effect of fire on flowering phenology is likely mediated by burn severity (defined as the proportion of vegetation killed by fire) and initial habitat type. For example, at moderate severity, fire is more likely to increase nutrient availability by removing biomass, whereas high-severity fire may decrease nutrient availability due to volatilization, leaching, erosion, and mineralization (Neary et al. 1999, Raison et al. 2009). Similarly, the effect of fire on soil



moisture depends on the pre-fire vegetation conditions; in areas dominated by herbaceous cover, such as meadows, fire-induced changes to soil hydrology were negligible within two years of fire, whereas tree-dominated landscapes tended to have long lasting changes to soil hydrology post-fire (Cerdà and Doerr 2005). As such, understanding the effects of fire on flowering plant phenology requires attention to both burn severity and initial habitat conditions.

In dry, temperate forests where fire is the dominant source of disturbance, herbs and shrubs are a small proportion of the biomass, however, they represent the majority of plant diversity and have important roles in erosion control, nutrient cycling, and energy flow (Gilliam 2007). Herbs and shrubs are typically found either in canopy gaps created by fire or other disturbance (Matonis and Binkley 2018) or in meadows formed by geography and hydrology and maintained by fire (DeBenedetti and Parsons 1979, Ratliff 1985). Because fire plays an important role in maintaining the herb and shrub layer, changes to the fire regime in this system are particularly concerning. Dry, mixed-conifer forest (henceforth, upland habitat) at mid-elevations (1,200-1,800m asl) in the Sierra Nevada historically had an average fire return interval of 5-25 years, with most fires burning in late summer at low-to-moderate severity, with some limited high-severity effects due to climatic conditions, topography, fuel loads, and extreme weather (Collins and Stephens 2010, Miller and Safford 2017, Safford and Stevens 2017). Meadows at similar elevations experienced low-severity fires every 40 years, with high-severity fires occurring every 200-300 years, typically during prolonged drought (Ratliff 1985, Caprio and Lineback 2002). Low-to-moderate severity fire is associated with high levels of plant diversity in the understory, which has been attributed to historic filtering effects (Ricklefs 1987, Miller and Safford 2020), colonization-competition tradeoffs (Grime 1977, Stevens et al. 2015), or increased habitat heterogeneity (Martin and Sapsis 1992, Richter et al. 2019). Following a

century of fire suppression, the number and size of canopy gaps in upland habitat has decreased significantly (Lydersen et al. 2013, Matonis and Binkley 2018) and in meadows, lack of fire leads to encroachment by woody species (DeBenedetti and Parsons 1979, Vale 1981, Norman and Taylor 2005), reducing landscape heterogeneity, altering water storage capacity, and shifting composition away from herbaceous cover (Fletcher et al. 2014, Boisramé et al. 2017b, 2017a). Thus, species that depend on flowering plants are also likely impacted by fire suppression; there are fewer plant-pollinator interactions and lower pollinator and plant diversity in green, unburned forests relative to burned forest (Burkle et al. 2015, 2022, LaManna et al. 2021).

Fire suppression has also led to a build-up of fuels and fire-intolerant species; combined with the hotter, drier, and longer fire seasons and multi-year severe droughts due to climate change, the Sierra Nevada mixed conifer forests and meadows now regularly experience extreme fire conditions (Westerling et al. 2006, Stephens et al. 2018). These conditions result in fires that burn with a greater proportion of high-severity effects. High-severity fire may affect plant survival and reproduction directly by the outright destruction of plants and seedbanks or indirectly by change to soil temperature, moisture, and chemistry and resource availability (Neary et al. 1999, Raison et al. 2009, Stoof et al. 2010). Consequently, fire may impact the flowering phenology of plants through these indirect effects, resulting in plants that bloom earlier, in greater numbers, or for longer duration due to increases in temperature, water, or other resources (Paritsis et al. 2006, LoPresti et al. 2018, Mola and Williams 2018). Additionally, fire may impact phenology by changing community composition; for example, annual plants may be better colonizers of post-fire systems (Keeley 2006) and more sensitive to phenological cues than perennial species (Fitter and Fitter 2002).

We aimed to better understand how fire severity impacts the diversity and phenology of plant communities in fire-suppressed Sierra Nevada mixed conifer forests and meadows by sampling flowering plant communities in the post-fire landscape of the King Fire that burned almost 40,000 ha in 2014, with nearly 50% at high severity. We compare phenological patterns in green (i.e., unburned), moderate-, and high-severity upland habitat and green and high-severity meadow habitat. Because we were primarily interested in understanding flowers as resources for pollinators, which are often long-lived or generalist foragers that rely on multiple species over the course of the season (Aldridge et al. 2011), we focused on the community phenology, i.e. the overall number of inflorescences and the diversity of species in bloom at a point in time, rather than species-level phenology.

We hypothesized that in upland habitat, moderate-severity conditions would have the highest diversity and abundance of plants in bloom and that these would be highest over the whole blooming season due to the increase in resource availability, and shifting of temperature and soil cues that stimulate flowering. We expected green forests to have the lowest floral diversity and abundance throughout the season due to the lower availability of resources and presumed cooler temperatures under the canopy that would delay blooming. We also predicted that the number and diversity of bloom may be high early in the season due to the increases in temperature that may stimulate flowering in high-severity upland habitat. We hypothesized that meadows would be more diverse and have higher floral abundance than upland habitat. Within meadow habitat, we expected floral diversity and abundance in high-severity meadows to be higher than in green meadows, due to decreased dominance by highly competitive species and a presumably large seed bank present after extended fire suppression. We did not expect

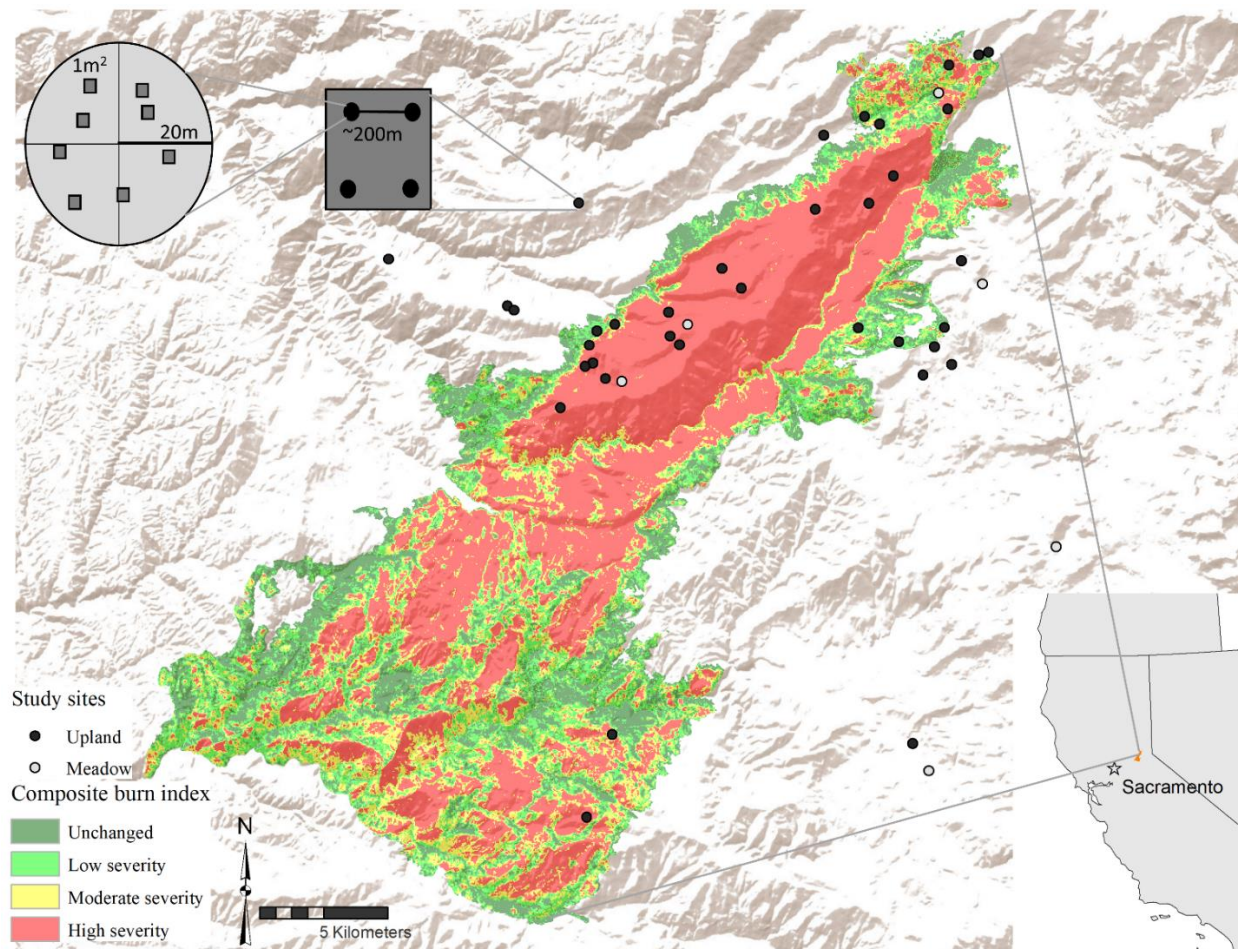
differences in the number or diversity of blooms over time in meadows due to the presumed similarity in resources among burned and green meadows.

## **Methods**

### Study Area

Our study area was located in and around the 2014 King Fire in the Eldorado National Forest, California (Fig.1). The study area was restricted to lower montane forest and meadow communities (between ~1300 and 1800m above sea level) to minimize the effects of elevation and related factors on our data. This region's climate is characterized by wet, cool winters with most precipitation falling as snow, and dry, warm summers with little precipitation. Pre-fire upland habitat was largely composed of dense stands of relatively young white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menziseii*) and incense cedar (*Calocedrus decurrens*). Pre-fire meadows were dominated by grasses (Poaceae) and graminoids (Juncaceae and Cyperaceae), forbs, and small shrubs, with some conifer encroachment (McKelvey et al. 1996, Skinner et al. 1996).

The King Fire was started by an arsonist outside of Pollock Pines, California (38.782° N, 120.604° W) on September 13, 2014. Its size, proportion of high-severity effects, and rate of spread led to its classification as a “megafire” (Stephens et al. 2014). The Sierra Nevada was experiencing a severe three-year drought at the time of the fire, with low precipitation and record high temperatures (Young et al. 2017). Fuel levels in the area were high due to effective fire suppression: much of the fire footprint had not burned in nearly 100 years (California Department of Forestry and Fire Protection 2022). Over a two-week period, nearly 39,545ha burned, about 50% at high severity (greater than 75% vegetation mortality, USDA Forest Service 2014).



**Figure 1.** Map of study area showing the region of the Sierra Nevada, California, where the King Fire burned in 2014; inset shows location of the King fire in California. Points on map indicate study sites within each burn-habitat class, with insets showing how sampling plots were organized within sites. Flowering plants in bloom were surveyed in eight randomly located -m2 quadrats within each plot.

### Sampling design

We identified sampling sites of a given burn severity in ArcGIS 10.6 (ESRI, Redlands, California, USA) using the US Forest Service King Fire RAVG (USDA Forest Service 2014) composite burn index to identify unburned (i.e., green) areas (unchanged), areas of moderate-severity (mix of surface fire and more severe fire, with some mortality of dominant vegetation) and high-severity (dominant vegetation has high-to-complete mortality) fire. The composite burn index is a vegetation severity rating based on composite of the changes to the dominant vegetation in the understory, midstory, and overstory. Ground-truthing ensured that sites were

assigned the appropriate burn severity category and where homogenous in a 200-m<sup>2</sup> area. We sampled green sites to compare the fire-suppressed condition to those created by fire. High- and moderate-severity sites were sampled to represent how flowering plant communities may differ under severe (high-severity) and more historic (moderate-severity) fire conditions and how this may differ across upland and meadow systems. Each site had between three and five 20-m radius circular plots separated by at least 100m (average distance = 198m) in either a linear or circular orientation that best characterized the habitat of interest (Fig. 1). In 2016, nine upland sites were established: six in high-severity and three in green habitat. All were visited three times following spring snowmelt. In 2017, twenty-seven new sites were established in upland forest with 9 each in unburned forest, moderate-severity, and high-severity burns. In 2017, upland sites were only visited twice due to a truncated floral season that resulted from a cold, snowy spring, and to accommodate simultaneous sampling at moderate-severity upland sites. This resulted in a total of 151 unique upland plots on 36 sites over both years of sampling. Because meadow habitat was limited within the fire footprint, we sampled the same sites (but not necessarily the same plots) in both years of the study. Meadow sites were located within the fire footprint in high-severity areas (n=3) or outside the fire footprint (n=3) and were visited three times per season in both years of the study. In 2016, each meadow site had five plots for a total of 30 meadow plots. This was reduced in 2017 to three or four plots per site for a total of 22 meadow plots due to the logistic constraints outlined above. We refer to the combination of habitat and burn conditions (e.g., high-severity meadow, green upland, etc.) as habitat-burn classes.

#### Floral diversity and abundance

We surveyed flowering plants in bloom in eight one-meter squared quadrats within each 20-m radius plot. Plots were divided into quarters using transects and two quadrats were randomly placed in each quarter. In each quadrat, we identified every plant in flower to species

following Jepson (Baldwin et al. 2012) and counted the number of inflorescences with open flowers per species. We estimated snowmelt dates for each year (June 6, 2016 and June 18, 2017) using data from the Greek Store and Robb's saddle weather stations located ~10km and at similar elevations (~ 1,700m asl) to our study area (California Department of Water Resources 2018). The time since snowmelt was the difference between the date of each visit and the regional date for snowmelt for each year in days. Floral richness of plants in bloom was the total number of unique species found across all quadrats in each plot on each visit. Floral abundance was the count of all inflorescences with open flowers observed in each plot on each visit.

#### Statistical Analysis

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

#### *Sampling Coverage*

From the field data, we derived several diversity measures (see below). Diversity estimates increase with increasing sampling effort; therefore, comparisons of communities require similar sampling coverage or standardization of effort to reduce bias. We tested sampling coverage across burn-habitat classes with the iNEXT function (iNEXT version 2.0.20; Chao et al. 2014; Hsieh et al. 2020) in R and found that coverage was high (>90%) and approximately equal for all burn-habitat classes, (Table 1), so we did not standardize our samples in order to preserve the ecologically meaningful differences in abundance in burn-habitat classes (LaManna et al. 2021).

#### *Alpha diversity*

Alpha diversity ( $\alpha$ ) represents species diversity at a local scale. To determine differences in  $\alpha$  among habitat-burn classes, we calculated diversity profiles for each class at each visit. A

diversity profile for a given community can be defined as a family of Hill's numbers, a function for Hill's diversity ( $D$ ) that varies in sensitivity to abundance by order,  $q$ :

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

where  $S$  is the number of species,  $p_i$  is the relative abundance of species  $i$ , and  $q$  is the sensitivity parameter ( $q > 0$ ; Chao et al. 2014). When  $q=0$ , relative 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). Plotting the Hill's diversity numbers at multiple values of  $q$  results in a curve with an intercept of species richness and slope that reflects the influence of evenness in that particular community (Chao et al. 2014). We plotted the Hill's diversity profiles of each burn-habitat class on each visit with a bootstrapped 95% confidence interval and considered profiles significantly different if the intervals were non-overlapping. We evaluated floral phenology of each class by comparing diversity metrics early and late in the season. For example, in burn-habitat classes with a longer blooming season, we would expect constant diversity values over the season, whereas an "early" season would show higher diversity on the first visit relative to later visits.

### *Beta diversity*

Beta diversity ( $\beta$ ) describes the variation in composition among subcommunities within a metacommunity and in the simplest definition is the ratio of the local ( $\alpha$ ) to regional ( $\gamma$ ) diversities (Whittaker 1960, Jost 2007). We defined  $\beta$  as the variation in the community matrix using an abundance-based Bray-Curtis dissimilarity index (Anderson et al. 2006; Legendre and De Cáceres 2013). Because this index is based on the proportion of species that are shared



among subcommunities, plots with zero species detections were dropped from this analysis. We calculated the among-plot (plot-level)  $\beta$ , the among-class (class-level)  $\beta$ , and compositional dissimilarity, all based on the Bray-Curtis dissimilarity index.

We defined class-level  $\beta$  as the spatial median of the community matrix for a given burn-habitat-visit class (Anderson 2006, Anderson et al. 2006), calculated with the betadisper function in vegan (version 2.5-7, Oksanen et al. 2020). This function takes the Bray-Curtis dissimilarity matrix and reduces its dimensionality with principal components analysis, such that the community composition of each plot can be located as a point in multidimensional space. The spatial median for each class is estimated as the point where the sum of the distances from all the plots of a burn-habitat class was minimized. The plot-level  $\beta$  is the distance of a plot from its respective spatial median, whereas the class-level  $\beta$  is the average distance of all plots within a class to their respective spatial median. At the plot level, high  $\beta$  indicates that a plot is unique relative to its burn-habitat class and low  $\beta$  suggests that a plot has a composition similar to other plots in its burn-habitat class, which may be a sign of homogenization. A high class-level  $\beta$  indicates that plots within that class are highly dissimilar. We used the permutest function in vegan to compare the class-level  $\beta$  among burn-habitat classes by visit for each year and adjusted for multiple comparisons with the false discovery rate, the expected proportion of Type II errors relative to all rejections of the null hypothesis (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001). Permutations were run 999 times. We modelled the plot-level  $\beta$  as described in the following section.

We defined the compositional dissimilarity as the difference in the spatial medians (ie, the location of each community in multidimensional space) described above for all classes by visit. This allowed us to test for differences in community composition through time with

permutational multivariate analysis of variance (PERMANOVA) using the `adonis` function in `vegan`. PERMANOVA assumes that variances within groups are homogeneous, which we tested with the `betadisper` function in `vegan` (Appendix A). Permutations were run 999 times. All classes by visits of interest had homogeneous variances (Appendix Table A1-A2). Multiple comparisons were corrected with the false discovery rate. Because we were only interested in understanding how burn-habitat classes differed from each other at a given time point, and how a given class differed across time, we only considered (and corrected for) these comparisons.

#### *Drivers of floral abundance and diversity*

In order to determine the factors that influence floral resources, we modeled estimates of floral abundance, floral richness (Hill's diversity for  $q=0$ , see equation 1), and plot-level  $\beta$  as functions of ecological measures obtained for each plot-visit. We used the `GLMMadaptive` package (version 0.8-2, Rizopoulos 2020) to build generalized linear mixed models (GLMM) with burn-habitat class, days since snowmelt and the interaction of these terms as the main effects and site as a random effect to account for spatial autocorrelation of plots within a site and repeated sampling. We interpreted the response of abundance or richness to days since snowmelt as a shorter bloom season if it was more negative and a longer blooming season if it was less negative. Elevation and year were also included in the models to account for the variation introduced by these variables. We tested for collinearity among variables and found that correlations among all continuous covariates were  $< 0.5$  (Appendix Table A3-A4). Continuous covariates were scaled and centered.

Floral abundance and species richness were modelled with GLMM with residuals following the negative binomial distribution. Plot-level  $\beta$  was modelled with a GLMM with residuals following the beta distribution. Model fit was checked using the `Dharma` package

(version 0.4.3, Hartig 2021) and GLMMadaptive wrapper (Rizopoulos 2020; Appendix Fig. A1-A3). Coefficient estimates were rescaled to determine how each burn and habitat variable and their interaction affected the response variable relative to its green control (i.e., rather than the default of comparing all burn-habitat classes against a single reference category, we compared high-severity meadow to green meadow, and high- and moderate-severity upland to green upland), and how the number of days since snowmelt affected the response variable in each burn-habitat class (i.e., rather than looking at how different the slope was in each burn-habitat category from that in a single reference category, we derived the actual slope in each burn-habitat class). We calculated standard errors and 95% Wald confidence intervals for each rescaled coefficient using the `deltamethod` function in the `msm` package (version 1.6.9, Jackson 2011). If the intervals did not overlap zero, we considered the effect of the covariate significant.

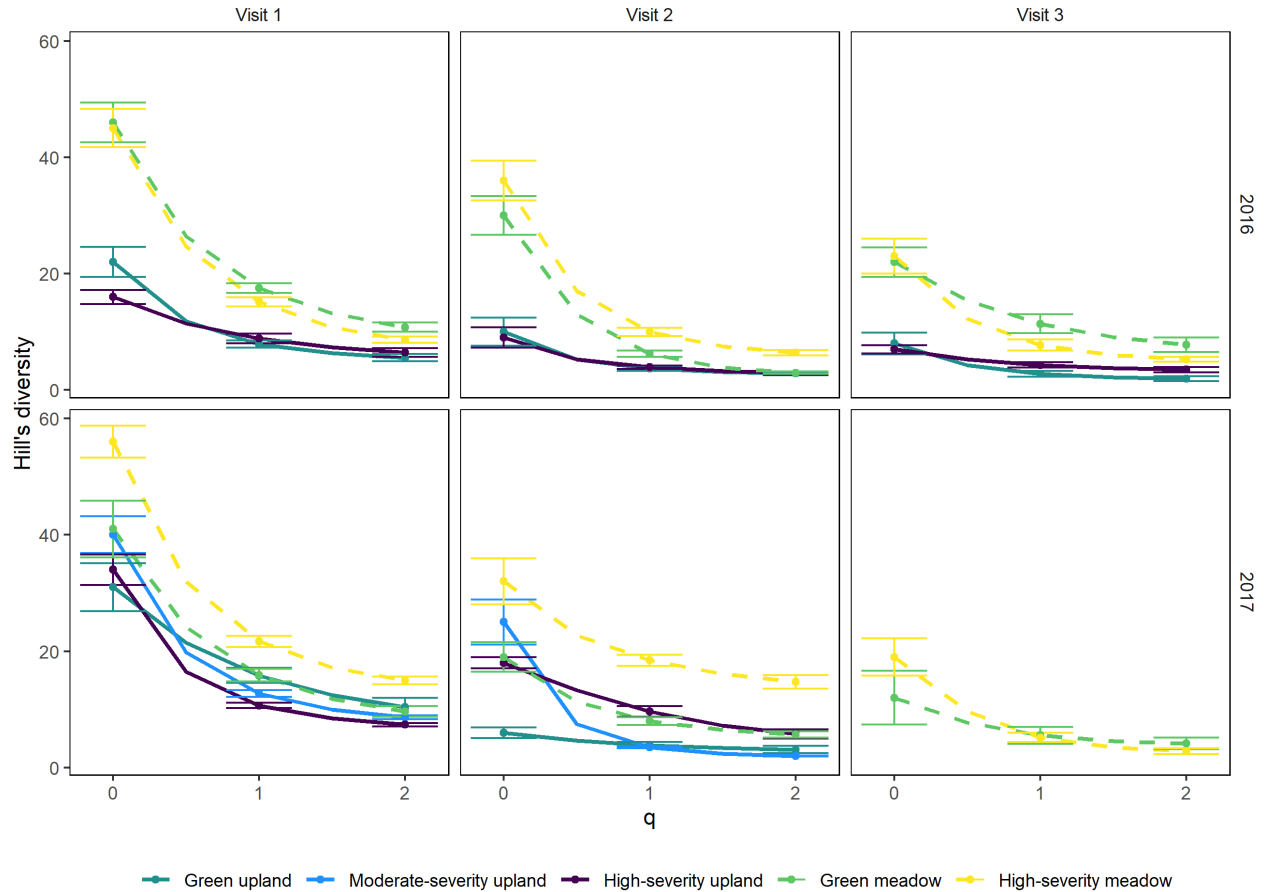
## **Results**

### Alpha diversity

We found that  $\alpha$  differed significantly across burn-habitat classes and visits (Fig. 2). As expected, meadows tended to be more diverse, but less even than upland habitat, although this pattern was weaker in 2017. In 2016, alpha diversity was similar among green and high-severity habitats early in the season. However, high-severity meadows tended to be more diverse than green meadows in the mid-season, while there was no difference in upland habitats. Later in the season, green meadows tended to be more diverse than burned meadows while high-severity upland habitats were slightly more diverse than green upland habitat. In 2017, burned habitats were consistently and significantly more diverse, though less even, than their green counterparts. Moderate-severity upland habitat was slightly more diverse than high-severity upland, although differences were not significant.

**Table 1.** Summary of floral abundance and diversity measured on multiple visits throughout the flowering season in green, moderate-, and high- severity burned upland and green and high-severity meadows of the Sierra Nevada of California, two and three years, after the 2014 King fire. SC=sample coverage, D=diversity.

2016	Visit	Abundance	SC	Species richness	Shannon D	Simpson D
Green upland	1	541	0.995	22	7.899	5.552
Green upland	2	339	0.991	10	3.66	2.825
Green upland	3	144	0.979	8	2.762	1.928
High-severity upland	1	363	0.995	16	8.843	6.42
High-severity upland	2	566	0.998	9	3.917	2.915
High-severity upland	3	206	1.000	7	4.321	3.492
Green meadow	1	2043	0.997	46	17.488	10.804
Green meadow	2	1303	0.995	30	6.233	2.988
Green meadow	3	497	0.994	22	11.395	7.784
High-severity meadow	1	1934	0.997	45	15.146	8.64
High-severity meadow	2	1357	0.996	36	9.987	6.419
High-severity meadow	3	223	0.982	23	7.715	5.286
2017	Visit	Abundance	SC	Species richness	Shannon D	Simpson D
Green upland	1	518	0.990	31	15.817	10.376
Green upland	2	89	1.000	6	3.829	3.071
Moderate-severity upland	1	2433	0.998	40	12.698	8.631
Moderate-severity upland	2	4584	0.999	25	3.483	1.988
High-severity upland	1	3551	0.999	34	10.667	7.359
High-severity upland	2	483	1.000	18	9.612	5.775
Green meadow	1	1080	0.994	41	15.887	9.614
Green meadow	2	647	0.995	19	7.955	5.701
Green meadow	3	77	0.909	12	5.555	4.126
High-severity meadow	1	2451	0.998	56	21.675	14.988
High-severity meadow	2	868	0.994	32	18.432	14.722
High-severity meadow	3	268	0.982	19	5.17	2.808



**Figure 2.** Floral alpha diversity in different burn-habitat classes in upland and meadow habitat in the Sierra Nevada, California, two and three years after the 2014 King Fire. Diversity profiles for each burn-habitat class where increasing order ( $q$ ) represents how decreasing contribution of rare species to diversity estimates, with bootstrapped 95% confidence interval. Estimates with non-overlapping confidence intervals are considered significantly different. Upland habitat is shown with solid lines and meadow habitat is shown with dashed lines.

### Beta diversity

We found that the class-level  $\beta$  (i.e., the mean plot-level distance to the respective spatial median) among visits within the same burn-habitat class, and those among classes within the same visit, did not differ significantly in 2016 ( $F_{11,23}=1.06$ ,  $p=0.419$ ; Table 2). In 2017, there were differences in class-level  $\beta$  ( $F_{11,149}=1.963$ ,  $p=0.037$ ), however, none of the pairwise comparisons of interest were significant (Appendix Table A2).

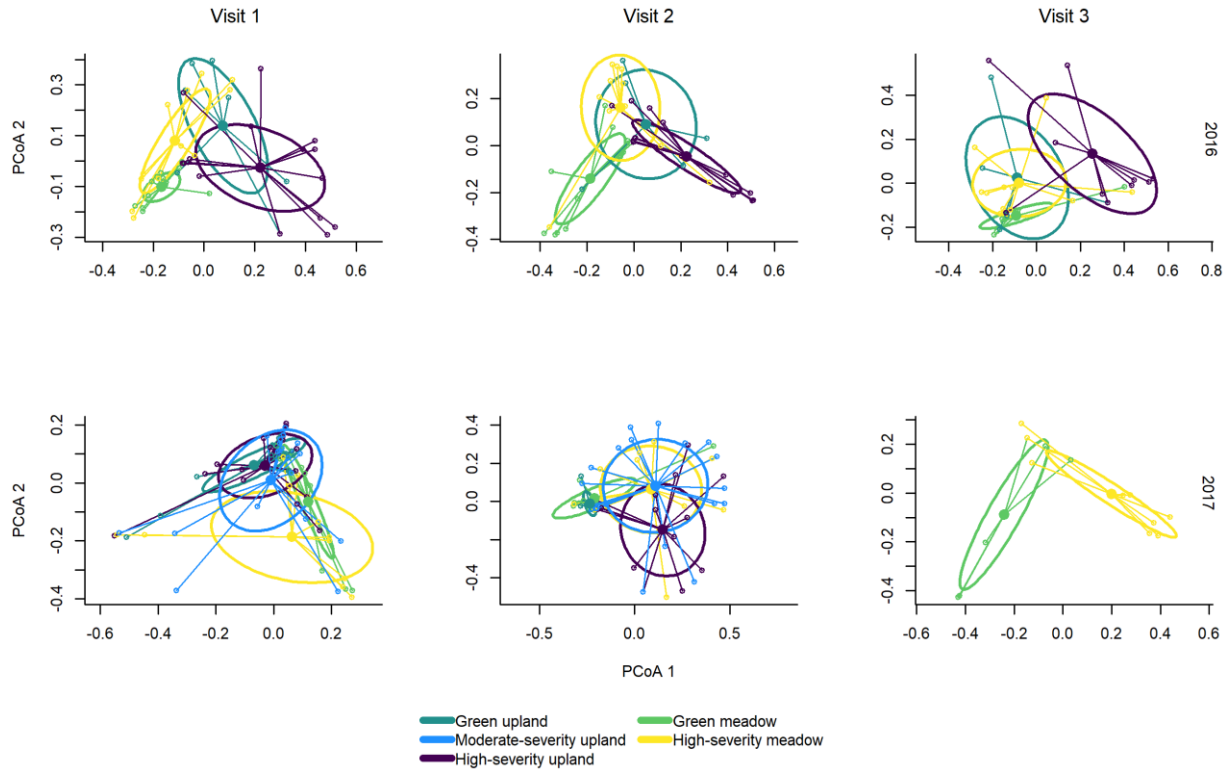
**Table 2.** Floral class-level  $\beta$  diversity by burn-habitat class and visit for green, moderate-, and high-severity upland and green and high-severity meadows of the Sierra Nevada of California in 2016 and 2017, following the 2014 King fire. For each visit,  $\beta$  is the mean distance of all sampling plots in a class to its spatial median of the Bray-Curtis dissimilarity matrix.

2016	Visit	$\beta$ diversity	2017	Visit	$\beta$ diversity
Green upland	1	0.618	Green upland	1	0.672
Green upland	2	0.599	Green upland	2	0.636
Green upland	3	0.627	Moderate-severity upland	1	0.676
High-severity upland	1	0.629	Moderate-severity upland	2	0.600
High-severity upland	2	0.633	High-severity upland	1	0.674
High-severity upland	3	0.551	High-severity upland	2	0.592
Green meadow	1	0.645	Green meadow	1	0.626
Green meadow	2	0.636	Green meadow	2	0.627
Green meadow	3	0.661	Green meadow	3	0.624
High-severity meadow	1	0.624	High-severity meadow	1	0.621
High-severity meadow	2	0.625	High-severity meadow	2	0.593
High-severity meadow	3	0.646	High-severity meadow	3	0.597

We found that there were overall significant differences in community composition among burn-habitat classes and visits in 2016 (pseudo  $F_{11, 123}=1.455$ ,  $p=0.001$ ,  $R^2=0.115$ ) and 2017 (pseudo  $F_{11, 149}=1.493$ ,  $p=0.001$ ,  $R^2=0.099$ ). Compositional dissimilarities were strongest across burn-habitat classes at a particular visit, rather than across visits in particular burn-habitat classes (Table 3, Fig. 3). When we compared classes at each visit, we found that about half of the pairwise comparisons were significant. When we considered each burn-habitat class across all visits, we found that there were few significant differences in communities (Table 3, Fig. 3). Green meadow community composition early in the season differed significantly from green meadow composition in the mid and late season in 2016. In 2017, both high-severity and moderate-severity upland habitat differed significantly in community composition between first and second visits. Burn-habitat class explained about 12% and 10% of the variation in community composition in 2016 and 2017, respectively.

**Table 3.** Floral community dissimilarity in green, moderate-, and high- severity upland and green and high-severity meadow habitat of the Sierra Nevada of California in 2016 and 2017, following the 2014 King fire. Adjusted pairwise p-values by visit (a,c) and burn-habitat class (b,d), Bold values are significant at  $\alpha=0.05$ .

<b>a. 2016 Visit pairwise comparison</b>			<b>c. 2017 Visit pairwise comparison</b>		
Visit 1		p-value	Visit 1		p-value
Green upland	High upland	0.511	Green upland	Moderate upland	0.658
Green upland	Green meadow	<b>0.005</b>	Green upland	High upland	0.309
Green upland	High meadow	0.150	Green upland	Green meadow	<b>0.004</b>
Green meadow	High meadow	<b>0.005</b>	Green upland	High meadow	<b>0.011</b>
Green meadow	High upland	<b>0.005</b>	Moderate upland	High upland	0.669
High upland	High meadow	<b>0.005</b>	Moderate upland	Green meadow	<b>0.004</b>
Visit 2		p-value	Moderate upland	High meadow	<b>0.030</b>
Green upland	High upland	0.511	High upland	Green meadow	<b>0.004</b>
Green upland	Green meadow	0.108	High upland	High meadow	<b>0.050</b>
Green upland	High meadow	0.805	High meadow	Green meadow	0.058
Green meadow	High meadow	<b>0.024</b>	Visit 2		p-value
Green meadow	High upland	<b>0.005</b>	Green upland	Moderate upland	<b>0.015</b>
High upland	High meadow	<b>0.024</b>	Green upland	High upland	<b>0.004</b>
Visit 3		p-value	Green upland	Green meadow	<b>0.018</b>
Green upland	High upland	0.233	Green upland	High meadow	<b>0.017</b>
Green upland	Green meadow	0.728	Moderate upland	High upland	0.116
Green upland	High meadow	0.831	Moderate upland	Green meadow	<b>0.004</b>
Green meadow	High meadow	0.152	Moderate upland	High meadow	0.625
Green meadow	High upland	<b>0.013</b>	High upland	Green meadow	<b>0.004</b>
High upland	High meadow	<b>0.035</b>	High upland	High meadow	0.309
			High meadow	Green meadow	0.129
			Visit 3		p-value
<b>b. 2016 Burn-habitat pairwise comparison</b>			High meadow	Green meadow	<b>0.013</b>
Green upland		p-value			
Visit 1	Visit 2	0.828	<b>d. 2017 Burn-habitat pairwise comparison</b>		
Visit 1	Visit 3	0.800	Green upland		
Visit 2	Visit 2	0.946	Visit 1	Visit 2	0.770
High upland			Moderate upland		
Visit 1	Visit 2	0.771	Visit 1	Visit 2	<b>0.036</b>
Visit 1	Visit 3	0.375	High upland		
Visit 2	Visit 2	0.430	Visit 1	Visit 2	<b>0.004</b>
Green meadow			Green meadow		
Visit 1	Visit 2	<b>0.005</b>	Visit 1	Visit 2	0.755
Visit 1	Visit 3	<b>0.015</b>	Visit 1	Visit 3	0.120
Visit 2	Visit 2	<b>0.004</b>	Visit 2	Visit 2	0.678
High meadow			High meadow		
Visit 1	Visit 2	0.946	Visit 1	Visit 2	0.309
Visit 1	Visit 3	0.511	Visit 1	Visit 3	0.168
Visit 2	Visit 2	0.946	Visit 2	Visit 2	0.897



**Figure 3.** Floral  $\beta$  diversity of in post-fire upland and meadow habitat in the Sierra Nevada, California in 2016 (top) and 2017 (bottom), sampled over three visits, following the 2014 King Fire. Each sampling plot per visit (hollow point) is located in space based on the abundance-based community matrix, the spatial median (larger, solid point) is the point in multidimensional space where the sum of the distances from all the plots of a burn-habitat class per visit is minimized, and the ellipse encompasses one standard deviation. The class-level  $\beta$  is the mean distance across plots from the spatial median for each class per visit, whereas the community composition of each class per visit is represented by the locations of the spatial medians. Note the difference in axis scales between plots. (Table 3, details in text).

#### Drivers of floral abundance and diversity

We found that the burn-habitat class affected the floral abundance at the plot-level (Table 4, Fig. 4a, Appendix Table B1). As predicted, the floral abundance in burned upland habitat increased significantly relative to green upland habitat, with a stronger positive effect observed in moderate-severity than high-severity upland. In meadows, we found that high-severity fire negatively affected the floral abundance relative to green meadows, although this relationship was not significant.

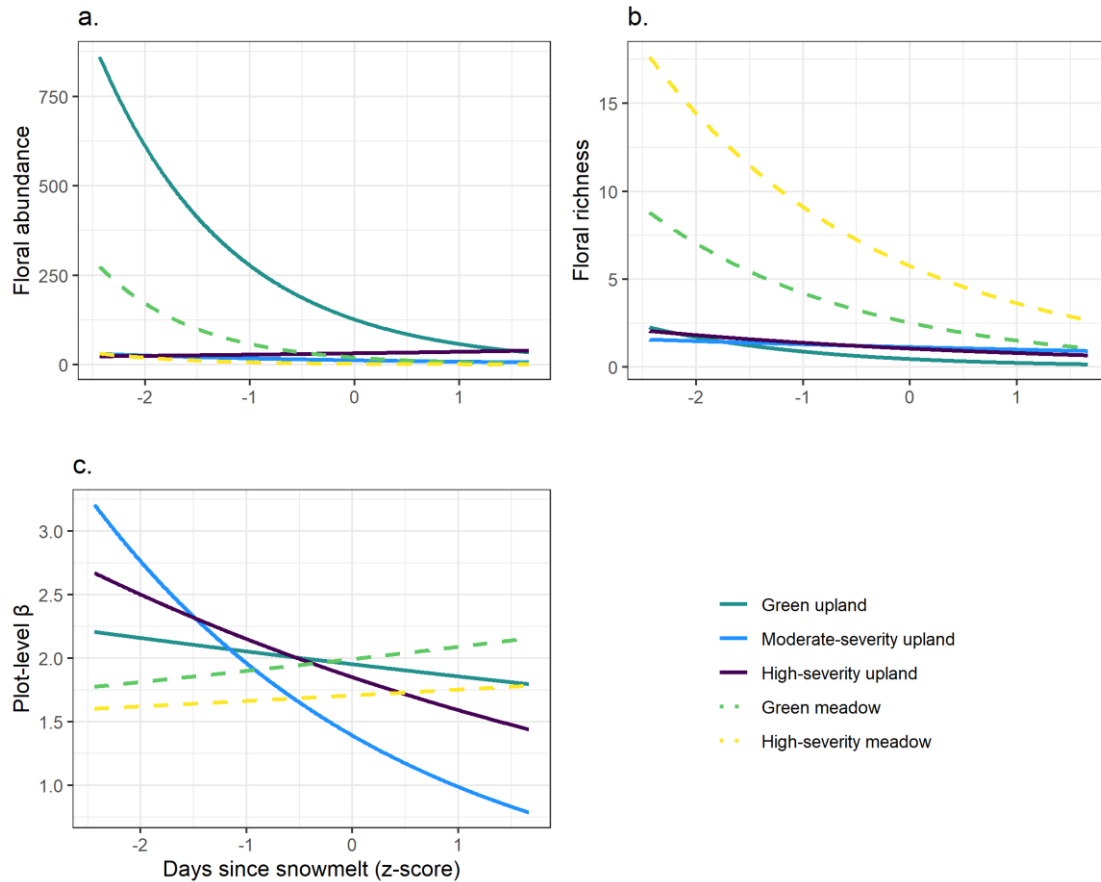


**Table 4.** Drivers of floral abundance and diversity in green, moderate-, and high- severity upland and green and high-severity meadows of the Sierra Nevada of California in 2016 and 2017, following the 2014 King fire. Results for generalized linear mixed models for floral abundance and richness (negative binomial) and beta diversity (beta). Intercepts and slopes were re-scaled to show the green (unburned) habitat as the reference category for upland and meadow habitats. DSS=days since snowmelt. Bold values are considered significant at  $\alpha=0.05$ . SE= standard error, CI = 95% confidence interval limits. Full model results in Appendix B.

<b>Floral abundance</b>				
Parameter	Estimate	SE	lower CI	upper CI
Intercept (Green upland)	1.352	0.568	0.238	2.465
$\beta$ (Moderate-severity upland)	2.720	0.760	1.231	4.209
$\beta$ (High-severity upland)	1.734	0.687	0.388	3.080
Intercept (Green meadow)	3.599	0.924	1.788	5.410
$\beta$ (High-severity meadow)	1.868	1.293	-0.667	4.403
$\beta$ (DSS, green upland)	-1.110	0.246	-1.592	-0.629
$\beta$ (DSS, moderate-severity upland)	0.129	0.296	-0.452	0.709
$\beta$ (DSS, high-severity upland)	-0.386	0.207	-0.791	0.020
$\beta$ (DSS, green meadow)	-1.087	0.224	-1.525	-0.649
$\beta$ (DSS, high-severity meadow)	-0.789	0.219	-1.218	-0.360
<b>Floral richness</b>				
Parameter	Estimate	SE	lower CI	upper CI
Intercept (Green upland)	-0.460	0.301	-1.049	0.129
$\beta$ (Moderate-severity upland)	0.907	0.396	0.132	1.683
$\beta$ (High-severity upland)	0.829	0.362	0.121	1.538
Intercept (Green meadow)	1.245	0.435	0.392	2.097
$\beta$ (High-severity meadow)	0.825	0.612	-0.374	2.024
$\beta$ (DSS, green upland)	-0.656	0.151	-0.952	-0.360
$\beta$ (DSS, moderate-severity upland)	-0.131	0.132	-0.389	0.127
$\beta$ (DSS, high-severity upland)	-0.275	0.110	-0.489	-0.060
$\beta$ (DSS, green meadow)	-0.513	0.078	-0.666	-0.361
$\beta$ (DSS, high-severity meadow)	-0.461	0.075	-0.608	-0.313
<b>Floral plot-level <math>\beta</math></b>				
Parameter	Estimate	SE	lower CI	upper CI
Intercept (Green upland)	0.615	0.096	0.428	0.803
$\beta$ (Moderate-severity upland)	-0.338	0.125	-0.582	-0.093
$\beta$ (High-severity upland)	-0.053	0.111	-0.271	0.164
Intercept (Green meadow)	1.245	0.435	0.392	2.097
$\beta$ (High-severity meadow)	0.825	0.612	-0.374	2.024
$\beta$ (DSS, green upland)	-0.050	0.066	-0.180	0.079
$\beta$ (DSS, moderate-severity upland)	-0.343	0.068	-0.477	-0.208
$\beta$ (DSS, high-severity upland)	-0.151	0.049	-0.246	-0.055
$\beta$ (DSS, green meadow)	-0.513	0.078	-0.666	-0.361
$\beta$ (DSS, high-severity meadow)	0.026	0.047	-0.066	0.118

Similarly, the effect of days since snowmelt was dependent on the burn-habitat class (Fig. 4a). Except for moderate-severity upland habitat, where the effect of days since snowmelt was close to 0, the floral abundance decreased with increasing days since snowmelt; this effect was significant except for high-severity upland habitat. The effects of burn-habitat and days since snowmelt were similar for floral richness (Table 4, Fig. 4b, Appendix Table B2). As expected, the floral richness increased significantly in both moderate- and high-severity upland habitat relative to green upland habitat and meadows tended to have high floral richness. Floral richness decreased in high-severity meadows relative to green meadows, but the effect was not significant. As the days since snowmelt increased, floral richness decreased significantly in all burn-habitat classes except moderate-severity upland.

Contrary to our expectations, fire tended to homogenize communities in upland habitat, but not in meadows (Table 4, Fig. 4c, Appendix Table B3). Plot-level  $\beta$  diversity decreased significantly in moderate-severity upland habitat relative to green upland; the effect of high-severity fire was not significant. Similarly, there was an increase in plot-level  $\beta$  diversity in high-severity meadow habitat, but this effect was not significant. Days since snowmelt interacted with burn-habitat class to impact plot-level  $\beta$ . In green upland, there was no effect of days since snowmelt, but in moderate- and high- severity upland habitat, as days since snowmelt increased, plot-level  $\beta$  decreased. Similarly, plot-level  $\beta$  decreased with increasing days since snowmelt in green meadows, but there was no significant effect of days since snowmelt in high-severity meadows.



**Figure 4.** The predicted response of a) floral abundance, b) floral richness, and c) floral plot-level  $\beta$  (y axis) to days since snowmelt (centered and standardized; x-axis) for green and burned meadow and upland habitat on Poisson generalized linear mixed models (GLMM) for abundance and richness, and beta GLMM for plot-level  $\beta$ . Upland habitat is shown with solid lines and meadow habitat is shown with dashed lines. Sampling occurred in the Sierra Nevada, California, two and three years after the 2014 King Fire.

## Discussion

We found that the effect of fire on the flowering plant community depended both on burn severity and on pre-fire habitat type, and that both of these factors also affected plant community phenology. As expected, meadows tended to have more diverse and abundant floral resources throughout the season; fire increased abundance and diversity in upland habitat. These effects, however, also depended on the scale at which they were studied, with clearer patterns at the sampling plot scale than when combining all data for a given burn-habitat class. Contrary to

our expectations, moderate-severity fire in upland habitat did not increase  $\beta$  diversity on either scale, but rather reduced plot-level  $\beta$ , indicating that these communities are more homogeneous. Whereas floral abundance and diversity generally declined as the season progressed, the importance of that decline depended on burn-habitat class and on the scale at which these patterns were studied. As expected, moderate-severity and, to a lesser extent, high-severity upland habitat had higher diversity and abundance of blooms throughout the season at both the class-level and plot-level than green upland habitat. Green and high-severity meadows were similar in floral diversity early in the season, but the decline in meadow resources occurred more slowly in burned habitat.

We expected to see high diversity of blooms early in the season in burned habitat due to fire-driven alterations to flowering cues such as temperature and soil moisture (Rathcke and Lacey 1985, Wroblewski and Kauffman 2003, Paritsis et al. 2006). We did observe this pattern in high-severity meadows, which tended to be higher in diversity earlier in the season than green meadows. Additionally, green meadows were dominated by perennial species, whereas high-severity meadows had more annual species (Appendix C), which also tend to bloom earlier in the season (Fitter and Fitter 2002). In upland forest, green habitat tended to be more diverse earlier in the season, and moderate- and high- severity burns were more diverse later, particularly in 2017, despite dominance by annual species in all upland habitat types. The upland plant community may have been less influenced by cues to initiate flowering earlier and more influenced by increased resource availability that prolong the flowering season. This may be due to the competitive release by fire from a system typically dominated by trees (Brodie et al. 2021). High-severity upland habitat showed highest diversity in the middle of the season, suggesting they provide important floral resources in between early and late blooming species. This is

particularly important given that climate change may cause divergent shifts in blooming, with early bloomers shifting earlier and late bloomer shifting later, leaving a mid-season “gap” in floral resources important to pollinators and other higher trophic levels (Aldridge et al. 2011, McKinney et al. 2012). Forests that have experienced some fire may be more resilient to species-level changes in phenology if the overall community can compensate for divergent shifts due to climate.

The interaction of burn severity and phenology in different habitats was also supported by the results of plot-level analysis: as the season progressed, floral abundance and richness generally declined in green upland and both meadow habitats. This suggests that green and high-severity meadows are similar in the rate of decline in flowers but green and burned habitat are not, and again highlights the importance of fire in upland habitat to provide floral resources throughout the growing season.

In upland habitats, we expected  $\alpha$  diversity of flowers to be highest in moderate-severity burns. Although we did not observe a clear pattern at the class-scale, at the plot-scale we did find that the positive effect on floral richness and abundance was higher in moderate-severity than high-severity fire and that floral richness was sustained across the season in moderate-severity burns. Other studies have found that diversity in understory species peaks at moderate severity, and attribute this to historic filtering effects (Miller and Safford 2020), colonization-competition tradeoffs (Stevens et al. 2015), or homogenizing effects of high-severity fire (Richter et al. 2019). Because we observed this pattern at the plot-scale but not the class-scale, there may be other local factors such as productivity (Brodie et al. 2021) or landscape factors, such as patch-size or distance to edge (Watson et al. 2012, Shive et al. 2018) influencing how diversity responds to fire.

Rather than increasing diversity in meadows by disrupting dominance, we found no effect of fire on  $\alpha$  at the class- or plot- level, or on abundance at the plot-level. Further, diversity profiles showed similar evenness (largely parallel profiles; Fig. 2) in burned and unburned meadow communities, with a tendency of green meadows to be more even. For example, in early and late 2016, burned and unburned meadows had similar richness, but unburned meadows had significantly higher Shannon and Simpson diversity indices (Fig. 2). High-severity meadows may be dominated disturbance-tolerant species, thus decreasing community evenness (Cadotte 2007, Biswas and Mallik 2011) which may explain the patterns observed in 2016. However, absolute differences in  $\alpha$  diversity between unburned and burned meadows were small. Because meadows are typically dominated by herbaceous cover and have higher moisture levels than upland habitat, fire may not have such profound effects in meadows as in upland, or these effects may be limited to the first year after fire. The effect of high-severity fire in meadow may be most dramatic when considering the changes to community composition, the transition from perennial to annual species, and the shifts to earlier flowering, rather than changes to  $\alpha$  or  $\beta$  diversity.

We expected  $\beta$  to be positively affected by fire relative to fire-suppressed green meadows and uplands. However, there were no significant differences in class-level  $\beta$ , indicating that all burn-habitat classes had similar amounts of heterogeneity in plant communities across the flowering season. All habitats in our study were fire-suppressed before the King fire occurred, which may have limited the amount of variability in source populations and regional diversity. Furthermore, when a community has fewer species, each subcommunity is likely to have a unique assemblage of species, resulting in high  $\beta$ , as in green upland plots, and observed in other systems (Legendre and De Cáceres 2013, Landeiro et al. 2018, Dubois et al. 2020). The reverse is also true: if a community is speciose, and is highly representative of the other communities

within its class, the  $\beta$  will be low, as in moderate-severity upland plots in 2017. Because moderate-severity fire increases species richness at the plot-level but not necessarily at the class-level, the  $\beta$  decreases as the plots become more similar. In both cases it is important to recall that this is a measure of heterogeneity within each class and visit and this does not indicate that community composition among classes or visits was similar.

Indeed, we found that compositional dissimilarity was high, particularly between classes at the same time period. We found that green and burned meadows differed significantly in composition on the first and second visits, with higher diversity of flowers early in the season. Similarly, we noted that floral diversity was higher in burned upland habitat later in the season, and we found significant differences in community composition among green and burned habitats on visit 2 but not visit 3. This suggests that fire affected phenology by altering community composition, rather than changing the timing of species- or individual-level flowering. Species in burned habitat may have endogenous cues that trigger flowering earlier, or be more sensitive to fire-induced changes to flowering cues (Rathcke and Lacey 1985, Wroblewski and Kauffman 2003).

Phenology tends to be a highly plastic trait in plants, allowing them to adjust to changes in light, water, and nutrients in order to time breeding to pulses in resources (Rathcke and Lacey 1985, Badeck et al. 2004, Forrest and Miller-Rushing 2010). Community phenology in burned habitat may differ from green habitat due to individual- or species-level shifts in phenology, or due to compositional dissimilarity. In meadows, we found that burned habitat had higher diversity of plants in bloom earlier in the season, whereas in uplands, burned habitat tended to have more species in bloom later in the season than green habitat. Both patterns are likely due to compositional dissimilarity among classes and other local or landscape processes (Pakeman and

Small 2005, Watson et al. 2012, Shive et al. 2018, Brodie et al. 2021). Fire-induced shifts to earlier flowering in meadows may be problematic if it causes a mismatch among plants and the resources they are tracking. Plants that bloom too early may be subject to late-season frost, or out of sync with resources, pollinators or seed dispersers (Kudo and Cooper 2019, Albert-Daviaud et al. 2020). Similarly, in burned upland habitats where the season extends later into summer, individual plants may reduce the number of flowers to compensate for the longer season, thereby missing out on outcrossing or peak resources for reproduction (Rathcke and Lacey 1985, Scheepens and Stöcklin 2013, Ehrlén et al. 2015). However, if plants in burned uplands are producing more flowers because the fire has created more resources, allowing plants to increase reproductive output when pollinators and dispersers are available, it may indeed be adaptive. Studies investigating the fitness of plants that vary in phenology due to fire are needed to assess if changes to the fire regime are negatively impacting plant reproduction, but our study does show that burned areas provide diverse and abundant floral resources across the blooming period for pollinators and tend to be complementary to unburned habitats in their phenology and composition.

Understanding how systems adapted to a moderate-severity, high-frequency fire regime respond to high-severity fire is critical (McKelvey et al. 1996, Stephens et al. 2018, Miller and Safford 2020), given that such fires are predicted to increase with climate change (Flannigan et al. 2000, Westerling et al. 2006, Cassell et al. 2019). Fire suppression reduces the total area that burns annually in the Sierra Nevada (North et al. 2012) and interacts with climate change to increase the high-severity patch-size relative to historic fires (McKelvey et al. 1996, Mallek et al. 2013, Safford and Stevens 2017). We found that fire in upland habitat increased floral diversity, abundance and flowering season and this response was stronger in moderate-severity upland



habitat. A lack of moderate-severity fire may result in fewer floral resources available later in the season, which is likely to impact pollinators. However, although the relationship with high-severity fire and late season resources was weaker, our study indicates that even high-severity fire provides important opportunities for understory species in fire-suppressed forest.

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## Appendices

### Appendix A.

PERMANOVA is analogous to univariate ANOVA, and as such, assumes that variances within groups are homogeneous. We tested this assumption by comparing the multivariate dispersion of each burn-habitat class with the betadisper function in vegan (Oksanen et al. 2020). None of the post-hoc comparisons (p-values adjusted with false discovery rate) were significant, indicating that variances among groups did not differ significantly. The adonis function in vegan finds the sum of squares distance from each plot to its respective burn-habitat spatial median and by repeating over many permutations, tests for significance with pseudo F-ratios. We used the false discovery rate method (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001) to adjust p-values for multiple comparisons in the pairwise.perm.manova function from the RVAideMemoire package (version 0.9-80, Hervé 2021).

**Table A1.** Class-level floral  $\beta$  diversity comparisons by burn-habitat class and visit in the Sierra Nevada, California after the 2014 King Fire. Bold values are significant at  $\alpha=0.05$ . SS= Sum of squares, DF= degrees of freedom, N Perm= number permutations.

<b>2016</b>						
	DF	SS	Mean SS	F	N Perm	p-value
Burn-habitat visit	11	0.092	0.008	1.06	999	0.419
Residuals	123	0.968	0.008			
<b>2017</b>						
	DF	SS	Mean SS	F	N Perm	p-value
Burn-habitat visit	11	0.180	0.016	1.963	999	<b>0.037</b>
Residuals	149	1.240	0.008			
*no pairwise comparisons were significant at $\alpha=0.05$ when corrected for multiple comparisons with the false discovery rate.						

**Table A2.** Pairwise comparisons of permutation test for floral class-level  $\beta$ , corrected with false discovery rate for data collected in 2017 only, in the Sierra Nevada, California after the 2014 King Fire.

<b>Within-class comparison of visits</b>	p-value
GreenUplandV1-GreenUplandV2	0.073
ModerateUplandV1-ModerateUplandV2	0.073
HighUplandV1-HighUplandV2	0.073
GreenMeadowV1-GreenMeadowV2	0.994
GreenMeadowV1-GreenMeadowV3	0.994
GreenMeadowV2-GreenMeadowV3	0.994
HighMeadowV1-HighMeadowV2	0.994
HighMeadowV1-HighMeadowV3	0.994
HighMeadowV2-HighMeadowV3	0.994
<b>Within visit comparison of classes</b>	p-value
GreenUplandV1-HighMeadowV1	0.097
GreenUplandV1-ModerateUplandV1	0.994
GreenUplandV1-HighUplandV1	0.994
GreenUplandV1-GreenMeadowV1	0.097
GreenMeadowV1-HighMeadowV1	0.994
ModerateUplandV1-HighUplandV1	0.994
ModerateUplandV1-GreenMeadowV1	0.073
ModerateUplandV1-HighMeadowV1	0.073
HighUplandV1-GreenMeadowV1	0.073
HighUplandV1-HighMeadowV1	0.073
GreenUplandV2-ModerateUplandV2	0.994
GreenUplandV2-HighUplandV2	0.994
GreenUplandV2-GreenMeadowV2	0.994
GreenUplandV2-HighMeadowV2	0.987
ModerateUplandV2-HighUplandV2	0.994
ModerateUplandV2-GreenMeadowV2	0.994
ModerateUplandV2-HighMeadowV2	0.994
HighUplandV2-GreenMeadowV2	0.994
HighUplandV2-HighMeadowV2	0.994
GreenMeadowV2-HighMeadowV2	0.994
GreenMeadowV3-HighMeadowV3	0.994

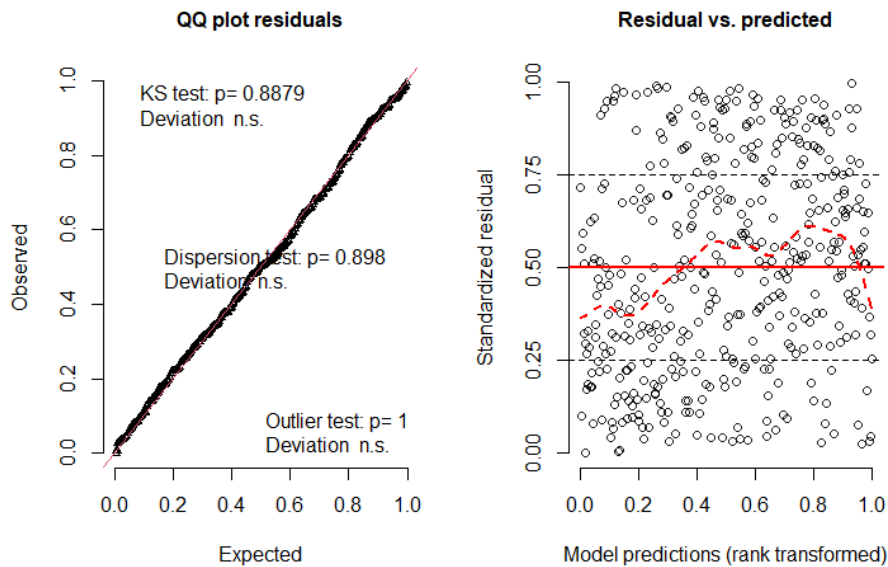
**Table A3.** Correlation among covariates for floral abundance and species richness models in the Sierra Nevada, California, two and three years after the 2014 King Fire.

	Elevation	Burn severity	Days since snowmelt
Elevation (m)	1	-0.023	-0.244
Burn severity	-0.023	1	0.166
Days since snowmelt	-0.244	0.166	1

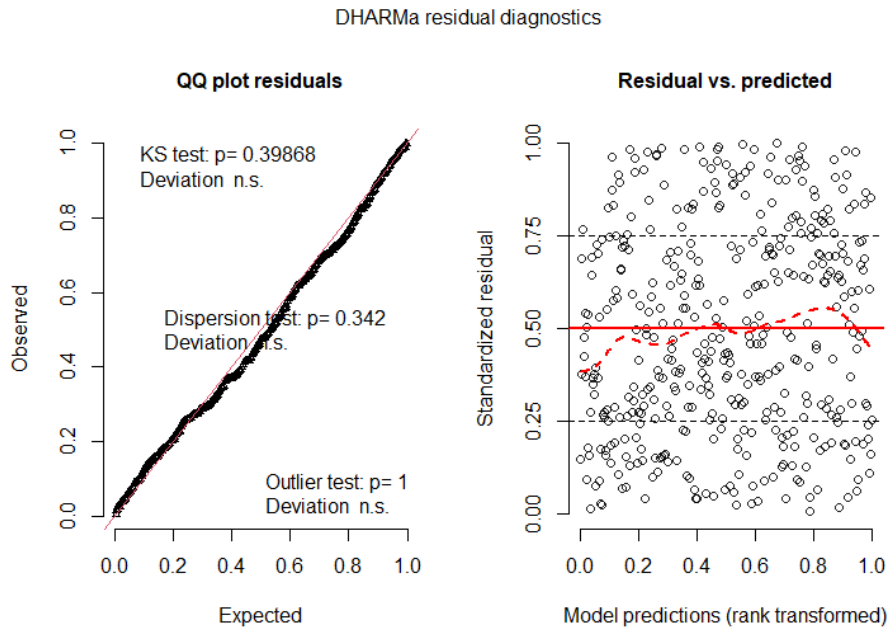
**Table A4.** Correlation among covariates for floral  $\beta$  diversity models in the Sierra Nevada, California, two and three years after the 2014 King Fire.

	Elevation	Burn severity	Days since snowmelt
Elevation (m)	1	-0.333	-0.116
Burn severity	-0.333	1	0.156
Days since snowmelt	-0.116	0.156	1

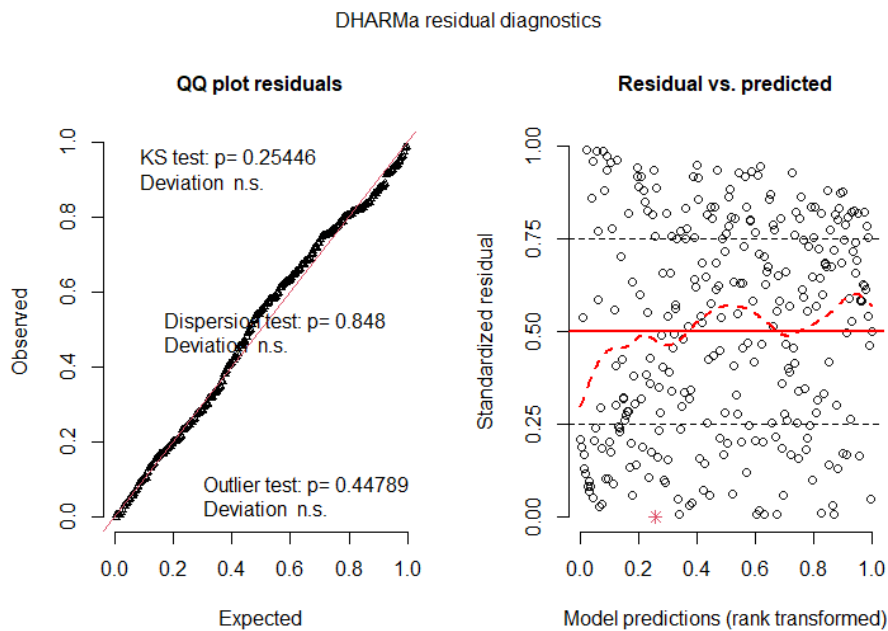
DHARMA residual diagnostics



**Figure A1.** Residual plot for generalized linear mixed model (negative binomial) for floral abundance in the Sierra Nevada, California, two and three years after the 2014 King Fire.



**Figure A2.** Residual plot for generalized linear mixed model (negative binomial) for floral species richness in the Sierra Nevada, California, two and three years after the 2014 King Fire.



**Figure A3.** Residual plot for generalized linear mixed model (beta distribution) for class-level floral  $\beta$  diversity in the Sierra Nevada, California, two and three years after the 2014 King Fire.

**Appendix B**

**Table B1.** Full results from generalized linear mixed model (negative binomial) for floral abundance in the Sierra Nevada, California, two and three years after the 2014 King Fire. Model contained site as random effect. Green meadow is the reference category. DSS = days since snowmelt, SD= standard deviation, SE= standard error.

Response: Floral abundance	Estimate	SE	z-value	p-value	Random effects covariance matrix	
Intercept	3.599	0.924	3.895	0.000	SD intercept	1.479
High Meadow	1.868	1.293	1.444	0.149		
Green Upland	-2.248	1.047	-2.146	0.032		
Moderate Upland	0.473	1.063	0.445	0.656	log(dispersions) parameter	
High Upland	-0.513	1.040	-0.494	0.622	Estimate	-0.822
DSS	-1.087	0.224	-4.861	0.000	SE	0.080
Elevation	0.881	0.285	3.091	0.002		
Year 2017	-0.630	0.266	-2.368	0.018		
High Meadow:DSS	0.298	0.312	0.954	0.340		
Green Upland:DSS	-0.023	0.332	-0.070	0.944		
Moderate Upland:DSS	1.216	0.371	3.276	0.001		
High Upland:DSS	0.701	0.304	2.304	0.021		

**Table B2.** Full results from generalized linear mixed models (negative binomial distribution) for floral richness in the Sierra Nevada, California, two and three years after the 2014 King Fire. Model contained site as random effect. Green meadow is the reference category. DSS = days since snowmelt, SD= standard deviation, SE= standard error.

	Estimate	SE	z-value	p-value	Random effects covariance matrix	
Intercept	1.245	0.435	2.863	0.004	SD intercept	0.706
Green Upland	-1.705	0.513	-3.322	0.001		
High Meadow	0.825	0.612	1.348	0.178		
High Upland	-0.875	0.499	-1.753	0.080	log(dispersions) parameter	
Moderate Upland	-0.798	0.511	-1.561	0.119	Estimate	2.215
DSS	-0.513	0.078	-6.602	0.000	SE	0.340
Elevation	0.388	0.143	2.716	0.007		
Year 2017	-0.320	0.104	-3.075	0.002		
Green Upland:DSS	-0.143	0.170	-0.841	0.400		
High Meadow:DSS	0.053	0.108	0.490	0.624		
High Upland:DSS	0.239	0.135	1.774	0.076		
Moderate Upland:DSS	0.382	0.153	2.501	0.012		

**Table B3.** Full results from generalized linear mixed models (beta distribution) for floral plot-level  $\beta$  diversity in the Sierra Nevada, California two and three years after the 2014 King Fire. Models contained site as random effect. Green meadow is the reference category. DSS = days since snowmelt, SD= standard deviation, SE= standard error.

	Estimate	SE	z-value	p-value	Random effects covariance matrix	
Intercept	0.636	0.106	5.985	<0.001	SD intercept	0.155
Green Upland	-0.020	0.136	-0.149	0.881		
High Meadow	-0.155	0.150	-1.028	0.304		
High Upland	-0.074	0.127	-0.580	0.562	phi parameter	
Moderate Upland	-0.358	0.138	-2.600	0.009	Estimate	3.606
DSS	0.047	0.045	1.056	0.291	SE	0.087
Elevation	-0.039	0.041	-0.954	0.340		
Year 2017	0.054	0.054	1.007	0.314		
Green Upland:DSS	-0.098	0.080	-1.222	0.222		
High Meadow:DSS	-0.021	0.065	-0.330	0.741		
High Upland:DSS	-0.198	0.066	-2.987	0.003		
Moderate Upland:DSS	-0.390	0.082	-4.767	<0.001		

Appendix C.

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Green Meadow	<i>Angelia breweri</i>	Brewer's angelica	90	0
Green Meadow	<i>Asteraceae</i>	Sunflower family	69	0
Green Meadow	<i>Bistorta bistortoides</i>	American bistort	27	6
Green Meadow	<i>Camassia quamash</i>	Common camas	1	2
Green Meadow	<i>Castilleja miniata</i>	Great red paintbrush	2	0
Green Meadow	<i>Castilleja tenuis</i>	Hairy owl's clover	8	13
Green Meadow	<i>Cirsium vulgare</i>	Bull thistle	2	0
Green Meadow	<i>Claytonia perfoliata</i>	Miner's lettuce	4	0
Green Meadow	<i>Drymacallis glandulosa</i>	Old cinque foil	5	1
Green Meadow	<i>Epilobium ciliatum</i>	Fringed willowherb	60	138
Green Meadow	<i>Epilobium species</i>	Willowherb species	85	20
Green Meadow	<i>Erigeron algidus</i>	Stalked fleabane	2	0
Green Meadow	<i>Erigeron canadensis</i>	Canada horseweed	1	0
Green Meadow	<i>Eriogonum nudem</i>	Naked buckwheat	2	0
Green Meadow	<i>Eurybia integrifolia</i>	Thickstem aster	11	12
Green Meadow	<i>Galium aparine</i>	Stickywilly bedstraw	22	0
Green Meadow	<i>Galium porrigens</i>	Climbing bedstraw	116	0
Green Meadow	<i>Gayophytum species</i>	Groundsmoke	16	59
Green Meadow	<i>Helenium bigelovii</i>	Sneezeweed	164	72
Green Meadow	<i>Heracleum maximum</i>	Cowparsnip	3	0
Green Meadow	<i>Hieracium albiflorum</i>	White hawkweed	12	0
Green Meadow	<i>Horkelia fusca</i>	Dusky horkelia	522	242
Green Meadow	<i>Hosackia oblongifolia</i>	Narrow-leaved lotus	26	0
Green Meadow	<i>Hypericum scouleri</i>	Scouler's St. John's wort	4	0
Green Meadow	<i>Kelloggia galioides</i>	Milk kelloggia	8	0
Green Meadow	<i>Ligusticum grayi</i>	Gray's lovage	66	0
Green Meadow	<i>Lilium parvum</i>	Alpine lily	4	0
Green Meadow	<i>Lupinus obtusilobus</i>	Bluntlobe lupine	8	0
Green Meadow	<i>Lupinus species</i>	Lupine species	1	0
Green Meadow	<i>Madia gracilis</i>	Gumweed madia	10	0
Green Meadow	<i>Mentha arvensis</i>	American wild mint	2	2
Green Meadow	<i>Mimulus guttatus</i>	Seep monkeyflower	143	1
Green Meadow	<i>Mimulus primuloides</i>	Primrose monkeyflower	36	27
Green Meadow	<i>Oreostemma alpigenum var. andersonii</i>	Tundra aster	431	40
Green Meadow	<i>Penstemon rydbergii</i>	Rydberg's penstemon	1	17
Green Meadow	<i>Perideridia bolanderi</i>	Bolander's yampah	173	0
Green Meadow	<i>Perideridia parishii</i>	Parish's yampah	895	0

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Green Meadow	<i>Phacelia egea</i>	Rock phacelia	2	0
Green Meadow	<i>Phalacroseris bolanderi</i>	Bolander's mock dandelion	15	4
Green Meadow	<i>Platanthera dilatata</i> var. <i>leucostachys</i>	Sierra bog orchid	39	0
Green Meadow	<i>Potentilla species</i>	Cinquefoil species	33	0
Green Meadow	<i>Prunella vulgaris</i>	Selfheal	22	5
Green Meadow	<i>Pseudostellaria jamesiana</i>	Sticky starwort	7	0
Green Meadow	<i>Ranunculus alismifolius</i>	Alisma leaved buttercup	4	0
Green Meadow	<i>Ranunculus occidentalis</i>	Western buttercup	16	29
Green Meadow	<i>Senecio triangularis</i>	Arrow head butterweed	51	37
Green Meadow	<i>Sidalcea glaucescens</i>	Waxy checkerbloom	15	35
Green Meadow	<i>Sidalcea malviflora</i>	Checkerbloom	20	0
Green Meadow	<i>Sidalcea oregana</i>	Oregon checkerbloom	1	0
Green Meadow	<i>Sisyrinchium elmeri</i>	Elmer's goldeneyed grass	34	2
Green Meadow	<i>Solidago canadensis</i>	Canada goldenrod	9	0
Green Meadow	<i>Spiranthes porrifolia</i>	Creamy lady tresses	1	1
Green Meadow	<i>Stachys ajugoides</i>	Hedge nettle	2	1
Green Meadow	<i>Stachys albens</i>	Cobwebby hedge nettle	11	0
Green Meadow	<i>Stellaria longipes</i>	Longstalk starwort	54	93
Green Meadow	<i>Symphotrichum ascendens</i>	Western aster	23	0
Green Meadow	<i>Symphotrichum spathulatum</i> var. <i>spathulatum</i>	Western mountain aster	85	293
Green Meadow	<i>Trifolium longipes</i>	Long-stalked clover	26	49
Green Meadow	<i>Triteleia hyacinthina</i>	Wild hyacinth	3	0
Green Meadow	<i>Veronica scutellata</i>	Skullcap speedwell	3	65
Green Meadow	<i>Achillea millefolium</i>	Yarrow	0	11
Green Meadow	<i>Allium validum</i>	Pacific mountain onion	0	1
Green Meadow	<i>Arnica chamissonis</i>	Chamisso arnica	0	7
Green Meadow	<i>Arnica mollis</i>	Hairy arnica	0	6
Green Meadow	<i>Calochortus minimus</i>	Sierra mariposa lily	0	2
Green Meadow	<i>Circaea alpina</i>	Enchanter's nightshade	0	5
Green Meadow	<i>Delphinium nuttallianum</i>	Meadow larkspur	0	11
Green Meadow	<i>Erigeron glacialis</i>	Wandering fleabane	0	6
Green Meadow	<i>Hypericum anagalloides</i>	Tinker's penny	0	4
Green Meadow	<i>Mimulus breweri</i>	Brewer's monkeyflower	0	6
Green Meadow	<i>Mimulus moschatus</i>	Musk monkeyflower	0	6
Green Meadow	<i>Oxypolis occidentalis</i>	Western cowbane	0	23
Green Meadow	<i>Perideridia species</i>	Yampah species	0	405
Green Meadow	<i>Potentilla gracilis</i>	Slender cinquefoil	0	5



**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Green Meadow	<i>Primula jeffreyi</i>	Sierra shooting star	0	4
Green Meadow	<i>Solidago elongata</i>	Cascade Canada goldenrod	0	27
Green Meadow	<i>Symphyotrichum foliaceum</i>	Alpine leafybract aster	0	1
Green Meadow	<i>Veratrum californicum</i>	California false hellebore	0	7
Green Upland	<i>Acmispon americanus</i>	Spanish lotus	427	3
Green Upland	<i>Asteraceae</i>	Sunflower family	41	6
Green Upland	<i>Cryptantha species</i>	Cryptantha species	1	30
Green Upland	<i>Drymacallis glandulosa</i>	Old cinque foil	3	0
Green Upland	<i>Epilobium brachycarpum</i>	Panicled willow herb	1	0
Green Upland	<i>Epilobium ciliatum</i>	Fringed willowherb	35	0
Green Upland	<i>Eriogonum nudem</i>	Eriogonum species	5	0
Green Upland	<i>Eriogonum nudem</i>	Naked buckwheat	206	7
Green Upland	<i>Galium species</i>	Galium species	6	0
Green Upland	<i>Gayophytum species</i>	Groundsmoke	187	84
Green Upland	<i>Gnaphalium species</i>	Gnaphalium species	5	0
Green Upland	<i>Helenium bigelovii</i>	Sneezeweed	1	0
Green Upland	<i>Hieracium albiflorum</i>	White hawkweed	14	8
Green Upland	<i>Hosackia oblongifolia</i>	Narrow-leaved lotus	4	0
Green Upland	<i>Kelloggia galioides</i>	Milk kelloggia	3	8
Green Upland	<i>Leptosiphon ciliatus</i>	Whiskerbrush	1	9
Green Upland	<i>Lilium parvum</i>	Alpine lily	2	0
Green Upland	<i>Lupinus breweri</i>	Brewer's lupine	4	0
Green Upland	<i>Lupinus species</i>	Lupine species	26	0
Green Upland	<i>Madia species</i>	Madia species	3	0
Green Upland	<i>Mimulus moschatus</i>	Musk monkeyflower	2	3
Green Upland	<i>Penstemon laetus</i>	Gay penstemon	3	0
Green Upland	<i>Perideridia parishii</i>	Parish's yampah	15	0
Green Upland	<i>Polemoniaceae</i>	Polemoniaceae species	12	0
Green Upland	<i>Prunella vulgaris</i>	Selfheal	2	0
Green Upland	<i>Senecio triangularis</i>	Arrow head butterweed	2	0
Green Upland	<i>Sidalcea glaucescens</i>	Waxy checkerbloom	10	26
Green Upland	<i>Viola purpurea</i>	Mountain violet	3	0
Green Upland	<i>Acmispon species</i>	Acmispon species	0	21
Green Upland	<i>Asyneuma prenanthoides</i>	California harebell	0	9
Green Upland	<i>Calyptridium monospermum</i>	One seeded pussypaws	0	13
Green Upland	<i>Castilleja miniata</i>	Great red paintbrush	0	11
Green Upland	<i>Ceanothus cordulatus</i>	Mountain whitethorn	0	17
Green Upland	<i>Chamaebatia foliolosa</i>	Mountain misery	0	1
Green Upland	<i>Collomia heterophylla</i>	Variableleaf collomia	0	1

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Green Upland	<i>Delphinium species</i>	Larkspur	0	3
Green Upland	<i>Epilobium species</i>	Willowherb species	0	2
Green Upland	<i>Eriophyllum lanatum</i>	Woolly sunflower	0	20
Green Upland	<i>Eucephalus breweri</i>	Brewer's aster	0	93
Green Upland	<i>Ligusticum grayi</i>	Gray's lovage	0	1
Green Upland	<i>Mimulus torreyi</i>	Torrey's monkeyflower	0	1
Green Upland	<i>Monardella odoratissima</i>	Desert mint	0	51
Green Upland	<i>Navarretia leptalea ssp. Leptalea</i>	Bridge's gilia	0	121
Green Upland	<i>Penstemon species</i>	Penstemon species	0	11
Green Upland	<i>Perideridia species</i>	Yampah species	0	3
Green Upland	<i>Phacelia hastata</i>	Silverleaf phacelia	0	5
Green Upland	<i>Phacelia species</i>	Phacelia species	0	1
Green Upland	<i>Ranunculus occidentalis</i>	Western buttercup	0	14
Green Upland	<i>Silene lemmonii</i>	Lemmon's catchfly	0	5
Green Upland	<i>Symphotrichum spathulatum var. spathulatum</i>	Western mountain aster	0	8
High Meadow	<i>Achillea millefolium</i>	Yarrow	6	35
High Meadow	<i>Acmispon americanus</i>	Spanish lotus	842	127
High Meadow	<i>Antenarria species</i>	Antenarria species	331	0
High Meadow	<i>Arabis species</i>	Arabis species	18	0
High Meadow	<i>Artemisia douglasiana</i>	California mugwort	2	0
High Meadow	<i>Asteraceae</i>	Sunflower family	6	0
High Meadow	<i>Asyneuma prenanthoides</i>	California harebell	11	8
High Meadow	<i>Calyptridium monospermum</i>	One seeded pussypaws	108	0
High Meadow	<i>Chamerion angustifolium</i>	Fireweed	1	0
High Meadow	<i>Cirsium vulgare</i>	Bull thistle	15	3
High Meadow	<i>Claytonia species</i>	Claytonia species	5	0
High Meadow	<i>Cornus sericea</i>	Creek dogwood	2	0
High Meadow	<i>Cryptantha species</i>	Cryptantha species	10	258
High Meadow	<i>Epilobium ciliatum</i>	Fringed willowherb	69	235
High Meadow	<i>Epilobium species</i>	Willowherb species	34	539
High Meadow	<i>Galium aparine</i>	Stickywilly bedstraw	20	11
High Meadow	<i>Gayophytum species</i>	Groundsmoke	604	372
High Meadow	<i>Geranium richardsonii</i>	Richardson's geranium	1	3
High Meadow	<i>Helenium bigelovii</i>	Sneezeweed	4	1
High Meadow	<i>Heterocodon rariflorum</i>	Rareflower heterocodon	22	5
High Meadow	<i>Hosackia oblongifolia</i>	Narrow-leaved lotus	83	49
High Meadow	<i>Hypericum perforatum</i>	Common St. John's wort	137	0
High Meadow	<i>Lathyrus sulphureus</i>	Sulphur pea	5	0

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
High Meadow	<i>Lupinus polyphyllus</i>	Bog lupine	1	1
High Meadow	<i>Lupinus polyphyllus</i>	Lupine species	11	0
High Meadow	<i>Madia elegans</i>	Common madia	2	0
High Meadow	<i>Madia gracilis</i>	Gumweed madia	1	0
High Meadow	<i>Madia species</i>	Madia species	10	48
High Meadow	<i>Mimulus breweri</i>	Brewer's monkeyflower	7	59
High Meadow	<i>Mimulus guttatus</i>	Seep monkeyflower	97	167
High Meadow	<i>Mimulus layneae</i>	Layne's monkeyflower	12	4
High Meadow	<i>Mimulus moschatus</i>	Musk monkeyflower	223	241
High Meadow	<i>Mimulus species</i>	Monkeyflower species	4	0
High Meadow	<i>Mimulus torreyi</i>	Torrey's monkeyflower	39	12
High Meadow	<i>Myosotis laxa</i>	Bay forget-me-not	605	122
High Meadow	<i>Navarretia intertexta</i>	Interwoven navarretia	14	0
High Meadow	<i>Navarretia leptalea ssp. Leptalea</i>	Bridge's gilia	106	5
High Meadow	<i>Perideridia parishii</i>	Parish's yampah	106	0
High Meadow	<i>Phacelia egena</i>	Rock phacelia	23	0
High Meadow	<i>Prunella vulgaris</i>	Selfheal	16	17
High Meadow	<i>Ranunculus occidentalis</i>	Western buttercup	10	58
High Meadow	<i>Rudbeckia occidentalis</i>	Western coneflower	22	27
High Meadow	<i>Senecio triangularis</i>	Arrow head butterweed	1	40
High Meadow	<i>Sericocarpus oregonensis</i>	Oregon whitetop aster	1	6
High Meadow	<i>Sidalcea glaucescens</i>	Waxy checkerbloom	8	0
High Meadow	<i>Solidago canadensis</i>	Canada goldenrod	44	8
High Meadow	<i>Stachys ajugoides</i>	Hedge nettle	4	23
High Meadow	<i>Stachys albens</i>	Cobwebby hedge nettle	2	0
High Meadow	<i>Stellaria longipes</i>	Longstalk starwort	7	14
High Meadow	<i>Symphotrichum ascendens</i>	Western aster	2	0
High Meadow	<i>Symphotrichum spathulatum var. spathulatum</i>	Western mountain aster	16	58
High Meadow	<i>Trifolium pratense</i>	Red clover	19	12
High Meadow	<i>Triteleia hyacinthina</i>	Wild hyacinth	1	0
High Meadow	<i>Veronica americana</i>	American speedwell	16	0
High Meadow	<i>Viola lobata</i>	Pine violet	11	16
High Meadow	<i>Viola sheltonii</i>	Shelton's violet	5	0
High Meadow	<i>Allophyllum integrifolium</i>	White allophyllum	0	2
High Meadow	<i>Anaphalis margaritacea</i>	Pearly everlasting	0	150
High Meadow	<i>Bistorta bistortoides</i>	American bistort	0	4
High Meadow	<i>Camassia quamash</i>	Common camas	0	3
High Meadow	<i>Claytonia perfoliata</i>	Miner's lettuce	0	15
High Meadow	<i>Collinsia parviflora</i>	Blue eyed mary	0	3
High Meadow	<i>Dianthus armeria</i>	Deptford pink	0	3

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
High Meadow	<i>Epilobium densiflorum</i>	Denseflower willowherb	0	41
High Meadow	<i>Erigeron canadensis</i>	Canada horseweed	0	3
High Meadow	<i>Erigeron glacialis</i>	Wandering fleabane	0	1
High Meadow	<i>Fabaceae spp</i>	Fabaceae species	0	192
High Meadow	<i>Hemizonella minima</i>	Opposite leaved tarweed	0	11
High Meadow	<i>Hieracium albiflorum</i>	White hawkweed	0	1
High Meadow	<i>Hypericum anagalloides</i>	Tinker's penny	0	118
High Meadow	<i>Kelloggia galioides</i>	Milk kelloggia	0	26
High Meadow	<i>Leptosiphon ciliatus</i>	Whiskerbrush	0	4
High Meadow	<i>Lupinus latifolius var. columbianus</i>	Columbia lupine	0	8
High Meadow	<i>Madia glomerata</i>	Mountain tarweed	0	13
High Meadow	<i>Perideridia species</i>	Yampah species	0	84
High Meadow	<i>Phacelia species</i>	Phacelia species	0	4
High Meadow	<i>Potentilla gracilis</i>	Slender cinquefoil	0	58
High Meadow	<i>Pseudognaphalium beneolens</i>	Cudweed	0	37
High Meadow	<i>Pseudognaphalium canescens</i>	Wright's cudweed	0	52
High Meadow	<i>Rudbeckia hirta</i>	Blackeyed susan	0	4
High Meadow	<i>Rumex acetosella</i>	Common sheep sorrel	0	29
High Meadow	<i>Senecio vulgaris</i>	Common groundsel	0	3
High Meadow	<i>Sidalcea malviflora</i>	Checkerbloom	0	1
High Meadow	<i>Sisyrinchium idahoense</i>	Idaho blue-eyed grass	0	5
High Meadow	<i>Solidago elongata</i>	Cascade Canada goldenrod	0	32
High Meadow	<i>Veratrum californicum</i>	California false hellebore	0	9
High Meadow	<i>Veronica scutellata</i>	Skullcap speedwell	0	2
High Upland	<i>Acmispon americanus</i>	Spanish lotus	38	920
High Upland	<i>Antenarria species</i>	Antenarria species	135	0
High Upland	<i>Asteraceae</i>	Sunflower family	32	18
High Upland	<i>Clarkia rhomboideae</i>	Diamond clarkia	6	0
High Upland	<i>Cuscuta californica</i>	California dodder	220	45
High Upland	<i>Draperia systyla</i>	Draperia species	13	0
High Upland	<i>Epilobium ciliatum</i>	Fringed willowherb	6	37
High Upland	<i>Epilobium species</i>	Willowherb species	56	300
High Upland	<i>Gayophytum species</i>	Groundsmoke	487	209
High Upland	<i>Heracleum maximum</i>	Cowparsnip	4	0
High Upland	<i>Hosackia oblongifolia</i>	Narrow-leaved lotus	2	72
High Upland	<i>Lathyrus nevadensis</i>	Sierra pea	1	0
High Upland	<i>Lathyrus species</i>	Lathyrus species	1	0
High Upland	<i>Lupinus fulcratus</i>	Greenstipule lupine	10	0

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
High Upland	<i>Madia gracilis</i>	Gumweed madia	30	0
High Upland	<i>Mimulus moschatus</i>	Musk monkeyflower	9	254
High Upland	<i>Mimulus torreyi</i>	Torrey's monkeyflower	68	268
High Upland	<i>Senecio flaccidus</i>	Shrubby ragwort	5	0
High Upland	<i>Sidalcea glaucescens</i>	Waxy checkerbloom	1	28
High Upland	<i>Stephanomeria lactucina</i>	Forest stephanomeria	4	0
High Upland	<i>Verbascum thapsus</i>	Woolly mullein	3	1
High Upland	<i>Apocynum androsaemifolium</i>	Bitter dogbane	0	3
High Upland	<i>Asyneuma prenanthoides</i>	California harebell	0	23
High Upland	<i>Calyptridium umbellatum</i>	Pussypaws	0	3
High Upland	<i>Calystegia occidentalis</i>	Bush morning glory	0	5
High Upland	<i>Chamaebatia foliolosa</i>	Mountain misery	0	12
High Upland	<i>Cirsium vulgare</i>	Bull thistle	0	15
High Upland	<i>Collinsia parviflora</i>	Blue eyed mary	0	17
High Upland	<i>Cryptantha species</i>	Cryptantha species	0	224
High Upland	<i>Epilobium brachycarpum</i>	Panicled willow herb	0	4
High Upland	<i>Erigeron canadensis</i>	Canada horseweed	0	16
High Upland	<i>Eriodictyon lobbii</i>	Matted yerba santa	0	507
High Upland	<i>Fabaceae</i>	Fabaceae species	0	5
High Upland	<i>Hemizonella minima</i>	Opposite leaved tarweed	0	6
High Upland	<i>Mimulus breweri</i>	Brewer's monkeyflower	0	610
High Upland	<i>Mimulus guttatus</i>	Seep monkeyflower	0	3
High Upland	<i>Monardella breweri</i>	Brewer's monardella	0	4
High Upland	<i>Navaretia species</i>	Navaretia species	0	34
High Upland	<i>Navarretia intertexta</i>	Interwoven navarretia	0	50
High Upland	<i>Navarretia leptalea ssp. Leptalea</i>	Bridge's gilia	0	40
High Upland	<i>Phacelia species</i>	Phacelia species	0	1
High Upland	<i>Prunella vulgaris</i>	Selfheal	0	22
High Upland	<i>Pseudognaphalium beneolens</i>	Cudweed	0	35
High Upland	<i>Pseudognaphalium canescens</i>	Wright's cudweed	0	170
High Upland	<i>Senecio triangularis</i>	Arrow head butterweed	0	12
High Upland	<i>Viola lobata</i>	Pine violet	0	12
Moderate Upland	<i>Acmispon americanus</i>	Spanish lotus	0	31
Moderate Upland	<i>Arnica dealbata</i>	Mock leopardbane	0	2
Moderate Upland	<i>Asteraceae</i>	Sunflower family	0	1
Moderate Upland	<i>Asyneuma prenanthoides</i>	California harebell	0	402
Moderate Upland	<i>Castilleja tenuis</i>	Hairy owl's clover	0	1
Moderate Upland	<i>Ceanothus cordulatus</i>	Mountain whitethorn	0	9
Moderate Upland	<i>Chamaesaracha nana</i>	Dwarf chamaesaracha	0	2
Moderate Upland	<i>Cirsium vulgare</i>	Bull thistle	0	116

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Moderate Upland	<i>Clarkia stellata</i>	Clarkia stellata	0	1
Moderate Upland	<i>Claytonia parviflora</i>	Miner's lettuce	0	2
Moderate Upland	<i>Claytonia perfoliata</i>	Miner's lettuce	0	63
Moderate Upland	<i>Collinsia species</i>	Collinsia species	0	11
Moderate Upland	<i>Collomia heterophylla</i>	Variableleaf collomia	0	3
Moderate Upland	<i>Cryptantha species</i>	Cryptantha species	0	74
Moderate Upland	<i>Cuscuta californica</i>	California dodder	0	3240
Moderate Upland	<i>Draperia systyla</i>	Draperia species	0	122
Moderate Upland	<i>Drymacallis glandulosa</i>	Old cinque foil	0	2
Moderate Upland	<i>Epilobium ciliatum</i>	Fringed willowherb	0	85
Moderate Upland	<i>Epilobium species</i>	Willowherb species	0	276
Moderate Upland	<i>Erigeron inornatus</i>	California rayless daisy	0	55
Moderate Upland	<i>Eriodictyon lobbii</i>	Matted yerba santa	0	397
Moderate Upland	<i>Eriophyllum lanatum</i>	Woolly sunflower	0	49
Moderate Upland	<i>Eucephalus breweri</i>	Brewer's aster	0	200
Moderate Upland	<i>Gayophytum species</i>	Groundsmoke	0	803
Moderate Upland	<i>Hackelia velutina</i>	Velvet stickseed	0	2
Moderate Upland	<i>Hieracium albiflorum</i>	White hawkweed	0	57
Moderate Upland	<i>Kelloggia galioides</i>	Milk kelloggia	0	12
Moderate Upland	<i>Lactuca serriola</i>	Prickly lettuce	0	27
Moderate Upland	<i>Lilium parvum</i>	Alpine lily	0	2
Moderate Upland	<i>Madia glomerata</i>	Mountain tarweed	0	9
Moderate Upland	<i>Mimulus breweri</i>	Brewer's monkeyflower	0	124
Moderate Upland	<i>Mimulus moschatus</i>	Musk monkeyflower	0	35
Moderate Upland	<i>Mimulus torreyi</i>	Torrey's monkeyflower	0	9
Moderate Upland	<i>Navarretia leptalea ssp. Leptalea</i>	Bridge's gilia	0	457
Moderate Upland	<i>Perideridia species</i>	Yampah species	0	1
Moderate Upland	<i>Phacelia hastata</i>	Silverleaf phacelia	0	4
Moderate Upland	<i>Phacelia species</i>	Phacelia species	0	10
Moderate Upland	<i>Polemoniaceae complex</i>	Polemoniaceae species	0	12
Moderate Upland	<i>Pseudognaphalium beneolens</i>	Cudweed	0	106
Moderate Upland	<i>Pseudognaphalium canescens</i>	Wright's cudweed	0	140
Moderate Upland	<i>Sambucus racemosa</i>	Red elderberry	0	1
Moderate Upland	<i>Senecio triangularis</i>	Arrow head butterweed	0	6
Moderate Upland	<i>Sidalcea glaucescens</i>	Waxy checkerbloom	0	33
Moderate Upland	<i>Silene laciniata ssp. Californica</i>	Californica indian pink	0	1
Moderate Upland	<i>Stephanomeria lactucina</i>	Forest stephanomeria	0	2
Moderate Upland	<i>Symphotrichum spathulatum var. spathulatum</i>	Western mountain aster	0	4
Moderate Upland	<i>Tragopogon dubius</i>	Yellow salsify	0	1
Moderate Upland	<i>Triteleia ixioides</i>	Golden brodiaea	0	5

**Table C1.** Floral abundance (count of inflorescences with open flowers) observed in green and high-severity meadows and green, moderate-severity, and high-severity upland habitats summed over all visits in the Sierra Nevada of California, two and three years after the 2014 King Fire.

Treatment	ScientificName	CommonName	2016	2017
Moderate Upland	<i>Viola lobata</i>	Pine violet	0	4

## **Chapter 2. Factors influencing pollinator abundance following megafire in uplands and meadows of the Sierra Nevada, California**

### **Abstract**

Many dry forests in the western United States are experiencing wildfires that burn outside the historic range of variation in size and severity. These fires impact the habitat and floral resources available for pollinators and the ecosystem services they provide, but how fire severity modulates these impacts is not well understood. We investigated the impacts of burn severity, habitat, and floral resources on pollinator abundance in post-fire mid-elevation forest and meadow habitat of the Sierra Nevada, California, by modeling counts of pollinators as functions of these variables. We used community models for floral visitors (split into *Bombus* and other insect visitors) and family-level models for butterflies and hummingbirds in a Bayesian framework. Nearly all pollinator taxa responded positively to floral richness, but not necessarily to floral abundance. Although most species-level effects were not significant, we found highly consistent negative effects of burn severity in meadows and variable effects of burn severity in dry, forested habitat. Only hummingbirds and some butterfly families responded positively to burn severity in meadows. For most species, the quadratic effect of burn severity in upland was negative and abundances tended to peak at moderate severity, indicating that even in large fires that burn largely at high severity, moderate-severity patches can improve habitat conditions for pollinator species in upland forest. In contrast, fire in meadows affected most pollinator abundances negatively. Given that much of the Sierra Nevada is predicted to burn at high severity, protecting meadow habitat from intense fire may be necessary to conserve pollinator communities.



## **Introduction**

Fire is the dominant source of disturbance that impacts the distribution and composition of species in ecosystems worldwide (Bond and Keeley 2005, Bond et al. 2005, Pausas and Keeley 2009). However, concerns are mounting that many fire-prone, historically diverse regions are becoming homogenized by the combined effects of climate change, fire suppression, logging, grazing, and urbanization (Bowman et al. 2011, Pausas and Fernández-Muñoz 2012, Seidl et al. 2016, Haggmann et al. 2021), resulting in landscapes with dense and contiguous fuels that experience hotter, drier, and longer fire seasons (Westerling et al. 2006, Pausas and Fernández-Muñoz 2012, Williams 2013). When fires do eventually escape suppression in these landscapes, they tend to occur during extreme weather events, resulting in fires that are larger, more severe and evade containment (Collins 2014, Lydersen et al. 2017). Consequently, several regions around the world experienced their largest and most destructive wildfires in recent years (Penney 2020). These so-called “megafires” burn outside the historic range of variation in size, severity, frequency and/or financial impact (Williams 2013, Stephens et al. 2014a, Singleton et al. 2019). These large and severe wildfires influence landscape patterns with major ecosystem-wide consequences, generating concerns that historically fire-prone systems may undergo state changes and no longer perform the same ecosystem functions (Williams 2013, Stephens et al. 2014b, Seidl et al. 2016).

Pollination is a prime example of an ecosystem function that is likely to be impacted by changes to fire regimes and the effects of megafires (Vanbergen and Initiative 2013, Van Nuland et al. 2013, Rodríguez and Kouki 2015). Direct ecosystem services provided by pollinators are well-recognized, for example, approximately one-third of the global food supply (Klein et al. 2007) and nearly 90% of all angiosperms (Ollerton et al. 2011) benefit from animal

pollination. Pollen-limitation is common among angiosperms and even self-compatible species often benefit from the increase in genetic variation, seed set, and germination rates provided by outcrossing (Ashman et al. 2004, Knight et al. 2005). The tightly interdependent nature of plant-pollinator communities indicates that loss or decline of one trophic level may have cascading and far-reaching impacts on the other (Biesmeijer et al. 2006, Kaiser-Bunbury et al. 2010, Potts et al. 2010). Evidence of global population declines (Biesmeijer et al. 2006, Goulson et al. 2015, Koh et al. 2016) and vulnerability to climate change of some pollinator species (Memmott et al. 2007, McKinney et al. 2012, Kerr et al. 2015) raises concerns that pollination services may be at risk. In fire-prone systems, such as forests with Mediterranean climates, the effects of fire on pollinators are generally positive (Potts et al. 2003; Potts et al. 2010; Galbraith et al. 2019). Fire creates openings in the canopy, which promotes the growth of floral resources that in turn benefit pollinator populations (Potts et al. 2003a, Burkle et al. 2015, Rodríguez and Kouki 2017). The habitat heterogeneity created by fire can also increase the diversity of floral resources and niche space available (Martin and Sapsis 1992, Turner et al. 1994, Bowman et al. 2016). In addition to increasing both the abundance and richness of floral resources, fire can also extend the flowering season (Chapter 1). High floral abundance may support and attract more pollinators and high floral richness may ensure that nectar and pollen resources are available for a variety of species throughout the season (Potts et al. 2003b, Ebeling et al. 2008, Aldridge et al. 2011). Increased floral diversity may also increase chances that pollinators “match” with available flowers temporally, spatially, physically or chemically (Fagan et al. 2014, Klumpers et al. 2019, Kudo and Cooper 2019). Further, nesting habitat for both cavity-nesting species and ground-nesting species is created when fire kills trees and exposes bare ground (Williams et al. 2010, Galbraith et al. 2019a). However, the effects of megafires on

pollinating species are not well-described, and may depend on burn severity, habitat type, and floral resources available after fire.

Whereas moderate-severity fire results in heterogeneous forest structure, high-severity fire tends to produce larger patches of homogeneous forest structure (Lydersen et al. 2013, Coppoletta et al. 2016, Kane et al. 2019). Similarly, the diversity and abundance of understory plants that pollinators rely upon in fire-prone systems tend to peak with moderate-severity fire (Richter et al. 2019). The impacts of severe fire on pollinators in a highly altered system are largely unknown, however, due to their dependence on angiosperms (Biesmeijer et al. 2006, Kaiser-Bunbury et al. 2010, Potts et al. 2010), pollinators may follow a similar pattern, with higher abundance observed in moderate-severity burns. High-severity fire may be especially problematic for pollinators if source populations are killed or dispersal is limited (Cane and Neff 2011; Galbraith et al. 2019; Lazarina et al. 2019) or if vegetative recovery is slow (DeBenedetti and Parsons 1984, Potts et al. 2003a). Previous studies that investigated pollinator abundance with respect to fire are equivocal, with studies reporting generally positive responses for bees (Carbone et al. 2019; Galbraith et al. 2019) and mixed responses for flies (Carbone et al. 2019, Lazarina et al. 2019), butterflies (Huntzinger 2003; Carbone et al. 2019) and hummingbirds (Kotliar et al. 2007, Bagne and Purcell 2011, Latif et al. 2016). Burn severity was not accounted for in these studies which may explain some of the differing results.

The impacts of megafires on pollinator abundance likely also depend on the habitat type. Meadows are relatively permanent habitats for forbs and graminoids and tend to harbor more pollinators than drier forested areas (Loffland et al. 2017). Severe fire in meadows typically occurs following prolonged drought, when moisture levels are low and fuels have accumulated over several years (DeBenedetti and Parsons 1979, Ratliff 1985, Caprio and Lineback 1997).

After severe fire, the organic soil and the seedbank of meadows may be damaged or destroyed, slowing vegetation recovery (DeBenedetti and Parsons 1979, 1984). Upland (i.e., dry forested habitat), on the other hand, is typically dominated by trees, with understory plants providing pollinator habitat in relatively small patches that may be ephemeral in space and time (Taki et al. 2013, Rodríguez and Kouki 2017, Matonis and Binkley 2018). Fire may improve pollinator habitat in forested habitats by increasing nesting and foraging resources or by competitive release of understory plant species; however, this response is likely mediated by burn severity (Kotliar et al. 2007, Ponisio et al. 2016, Lazarina et al. 2019). Habitat type may be more important to some taxa than others. For example, many butterfly (Lepidoptera) species have larval phases that are dependent on particular host plants that tend to be found in meadow habitats (Dennis and Shreeve 1988, Fleishman 2000), whereas some beetle larva (e.g., Coleoptera: Cerambycidae) are associated with dead or decaying wood that is more abundant in upland habitats (Grove 2002, Bouget et al. 2013). Because bee, wasp (Hymenoptera, suborder: Apocrita) and fly (Diptera) species vary greatly in nesting and foraging behavior, the response to different habitat types may also depend on species-specific preferences and adaptations. Migrating hummingbirds (Trochilidae), on the other hand, may prefer meadows that are more predictable in space and time than upland habitat (Russell et al. 1994, Moore and Aborn 2000).

The importance of floral resources to pollinator species is well-documented and fire may impact the availability of these resources (Steffan-Dewenter and Tschardtke 1999, Potts et al. 2003b, Robinson et al. 2018). Bumble bees (*Bombus* species) and other bees (Anthophila) depend on pollen and nectar during all life stages, suggesting that their abundance may be strongly and positively influenced by floral abundance and richness (Häussler et al. 2017). Unlike bees, species in the Lepidoptera, Diptera, and Coleoptera families do not rely upon floral

resources in all life stages, and may not be as strongly influenced by floral resources (Steffan-Dewenter and Tscharrntke 1999, Robinson et al. 2018). Additionally, most insect pollinators are generalists (Waser et al. 1996, Amaya-Márquez 2009) and many rely upon multiple flower species that bloom asynchronously to support them over the course of the season, thus floral richness may be important (Ebeling et al. 2008, Vaca-Urbe et al. 2021).

The Sierra Nevada Mountains of California, USA, are an ideal system to study how pollinators are affected by burn severity, habitat, and floral resources in a highly modified fire regime. Fires in the mid-elevation, mixed coniferous forests of the Sierra Nevada historically burned every 5-25 years at moderate-severity with some high-severity effects (Beaty and Taylor 2008, Collins and Stephens 2010) due to local fuel conditions (Coppoletta et al. 2016), climate (Taylor and Beaty 2005, Westerling et al. 2006), and topography (Beaty and Taylor 2001). Mid-elevation meadows historically experienced severe fire every 200-300 years, typically following prolonged drought, with low-severity fires occurring every 40 years (Ratliff 1985, Caprio and Lineback 1997). Prior to colonization by Euro-Americans in the mid-1800s, both lightning and indigenous peoples started fires. The Nisenan, Washoe, and Maidu peoples managed the forest, woodlands, and meadows with low-severity, frequent fires to stimulate growth of understory plants that were important for food, fiber, medicine, or to attract game (Anderson and Moratto 1996, Lake et al. 2017, Klimaszewski-Patterson et al. 2018). The result of this fire activity was three-fold: first, it created a heterogeneous patchwork of uneven-aged stands that were resilient to large, high-severity fire (Perry et al. 2011, Bowman et al. 2016), second, it regularly removed ground and ladder fuels (Parks et al. 2015, Ritter et al. 2020), and third, it prevented encroachment of meadows by woody species (Lepofsky et al. 2003, Norman and Taylor 2005, Boisramé et al. 2017a). However, with Euro-American colonizers came fire suppression,

logging, and urbanization (Williams 2013, Dennison et al. 2014, Stephens et al. 2014b). Contemporary western forests are densely packed with fuels and competition-, disease- and pest-stressed trees (Donovan and Brown 2007) and meadows are encroached by woody species (DeBenedetti and Parsons 1979, Vale 1981, Norman and Taylor 2005) that reduce water storage capacity (Fletcher et al. 2014, Boisramé et al. 2017b, 2017a) and increase fuel loads (Briggs et al. 2005). The sheer scale of the acreage overdue to burn in the Sierra Nevada combined with the extreme weather conditions created by climate change indicate that western North America is due for many more large-scale, high-severity fires (North et al. 2012, Stephens et al. 2014a, Abatzoglou and Williams 2016). The impacts of these fires on pollinator communities remains largely unknown (but see Simanonok and Burkle 2020).

We investigated how burn severity affected the abundance of pollinators in upland and meadow habitat in and around the King Fire, a first-entry megafire that burned in 2014 in the Sierra Nevada. We predicted that the response of pollinators to fire would differ by both habitat type (meadow versus upland) and burn severity. We expected that fire would increase pollinator abundance in upland habitat due to an increase in foraging/nesting resources, and that moderate-severity upland habitat would have higher pollinator abundance than high-severity upland habitat because pollinators are less likely to be limited by dispersal or the loss of source populations under these conditions. We also predicted that green meadows would support more pollinators than burned meadows due to negative impacts of high-severity fire on seedbanks, soil, and pollinator recolonization. Because pollinators are highly dependent on floral resources, we also predicted that pollinator abundance would be positively influenced by increasing floral abundance and richness.

Our study system is home to a diverse community of diurnal pollinator species including

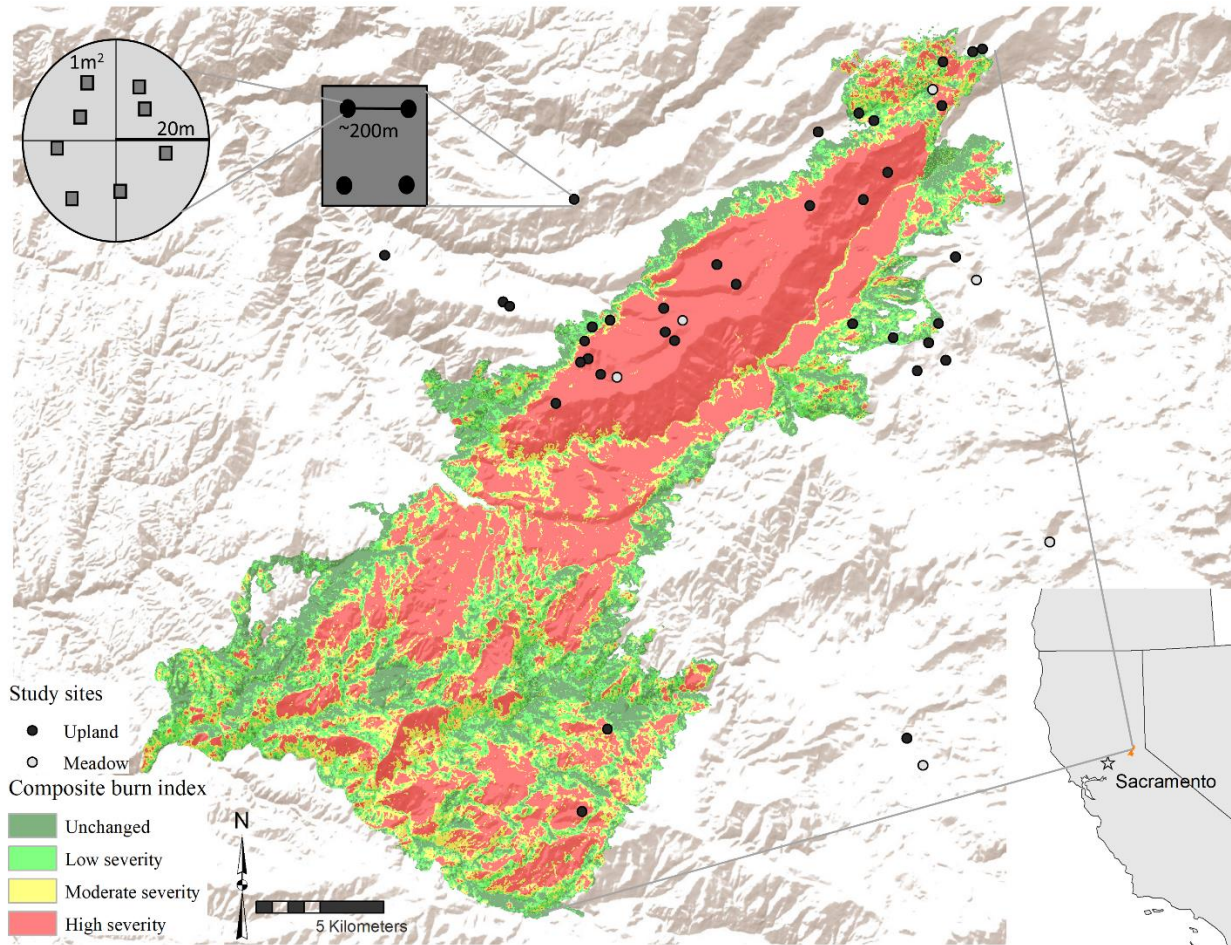
hummingbirds (Trochilidae), butterflies (Lepidoptera), bees and wasps (Hymenoptera: Apocrita), flies (Diptera), and beetles (Coleoptera) that evolved with frequent low- to moderate-severity fire (Bond and Keeley 2005, Brook et al. 2008). We expected these groups to be fairly similar in their response to burn severity and habitat, with differences attributable to life history traits. We expected the bees and hummingbirds to have a positive or hump-shaped relationship with burn severity, since their high mobility makes survival or escape from fire likely, and they are unlikely to face dispersal limitations. We hypothesized that butterflies would be more abundant in meadows than upland habitat because many host plants are dependent on mesic habitat, and response to fire would be positive at moderate levels. We expected hummingbird abundance to be greater in meadow habitat due to their predictability of resources in space and time. We predicted that all pollinator species would be positively associated with floral abundance and richness and that this effect would be strongest in bumble bees because they rely on floral resources throughout their life and are their longevity requires multiple species of asynchronous flowers for successful reproduction.

## **Methods**

### Study Area

Our study area was located in and around the 2014 King Fire in the Eldorado National Forest, California (Fig.1). The study area was restricted to lower montane forest and meadow communities (between ~1300 and 1800m above sea level) to minimize the effects of elevation and related factors. This region's climate is characterized by wet, cool winters with most precipitation falling as snow and dry, warm summers with little precipitation. Pre-fire forest was largely composed of dense stands of relatively young white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menziseii*) and incense cedar (*Calocedrus decurrens*). Pre-fire meadows were dominated by grasses (Poaceae)

and graminoids (Juncaceae, and Cyperaceae), forbs, and small shrubs, with some conifer encroachment (McKelvey et al. 1996, Skinner et al. 1996). Given our focus of upland forest and meadows we avoided areas classified as montane chaparral or riparian.



**Figure 1.** Map of study area showing the region of the Sierra Nevada, California where the King Fire burned in 2014; inset shows location of the King Fire in California. Points on map indicate study sites within each burn-habitat class, with insets showing how plots were organized within sites. Pollinators were surveyed within each 20m-radius circular plot, plants in bloom were surveyed in eight randomly located 1-m<sup>2</sup> quadrats within each plot.

The King Fire was started by an arsonist outside of Pollock Pines, California (38.782° N, 120.604° W) on September 13, 2014. Its size, proportion of high-severity effects, and rate of spread led to its classification as a “megafire” (Stephens et al. 2014b). The Sierra Nevada was experiencing a severe three-year drought at the time of the fire, with low precipitation and record



high temperatures (Young et al. 2017). Fuel levels in the area were high due to effective fire suppression: much of the fire footprint had not burned in nearly 100 years (Department of Forestry and Fire Protection 2018). Over the two-week period, nearly 39,545ha burned, about 50% at high severity (greater than 75% basal area mortality, USDA Forest Service 2014).

### Sampling design

Sites were selected using ArcGIS 10.6 (ESRI, Redlands, California, USA) in green and high-severity upland sites and green and burned meadow sites in 2016 and 2017, with low-to-moderate-severity upland sites added in 2017. We excluded private lands, areas slated 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 located in patches of a given burn severity determined using the US Forest Service King Fire RAVG (USDA Forest Service 2014) composite burn index to identify areas of green (unchanged), 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; Fig. 1). Ground-truthing ensured that sites were assigned the appropriate burn severity category and habitat type and were homogenous in a 200-m<sup>2</sup> area. We sampled green sites to characterize pre-fire conditions. High- and moderate-severity sites were sampled to represent how pollinator communities may differ under severe (high-severity) and more historic (moderate-severity) fire conditions and how this may differ across upland and meadow systems. Each site had between three and five 20-m radius circular plots separated by at least 100m (average distance = 198m) in either a linear or circular orientation that best characterized the habitat of interest (Fig. 1). In 2016, nine upland sites were established: six in high-severity and three in green habitat. All were visited three times following spring snowmelt to account for some of the variation in phenology in the plant-pollinator communities. In 2017, twenty-seven new sites were established in upland

forest with nine each in unburned forest, forest that burned with moderate severity, and forest that burned with high severity. In 2017, upland sites were only visited twice due to a truncated floral season that resulted from a cold, snowy spring, and to accommodate simultaneous sampling at moderate-severity upland sites. This resulted in a total of 151 unique upland plots on 36 sites over both years of sampling. Because meadow habitat was limited within the fire footprint, we sampled the same sites (but not necessarily the same plots) in both years of the study. Meadow sites were located within the fire footprint (n=3) or outside the fire footprint (n=3) and were visited three times per season in both years of the study. In 2016, each meadow site had five plots for a total of 30 meadow plots. This was reduced in 2017 to three or four plots per site for a total of 22 meadow plots due to the logistic constraints outlined above. Surveys were completed June-September during daylight hours when weather conditions supported insect activity: temperatures were  $> 2^{\circ}\text{C}$ , wind speeds were below 25 mph ( $\geq 6$  on the Beaufort scale), with no precipitation. In each plot, we surveyed pollinators and plants with open inflorescences. We targeted bumble bees, butterflies, and hummingbirds in separate surveys in 2016. In 2017, we focused on floral visitors, although hummingbirds were still recorded opportunistically during site visits.

#### Flower-visitor surveys

We selected plot size and sampling period following other studies to allow comparison of our study with *Bombus* populations in other Sierra Nevada fires (Loffland et al. 2017, Cole et al. 2020). Two observers used a 40-mm sized insect net to capture all *Bombus* species in two consecutive 16-minute fixed area surveys (2016 and 2017) and all other species visiting flowers in one separate 16-minute fixed area surveys (2017 only). These times reflect the minimum amount needed for a surveyor to scan the entire plot, maximizing captures while minimizing movement of pollinators in and out of the plot (i.e. to ensure population closure). Each

individual was captured, placed in a vial and held in a cooler until the end of the flower-visitor survey period, then either identified to species and released or collected for later identification to species or morphospecies using published keys or expert opinion (Triplehorn and Johnson 2005, UC Davis Bohart Museum). We planned to use multiple sampling periods with *Bombus* to account for detectability using a removal model (Farnsworth et al. 2002), however, we did not observe a decline in detections from the first to the second period, thus we pooled data from the two sampling periods. We also recorded the plant species visited and whether the pollinator was captured in the air or on another substrate. 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.

#### Butterfly surveys

In 2016, we conducted a five-minute point count for butterflies in which an observer stood in the middle of the plot and attempted to count every individual that entered the plot during this time (Henry et al. 2015, Lang et al. 2019). Five-minute point count surveys for butterflies provide unbiased density estimates, particularly in dense or heterogeneous habitats, (Van Swaay et al. 2012, Henry et al. 2015). Butterflies were identified to family or lower taxonomic classification on the wing or captured in a 40-mm insect net for identification in the hand as needed (surveys were paused while capturing and identifying species). In 2017, we dropped the point counts, but included butterflies in the flower-visitor surveys.

#### Hummingbird surveys

Hummingbirds were sampled using a mix of passive and broadcast surveys in an attempt to improve detection. We followed protocols typically used to detect other elusive avian species (Saracco et al. 2011). In 2016, a five-minute passive survey was immediately followed by a six-minute broadcast survey (30 seconds of broadcasting, then 90 seconds of observing, repeated

three times) for each species: *Calypte anna*, *Selasphorus rufus*, and *Selasphorus calliope*. Each 30-second recording consisted of wing and tail buzz sounds, dive display calls, and chip notes (Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, <https://macaulaylibrary.org>). Broadcast surveys are often used to detect rare or elusive species (Saracco et al. 2011), and we hypothesized that the territorial nature of hummingbirds suited them for this sampling method. If a hummingbird was detected, the detection was noted as occurring during one of the sampling intervals (1 passive interval, 3 active intervals per species). Because many detections of hummingbirds were incidental while collecting data on other taxa, we dropped the broadcast surveys in 2017. Hummingbirds were included in the flower-visitor surveys, and in addition, observations of hummingbirds were collected opportunistically at each visit while sampling for other species.

#### Floral resources

We estimated the abundance and richness of angiosperms in bloom in eight 1-m<sup>2</sup> quadrats in each plot. We chose to only include plants with open flowers because they best represented the food resources of nectar and pollen available to pollinators at that point in time. Plots were divided into quarters using transects and two quadrats were randomly placed in each quarter. In each quadrat, we identified every plant in flower to species following the Jepson manual (Baldwin et al. 2012) and counted all inflorescences with open flowers. Because pollinators were rarely or never observed visiting some plant species, we only included the subset of 30 plants that were frequently visited ( $\geq 10$  visits) by pollinators (Appendix Table A1). Floral abundance was defined as the sum of inflorescences with open flowers on frequently visited species in each plot for each visit. Floral richness was the number of frequently visited species with open flowers found in all quadrats of a plot on each visit.

## Analysis

To investigate how burn severity, habitat type and floral resources affect pollinator abundance, we created generalized linear mixed models (GLMMs) for each of the following taxonomic groups: bumble bees, butterflies, other insects, and hummingbirds. We modelled abundance of pollinators groups separately to account for differences in sampling effort/method and number of individuals detected. Abundance was calculated for each visit, point, and year (when applicable) of sampling as the total number of detections of a given species. Because the community changed over time due to differences in phenology in emergence, migration, or death, we considered each visit independently. Only species observed in at least three plots were included in the analysis. Bumble bees and other insects were each modelled with hierarchical multi-species abundance models, where species-specific parameters come from a hyper-distribution that is shared by all species and described by hyperparameters (Dorazio and Royle 2005, Dorazio et al. 2006). Multi-species abundance models share information across species, allowing us to model species that were relatively rare, but they require a sufficient number of species (typically 6 or more). We did not have enough taxonomic resolution to use these models on butterflies or hummingbirds. Instead, we created GLMMs for each butterfly family and one GLMM for all hummingbirds. Abundances of each taxon were modelled with the following covariates: burn severity and habitat type (upland or meadow) and an interaction term, year (for *Bombus* and hummingbirds only), floral abundance and richness, elevation, and days since snowmelt.

Although sites were selected using categorical assessment of burn severity, we modeled abundance with a continuous value of burn severity, the Relative Differenced Normalized Burn Ratio (RdNBR) due to its greater accuracy in high-severity, heterogenous landscapes and the finer resolution possible with this metric. RdNBR is derived from the Normalized Burn Ratio, a

vegetation index that detects differences in live green vegetation from dead wood, moisture content, and mineral and soil conditions. By comparing pre- and post-fire imagery, we can estimate the change in vegetation due to fire (Miller and Thode 2007), with higher RdNBR values indicating more severe burns. We used the US Forest Service King Fire RAVG (USDA Forest Service 2014) GIS data with 30x30m resolution to assign a scaled and centered RdNBR value to each plot. In upland habitat we also included a quadratic term for burn severity to account for non-linear response that has been observed for understory plants in this region (Richter et al. 2019). This was not evaluated for meadows because intermediate RdNBR values were not well-represented in meadow habitat. Because the response of pollinators to burn severity may be mediated by habitat type, we included an interaction term between these two variables.

We included two floral metrics to account for importance of these resources to pollinators: floral abundance and richness. Because the floral resource variables were correlated with the habitat type (Appendix Fig. A2), we standardized the floral abundance and richness with the mean and standard deviation of its respective habitat. Thus, the baseline difference in floral resources among meadow and upland habitat is incorporated into the categorical habitat covariate, and the floral abundance and richness covariates describe the deviation from the habitat-level mean.

Elevation, days since snowmelt, and year were included in models to explain additional variation in abundance due to unmeasured environmental factors likely correlated with these variables (e.g., temperature) and to improve model fit. Elevation was derived from digital elevation models in ArcGIS. We estimated snowmelt dates for each year (June 6, 2016 and June 18, 2017) using data from the Greek Store and Robb's saddle weather stations located close to

(~10km) and at similar elevations (~ 1,700m asl) as the study area (California Department of Water Resources 2018). The days since snowmelt was the difference between the date of each visit and the regional date for snowmelt for each year, scaled to have a mean of 0 and standard deviation of 1. Year was included to incorporate annual variation in pollinator communities and changes in sampling protocols for bumble bees and hummingbirds.

Seven *Bombus* species were included in one multi-species (community) abundance model, and 30 other insect visitors in another. Abundance  $N_{ijk}$  of species  $i = 1, 2, \dots, n$  at each of the  $j = 1, 2, \dots, J$  plots at each visit  $k = 1, 2, \dots, K$  was modeled as a negative binomial random variable with species and plot-specific mean ( $\lambda_{ijk}$ ) and a common dispersion parameter  $r$ :

$$N_{ijk} \sim \text{Negative binomial}(\lambda_{ijk}, r)$$

$$\log(\lambda_{ijk}) = \beta_{0i} + \beta_{1i}\text{Snowmelt}_{jk} + \beta_{2i}\text{Richness}_{jk} + \beta_{3i}\text{Inflor}_{jk} + \beta_{4i}\text{Elevation}_j + \beta_{5i}\text{Year}_{jk} \\ + \beta_{6i}\text{Burn}_j + \beta_{7i}[\text{Habitat}=\text{upland}]\text{Burn}_j^2 + \beta_{8i}\text{Habitat}_j\text{Burn}_j + \varepsilon_{\text{site}[j]}$$

Here,  $\beta_{0i} \sim \text{Normal}(\mu, \beta_0, \sigma, \beta_0)$  and analogous for all other coefficients;  $\mu, \beta_0$  is the community mean coefficient and  $\sigma, \beta_0$  the community standard deviation that describes variation of species-level coefficients about the community mean. Snowmelt is the days since snow melt in days, Richness is floral richness, Inflor is floral abundance, and Elevation is elevation in meters, and  $\varepsilon_i$  is the random effect of site, accounting for both the study design (plots nested within sites) and repeated sampling. Year (reference=2016) was included as a fixed effect in the *Bombus* model to account for interannual variation. The quadratic term for burn severity was only included for upland habitat, i.e.,  $\beta_7$  was fixed at 0 for meadow habitat. All continuous variables were centered and standardized.

We modeled abundance separately for each family of butterfly and for all hummingbirds combined, using single-species negative binomial models with the same general model structure

(covariates and random effect) as described above. Year and the quadratic burn severity term were not included in the butterfly model because they were only surveyed in 2016, at green and high-severity plots.

We implemented all models in a Bayesian framework using the software JAGS version 4.3.0 (Plummer 2003) accessed through the jagsUI package 1.5.1 (Kellner 2021) in R (R version 3.4.4). All parameters were assigned vaguely informative priors. The posterior distributions were sampled using three Markov Chain Monte Carlo (MCMC) chains, each with 100,000 samples and a burn-in of 50,000 samples. Convergence of MCMC chains was evaluated using traceplots and the Gelman-Rubin statistic (where  $\hat{R} \leq 1.1$  is considered convergence; Gelman et al. 2004). We report posterior means, standard deviations (SD) and the 2.5th and 97.5th percentiles as the Bayesian 95% credible interval (BCI) for each parameter; we considered coefficients whose 95% BCI did not overlap zero as significant. We calculated Bayesian p-values for the species and community abundances to evaluate goodness-of-fit (Bayesian p-value between 0.1 and 0.9 indicate fit; Gelman et al. 1996; Kéry and Royle 2020; Appendix A ). All chains in all models converged and all models fit their respective data appropriately (Appendix Tables B2-B5).

## **Results**

### Flower-visitors

#### **Bombus species**

In 2016, we captured 812 bumble bees from nine species; eight individuals escaped prior to identification and were dropped from further analysis. In 2017, we captured 233 *Bombus* individuals from nine species; two individuals escaped prior to identification and were dropped from further analysis (Fig. 2, Appendix Table A3). *B. vosnesenskii* was the most commonly encountered species in all burn severity-habitat combinations in both years of sampling. Across

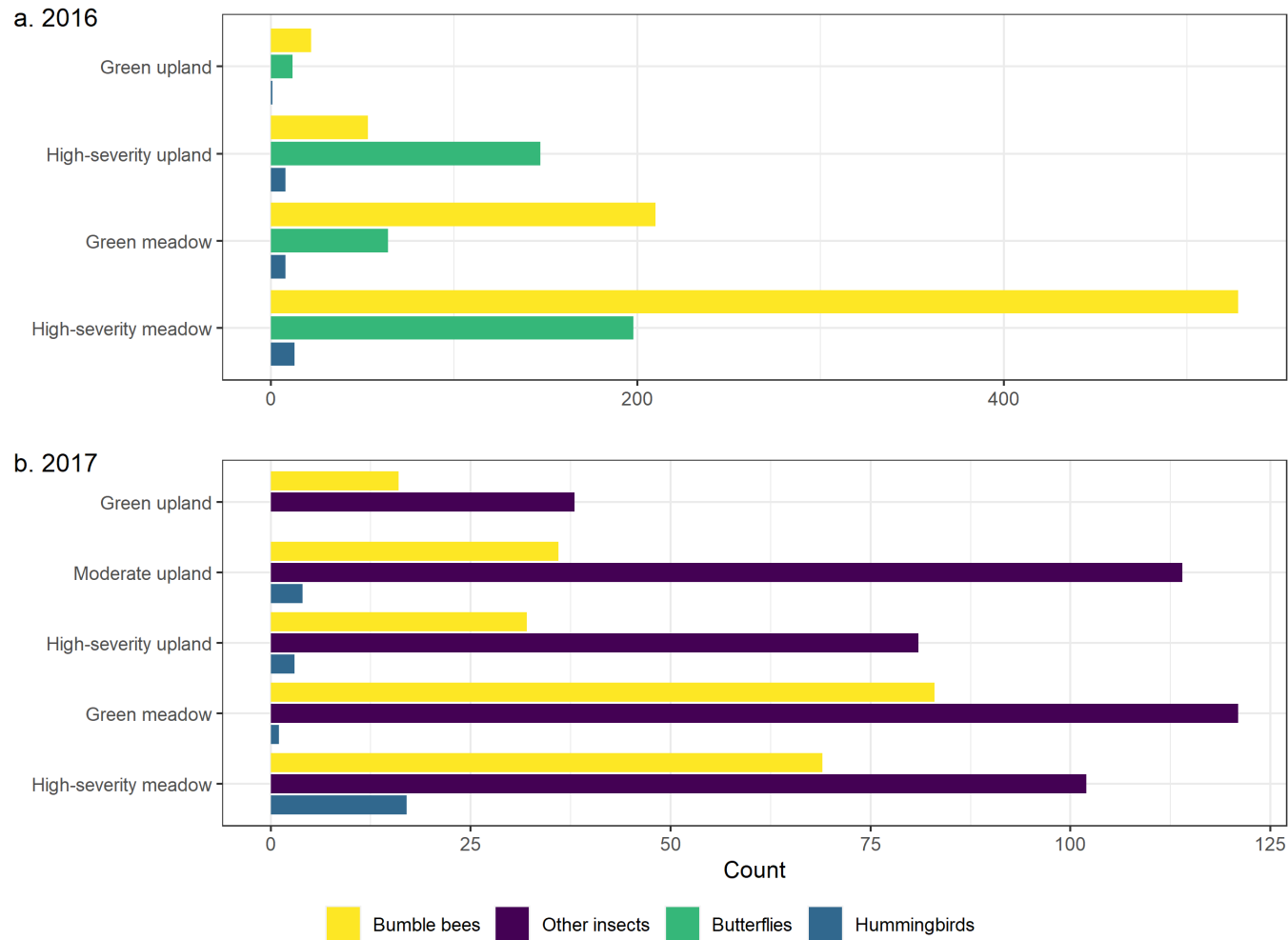


both years, 1,019 observations of seven species of *Bombus* were included in the community model ( Appendix Table B1-B2).

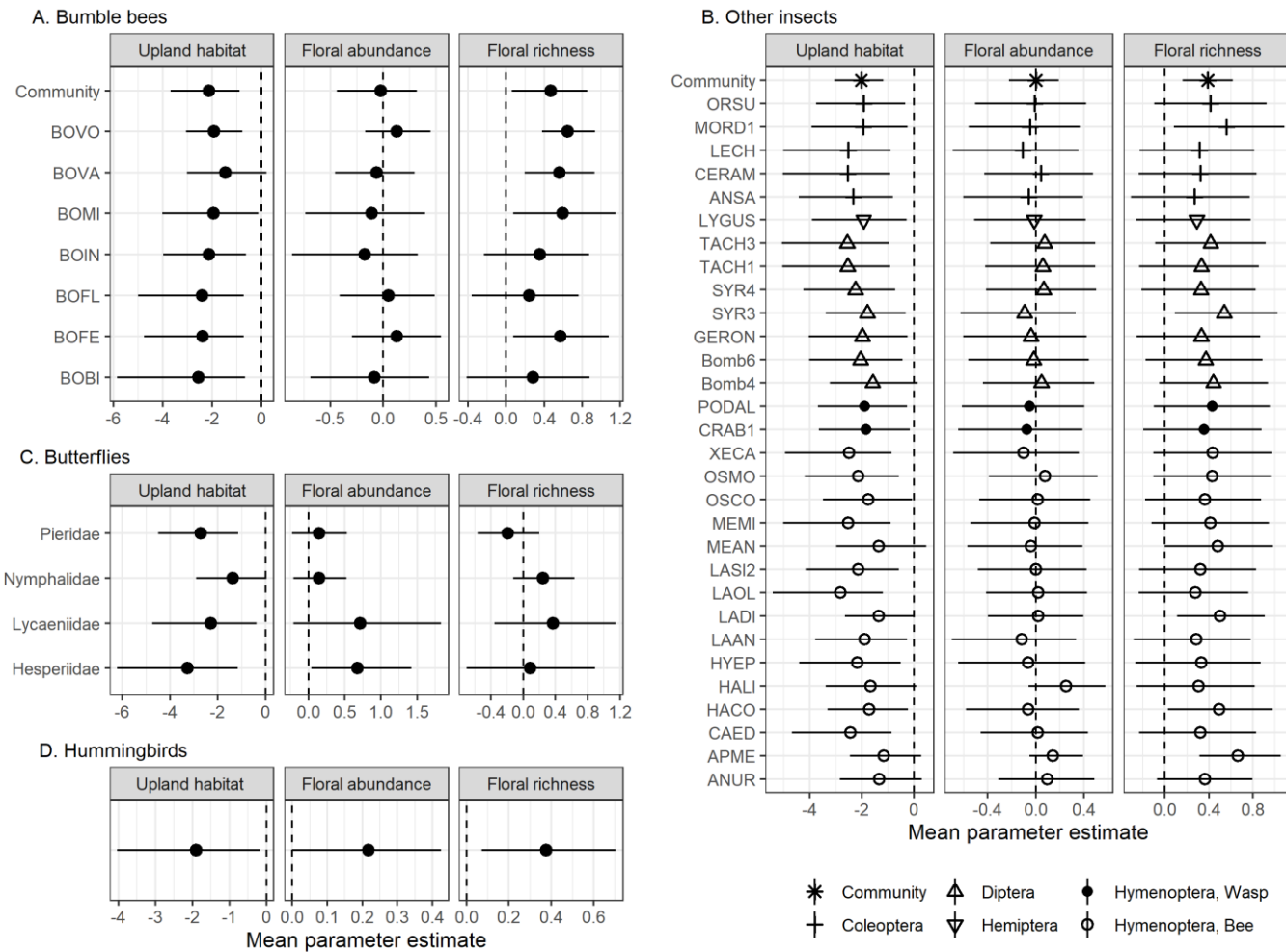
As predicted, bumble bee abundance in upland habitat was lower than in meadow habitat at the community- and species- level, and significantly so for the community and all but one species (Fig. 3A). We expected abundance of bumble bees to be positively associated with the continuous RdNBR burn severity metric, however, at the community-level, we did not find significant effects of either the linear or quadratic burn severity term in either habitat type (Fig. 4A). On the species-level bumble bee abundance tended to decrease in meadows with increasing burn severity, and that effect was significant for one species. In upland habitat, the effect of burn severity varied but was never significant; the effect of squared burn severity was always negative, and significantly so for one species. At the community-level and for four species, floral richness had a significant positive effect on bumble bee abundance; all other species also showed positive, though non-significant, responses. There were no significant effects of floral abundance and community effects were close to zero (Fig. 3A). There were no significant effects of time since snowmelt or elevation, but two species were significantly more abundant in 2016 and one was significantly more abundant in 2017 (Appendix Table B2).

### **Other insects**

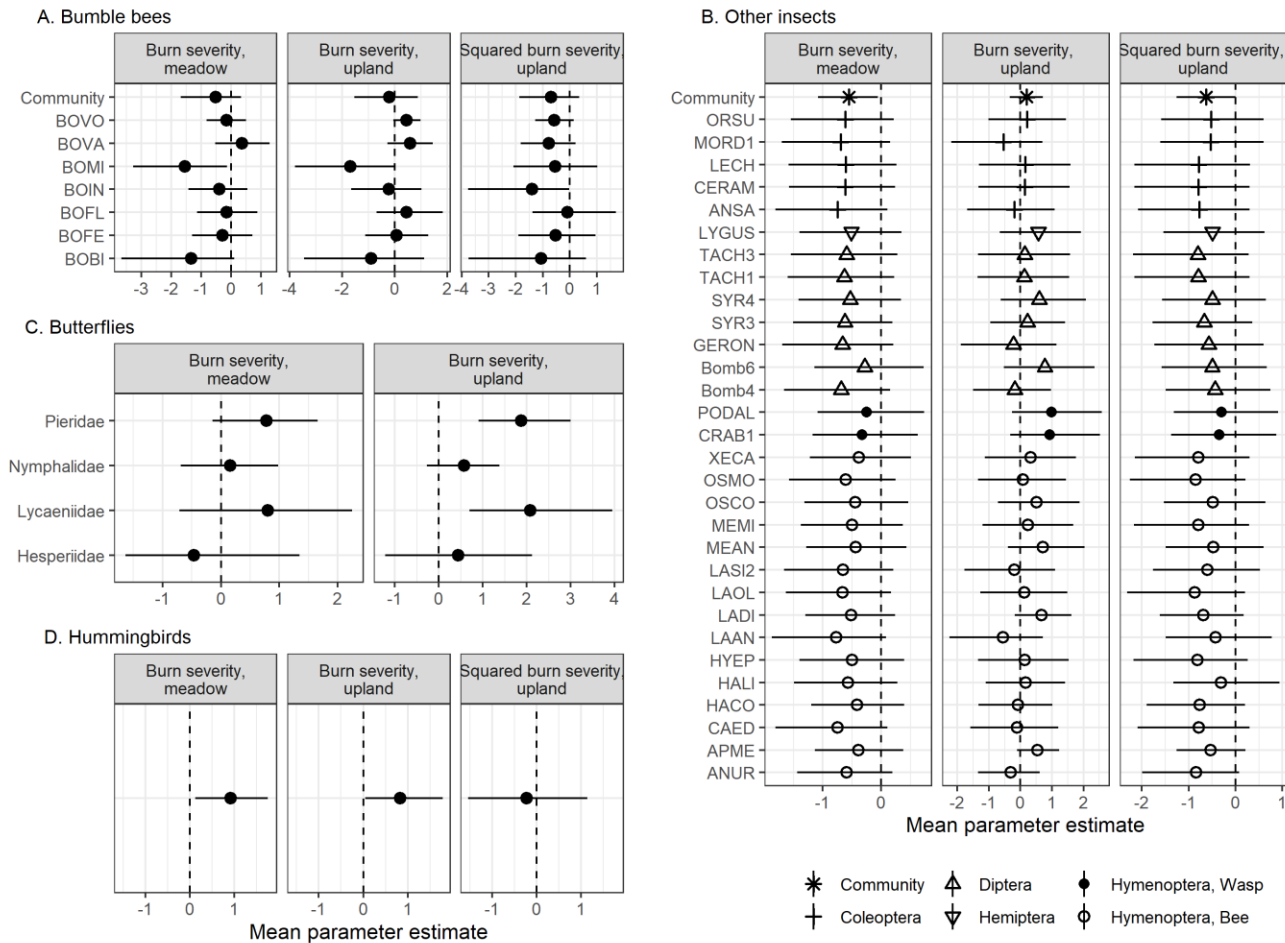
In 2017, we observed 681 individuals representing 132 species or morphospecies from six orders of insects (Fig. 2, Appendix Table A3). The vast majority of individuals were of the order Hymenoptera, family Apidae (n=381). After omitting species that were detected in fewer than three plots, we included 286 individuals of 30 species from five orders in the community model for non-*Bombus* insects.



**Figure 2.** Observed counts of pollinators by year, burn-habitat class, and taxon, during surveys in the Sierra Nevada, California, two and three years after the 2014 King Fire. Moderate-severity habitat was only sampled in 2017. Butterflies were only sampled in 2016 and other insects (including non-*Bombus* bees, wasps, flies, true bugs and beetles) were only sampled in 2017. Note the difference in scales on the x-axes; different taxa were sampled with different methodologies, precluding among-taxon comparison of counts (see main text for details).



**Figure 3.** Factors influencing abundance of pollinator taxa in meadow and upland habitat in the Sierra Nevada, California, two and three years after the 2014 King Fire, estimated using Negative binomial Generalized Linear Mixed Models (single-species models for butterflies and hummingbirds, multi-species models for bumble bees and other insects). Covariate coefficients for habitat type and abundance and richness of blooming plant species visited at least ten times by pollinators for a) the bumble bee community on average and individual species, b) the community of other flower-visiting insects on average and individual species, c) butterfly families, and d) hummingbirds. Coefficients are considered significant when 95% confidence intervals do not overlap 0. Species codes in Appendix Table A3.



**Figure 4.** Factors influencing abundance of pollinator taxa in meadow and upland in the Sierra Nevada, California, two and three years after the 2014 King Fire, estimated with negative binomial generalized linear mixed models (single-species models for butterflies and hummingbirds, multi-species models for bumble bees and other insects). Covariate coefficients for the interaction of burn severity and habitat, and the quadratic term for burn severity applied in upland habitat only for a) the bumble bee community on average and individual species, b) the community of other flower-visiting insects on average and individual species, c) butterfly families (not sampled in moderate-severity habitat, so no quadratic burn effect), and d) hummingbirds. Coefficients are considered significant when 95% confidence intervals do not overlap 0. Species codes in Appendix Table A3.

As predicted, the insect community was significantly less abundant in upland than in meadow habitat (Fig. 3B, Appendix Table B1, B3). The effect of upland habitat was negative for all species and significantly so for 24 species. Community insect abundance was significantly negatively associated with burn severity in meadow habitat; even though all species-level parameter estimates were negative, none of them were significant. In upland habitat, the community-level effect and the majority of species-level effects of burn severity were positive, but none were significant (Fig. 4B). In addition, the quadratic burn term was significant and negative on the community (and negative but non-significant for all species), indicating that insect abundance was highest at moderate-severity in upland habitat. We found a positive and significant effect of floral richness on the community-level insect abundance (Fig. 3B). The species-level response to floral richness was positive for all species and significant for one beetle, one fly, and three bee species. There was no significant response at the community- or species- level to floral abundance. Elevation did not have a significant effect, but the abundance of ten species decreased significantly with increasing number of days since snowmelt.

### **Butterflies**

In 2016, we observed 421 individuals from five butterfly families (Fig. 2, Appendix Table A3). Pieridae was the most frequently observed family in high-severity habitat, and Nymphalidae was the most frequently observed family in green habitat. We included 419 butterfly observations from four families in the abundance model.

As expected, we observed more butterfly pollinators in meadow habitat than upland habitat, and this relationship was significant for three out of four families and marginally significant for the fourth (Fig. 3C, Appendix Table B1, B4). There was no significant response of

butterfly abundance to burn severity in meadows, but two families, Pieridae and Lycaenidae, increased significantly with increasing burn severity in uplands (Fig. 4C). Only one family was significantly associated with increasing floral abundance, although we did observe a nonsignificant positive trend for all families (Fig. 3C). Similarly, although no families were significantly influenced by floral richness, three out of four families tended toward higher abundance with increasing richness. Nymphalidae and Lycaeniidae both decreased significantly with increasing elevation, while Pieridae and Herperiidae both decreased significantly with increasing number of days since snowmelt (Appendix Table B4).

### **Hummingbirds**

In 2016, we detected 30 hummingbirds in both broadcast surveys and incidental observations that occurred as other sampling took place (Fig. 2, Appendix Table A3). In 2017, we observed 25 hummingbirds incidentally. We included all 55 observations in our hummingbird abundance model.

We found that the effect of burn severity was significantly positive for hummingbird abundance in both meadow and upland habitat (Fig. 4D, Appendix Table B1, B5). As we predicted, hummingbird abundance responded positively to increasing floral resources, although this was only significant for floral richness (Fig. 3D). Hummingbirds decreased significantly with increasing number of days since snowmelt but had no significant response to elevation or year (Appendix Table B5).

### **Discussion**

Pollinator abundance tended to be highest in meadows, moderate-severity uplands, and habitats with high floral richness. We expected pollinator abundance to peak in moderate-severity upland habitat and decrease with increasing burn severity in meadow habitat. We found

evidence for this relationship at the community-level for other floral visitors, and partial (and non-significant) support for the *Bombus* community, who responded weakly negatively to burn severity in meadows and to squared burn severity in upland habitat. For species within the *Bombus* and other floral visitor communities, the response to burn severity in meadows was highly consistent and negative, but rarely significant, whereas it varied in upland habitat. Meanwhile, hummingbirds responded positively to burn severity in both habitats, and most butterfly families responded positively, though rarely significantly, to burn severity. The pollinators of the mixed-conifer forests of the Sierra Nevada evolved under a disturbance-prone system that may have filtered out species that are intolerant of rapid environmental change (Kelt et al. 2017), resulting in a community that is resilient to the changes associated with frequent, albeit moderate-severity fire. This may explain why they seem to prefer green meadow and moderately burned upland habitat, but can tolerate a wide variety of habitat conditions (Waser et al. 1996).

All communities and most species had significantly higher abundance in meadows than upland habitat. Meadows have denser floral resources, may be easier to find, with floral resources that are more predictable in space and time than upland habitat (Gass 1979, Clark and Russell 2020). Meadows in this area had higher floral diversity and abundance than uplands, particularly earlier in the season (Chapter 1). Because there was a strong correlation between habitat type and both floral resource metrics, we scaled the resources relative to the mean for the habitat. As such, the baseline difference in floral richness and abundance is incorporated into the habitat variable, which may partially explain the consistently positive effect of meadows on pollinator abundance. Meadows may also provide other non-floral benefits to pollinator species. For example, caterpillars of many butterfly species are dependent on a particular host species or

genera, which are often associated with or limited to mesic habitats (Fleishman 2000). For hummingbirds, burned meadows may be especially attractive to long-distance and elevational migrants if fire increased the abundance or richness of floral resources during migration or breeding (Russell et al. 1994, McKinney et al. 2012). Hummingbird abundance declined significantly with time since snowmelt, suggesting that they will target habitats with relatively early-blooming flowers. We found that floral resources increased in abundance and richness in burned meadows relative to green meadows, and floral richness was higher in burned meadows earlier in the season (Chapter 1), suggesting that the resource pulse may align with the needs of hummingbirds. Meadows may also have more nest sites for ground-nesting bee species (Antoine and Forrest 2021; Pugsek and Crone 2021), although this will likely depend on species-specific preferences.

Pollinator abundance is associated with increased seed set and reduced pollen limitation in flowering plants (Steffan-Dewenter and Tschardtke 1999, Cusser et al. 2016, Thomson 2019), therefore identifying drivers of abundance is critical in supporting pollination services. Floral richness was positively associated with nearly all pollinator communities and taxa (although not always significant), and the effect of floral richness was strongest for bumble bees and the European honey bee. Multiple species of angiosperms that bloom sequentially will be necessary to support bumble bees and honey bees that rely upon pollen and nectar in all life stages, and forage to support their colony over an entire season (and beyond for honey bees storing honey for winter) (Aldridge et al. 2011). Increasing floral richness may positively impact pollinators by providing pollen and nectar resources that vary temporally and spatially, providing reliable food resources for long-lived, early, and late emerging species, as well as multiple generations of social bees (Ebeling et al. 2008, Roulston and Goodell 2011, Ogilvie and Forrest 2017, Kaluza et



al. 2018). High floral diversity increase attraction through large mixed species displays (Ghazoul 2006, Vaca-Uribe et al. 2021) or reduce competition among pollinators (Brosi et al. 2017, Kaluza et al. 2017). High floral diversity may also increase the likelihood of specialist pollinators finding their preferred species or family due to sampling effects (Loreau et al. 2001). However, most species of pollinators were not influenced by the abundance of open flowers. For non-bee species this may be explained by the reliance of larval stages on non-floral resources, a pattern that has been observed for flies (Robinson et al. 2018), beetles (O'Neill et al. 2008), and butterflies (Woodcock et al. 2012) in other systems. Floral abundance may not affect abundance of bees and other pollinators if there is a mismatch in the flower and pollinator morphology (Stang et al. 2009, Klumpers et al. 2019). Many plants with flowers densely packed into inflorescences have individual flowers that are inaccessible or not worth the handling time (Stang et al. 2009, Klumpers et al. 2019). Additionally, because the number of inflorescences was scaled to the meadow and upland habitat means, the variation in this covariate was reduced, making it more difficult to detect a pattern.

Drought may reduce floral resources for pollinators by reducing the number of flowers or the amount of nectar or pollen that a plant produces (Thomson 2016, Phillips et al. 2018, Descamps et al. 2021). One of the worst droughts on record in the Sierra Nevada occurred from 2012 to 2016 (Griffin and Anchukaitis 2014, Bales et al. 2018) and was followed by record high snowpack in winter 2017 (Painter et al. 2017, Behrangi et al. 2018). Despite evidence that drought may negatively impact pollinator abundance (Thomson 2016, Phillips et al. 2018, Descamps et al. 2021), we observed more bumble bees in 2016 than in 2017 (Fig. 2). Perhaps the lower abundance observed in 2017 was due to a lag effect of the drought, since the size of the current population is limited by resource availability in the previous season (Minckley et al.

1994, Larsson and Franzén 2007). Conversely, the habitat conditions produced by moderate-severity fire may buffer pollinator populations from the negative effects of drought (Ponisio et al. 2016), and we did observe the highest abundance for many pollinator species in this fire severity in uplands. The reduced abundance observed for some species in 2017 may also be due to the heavy snow year, including some late-season frost (California Department of Water Resources 2018). Late-season frost can reduce floral abundance and pollinator visitation (Inouye 2008, Pardee et al. 2018), and presumably kill early-emerging pollinators (Krunić and Stanisavljević 2006, Owen et al. 2013, Bennett 2017). High variability is typical of California precipitation patterns, with even more extreme weather predicted under climate change (Lubchenco and Karl 2012, Arnold et al. 2014). Long-term studies of plant-pollinator communities are needed to better understand how fire, precipitation and flowering resources interact to affect pollinators.

The mobility of pollinators is often highlighted as an advantage for repopulating disturbed or restored habitats, however, this same mobility may affect our ability to discern preferences with regard to habitat type and burn severity. Areas of high and moderate severity were interspersed in the King Fire (Fig. 1) and the distances between sampling sites did not preclude travel between them for many species, bees and hummingbirds in particular. For floral visitors, we were able to qualitatively observe them “using” the habitat in a sampling plot, i.e., foraging on flowers, suggesting that this habitat was indeed important. Similarly, although we did not observe hummingbirds visiting flowers, we did observe territorial behavior (vocalizing, chasing, and diving) that suggested these habitats were important to hummingbirds (Armitage 1955, Cody 1968, Hixon et al. 1983). In contrast, butterflies were typically observed moving through the sampling plot during point counts rather than foraging, and we did not observe butterflies during floral visitor surveys. During the breeding season, many butterfly species are

searching for mates, males in particular tend to “guard” larval host plants (Dennis and Shreeve 1988). We found that butterflies tended to respond positively to burn severity and floral abundance, suggesting that burned habitats may provide resources, but targeting host plants would help us better understand how these habitats are used.

In spite of most effects of burn severity being non-significant, there is some evidence that high-severity fire has negative impacts on pollinator communities in the Sierra Nevada. First, in meadow habitat, bumble bee and other insect pollinators very consistently occurred at lower abundance with increasing burn severity. Even though these effects were mostly non-significant, this consistency in negative response suggests that high-severity fire is more likely to decrease habitat quality in meadows than improve it. This is also reflected in the community-level significant negative effect for insect pollinators. In upland habitat, burning had inconsistent effects on pollinator species abundance (though more species responded positively), but with consistently negative quadratic effects – i.e., at high severity, fire reduced pollinator abundance. Again, the consistency in that second response (even though largely non-significant) may be an indication that high-severity fire has the potential to affect pollinators negatively, whereas moderate severity fire in upland habitat is more likely beneficial or neutral, at least for the majority of species. Our study suggests that even when embedded in large fires that burn largely at high severity, moderate-severity upland patches improve habitat conditions for pollinator species in fire-suppressed forests. Given the uncertainty in effects of burn severity on pollinator abundance, as well as the finding that abundance and diversity of floral resources is higher in high-severity upland habitat compared to unburned upland (Chapter 1), even high-severity fire may create suitable pollinator habitat. This is reassuring, given that much of the Sierra Nevada is overdue to burn (North et al. 2012) and fire effects are likely to be severe (Collins 2014, Cassell

et al. 2019). Pollinators of this and other regions have shown themselves tolerant of and even amenable to moderate-severity fire (Ponisio et al. 2016, Rodríguez and Kouki 2017, Lazarina et al. 2019). Our study shows that pollinators can survive and repopulate megafires; however, their ability to do so will depend on landscape effects of connectivity (Brown et al. 2017, Adedoja et al. 2019, Carbone et al. 2019), post-fire management (Heil and Burkle 2018, Galbraith et al. 2019b), and life history traits (Williams et al. 2010, Enright et al. 2014, Peralta et al. 2017). Addressing these issues will require future studies across multiple fires.

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## Appendices

### Appendix A.

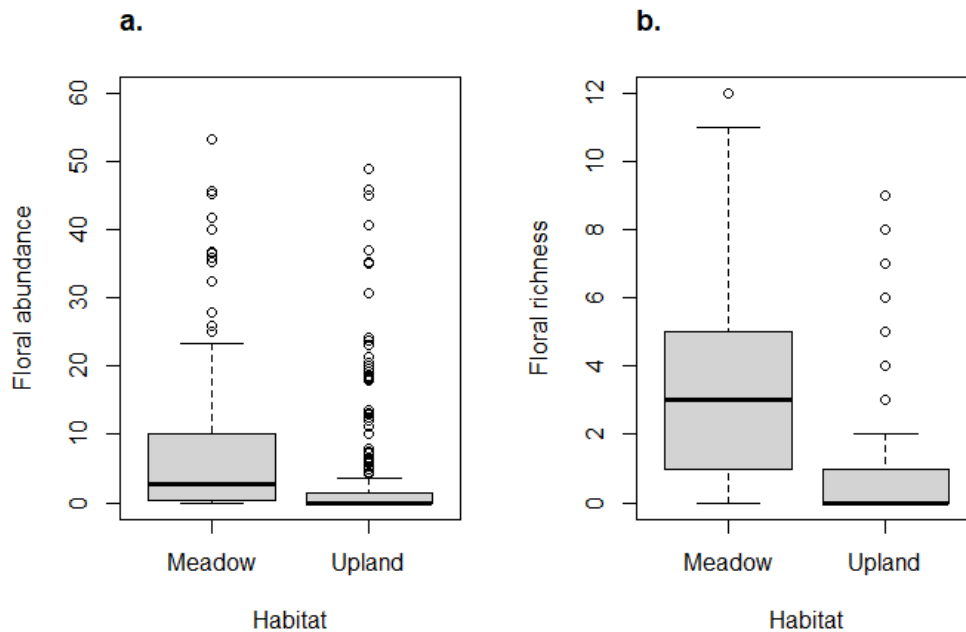
**Table A1.** Species or morphospecies of plants that had least 10 pollinator visits in the Sierra Nevada, California, two and three years after the 2014 King Fire.

ScientificName	Family	Native	Pollinator visits
<i>Erigeron</i> species	Asteraceae	Native	26
<i>Asyneuma prenanthoides</i>	Campanulaceae	Native	43
<i>Bistorta bistortoides</i>	Polygonaceae	Native	25
<i>Cirsium andersonii</i>	Asteraceae	Native	11
<i>Cirsium vulgare</i>	Asteraceae	Invasive	198
<i>Cuscuta californica</i>	Convolvulaceae	Native	50
<i>Drymacallis glandulosa</i>	Rosaceae	Native	13
<i>Eriodictyon lobbii</i>	Boraginaceae	Native	50
<i>Eriophyllum lanatum</i>	Asteraceae	Native	17
<i>Helenium bigelovii</i>	Asteraceae	Native	21
<i>Horkelia fusca</i>	Rosaceae	Native	51
<i>Hypericum perforatum</i>	Hypericaceae	Invasive	19
<i>Hypericum scouleri</i>	Hypericaceae	Native	11
<i>Lupinus latifolius</i> var. <i>columbianus</i>	Fabaceae	Native	13
<i>Lupinus</i> species	Fabaceae	Native	70
<i>Mimulus guttatus</i>	Phrymaceae	Native	17
<i>Mimulus moschatus</i>	Phrymaceae	Native	16
<i>Monardella odoratissima</i>	Lamiaceae	Native	14
<i>Oreostemma alpigenum</i> var. <i>andersonii</i>	Asteraceae	Native	15
<i>Perideridia parishii</i>	Apiaceae	Native	11
<i>Phacelia hastata</i>	Boraginaceae	Native	13
<i>Phacelia</i> species	Boraginaceae	Native	30
<i>Rudbeckia occidentalis</i>	Asteraceae	Native	10
<i>Senecio triangularis</i>	Asteraceae	Native	23
<i>Sidalcea glaucescens</i>	Malvaceae	Native	18
<i>Solidago canadensis</i>	Asteraceae	Native	19
<i>Solidago elongata</i>	Asteraceae	Native	13
<i>Symphyotrichum spathulatum</i> var. <i>spathulatum</i>	Asteraceae	Native	122
<i>Trifolium pratense</i>	Fabaceae	Non-Native	44
<i>Veratrum californicum</i>	Melanthiaceae	Native	21



**Table A2.** Tests for correlations among predictor variables used to model pollinator abundance, with Pearson's correlation and variance inflation factor (VIF), stratified by upland and meadow habitat. Data were collected in the Sierra Nevada, California, two and three years after the 2014 King Fire. Floral abundance and richness were derived from the 30 most commonly visited plant species (Table A1). Elevation and burn severity were derived from remote-sensed data.

Upland				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.013		Burn severity	1.019
Floral richness	0.128	0.454	Floral abundance	1.264
			Floral richness	1.284
Meadow				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.203		Burn severity	1.092
Floral richness	0.290	0.676	Floral abundance	1.842
			Floral richness	1.928
All				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.024		Burn severity	1.293
Floral richness	0.163	0.397	Floral abundance	1.190
			Floral richness	1.221



**Figure A1.** Correlation between meadow and upland habitats and a. floral abundance and b. floral richness in the Sierra Nevada, California, two and three years after the King Fire.

**Table A3.** Counts of pollinator species or morphospecies detected in the Sierra Nevada of California two and three years after the 2014 King Fire. Moderate-severity habitat was only sampled in 2017. Butterflies were only sampled in 2016 and other insects (bees, wasps, flies, true bugs and beetles) were only sampled in 2017. Different taxa were sampled with different methodologies (see main text for details). GU=Green upland, MU=Moderate-severity upland, HU=High-severity upland, GM=Green meadow, and HM=High-severity meadow; Code=species code used in figures.

Order	Family	Scientific name	Code	GU	MU	HU	GM	HM
Apodiformes	Trochilidae	NA	NA	1	4	11	9	30
Lepidoptera	Hesperiidae	NA	NA	3	NA	3	16	6
Lepidoptera	Lycaenidae	NA	NA	2	NA	22	4	21
Lepidoptera	Nymphalidae	NA	NA	6	NA	59	23	61
Lepidoptera	Papilionidae	NA	NA	0	NA	0	0	2
Lepidoptera	Pieridae	NA	NA	1	NA	63	21	108
Hymenoptera	Apidae	<i>Bombus bifarius</i>	BOBI	0	0	0	19	0
Hymenoptera	Apidae	<i>Bombus fervidus</i>	BOFE	2	0	2	3	29
Hymenoptera	Apidae	<i>Bombus flavifrons</i>	BOFL	4	1	2	8	9
Hymenoptera	Apidae	<i>Bombus fernaldae</i>	BOFN	1	0	0	0	4
Hymenoptera	Apidae	<i>Bombus insularis</i>	BOIN	1	1	1	4	8
Hymenoptera	Apidae	<i>Bombus melanopygus</i>	BOME	2	0	0	1	2
Hymenoptera	Apidae	<i>Bombus mixtus</i>	BOMI	6	1	0	22	1
Hymenoptera	Apidae	<i>Bombus rufocinctus</i>	BORU	0	0	0	3	3
Hymenoptera	Apidae	<i>Bombus vandykei</i>	BOVA	1	6	16	4	37
Hymenoptera	Apidae	<i>Bombus vosnesenskii</i>	BOVO	20	27	63	208	513
Coleoptera	Cerambycidae	<i>Anastrangalia sanguinea</i>	ANSA	0	1	0	2	4
Coleoptera	Cerambycidae	Cerambycidae	CERAM	0	0	0	1	2
Coleoptera	Cerambycidae	<i>Lepturobosca chrysocoma</i>	LECH	0	0	0	3	0
Coleoptera	Dermestidae	<i>Orphilus subnitidus</i>	ORSU	0	2	0	1	1
Coleoptera	Mordellidae	Mordella 1	MORD1	0	4	0	1	1
Diptera	Bombyliidae	Bombyliidae 4	Bomb4	1	2	0	1	0
Diptera	Bombyliidae	Bombyliidae 6	Bomb6	0	0	1	0	1
Diptera	Bombyliidae	Geron	GERON	0	1	0	0	0
Diptera	Syrphidae	Syrphidae 3	SYR3	0	2	1	5	1
Diptera	Syrphidae	Syrphidae 4	SYR4	0	0	1	5	0
Diptera	Tachinidae	Tachinidae 1	TACH1	0	0	0	1	2
Diptera	Tachinidae	Tachinidae 3	TACH3	0	0	0	2	2
Hemiptera	Miridae	<i>Lygus</i> spp	LYGUS	0	1	3	1	1
Hymenoptera	Andrenidae	<i>Calliopsis edwardsii</i>	CAED	0	1	0	7	1
Hymenoptera	Apidae	<i>Anthophora urbana</i>	ANUR	4	11	0	7	6
Hymenoptera	Apidae	<i>Apis mellifera</i>	APME	4	39	25	24	11
Hymenoptera	Apidae	<i>Melissodes microsticta</i>	MEMI	0	0	0	2	1
Hymenoptera	Apidae	<i>Xeromelecta californica</i>	XECA	0	0	0	1	3
Hymenoptera	Collectidae	<i>Hylaeus episcopalis</i>	HYEP	1	0	0	0	2
Hymenoptera	Crabronidae	Crabronidae 1	CRAB1	0	0	2	0	1
Hymenoptera	Halictidae	Halictidae	HALI	0	2	1	1	0
Hymenoptera	Halictidae	<i>Halictus confusus</i>	HACO	3	2	0	1	5

**Table A3.** Counts of pollinator species or morphospecies detected in the Sierra Nevada of California two and three years after the 2014 King Fire. Moderate-severity habitat was only sampled in 2017. Butterflies were only sampled in 2016 and other insects (bees, wasps, flies, true bugs and beetles) were only sampled in 2017. Different taxa were sampled with different methodologies (see main text for details). GU=Green upland, MU=Moderate-severity upland, HU=High-severity upland, GM=Green meadow, and HM=High-severity meadow; Code=species code used in figures.

Hymenoptera	Halictidae	<i>Lasioglossum 2</i>	LASI2	0	1	0	1	1
Hymenoptera	Halictidae	<i>Lasioglossum anhypops</i>	LAAN	0	2	0	1	0
Hymenoptera	Halictidae	<i>Lasioglossum dialictus</i>	LADI	1	4	11	8	3
Hymenoptera	Halictidae	<i>Lasioglossum olympiae</i>	LAOL	0	0	0	8	4
Hymenoptera	Megachilidae	<i>Megachile angularum</i>	MEAN	0	2	2	1	0
Hymenoptera	Megachilidae	<i>Osmia coloradensis</i>	OSCO	0	1	1	0	1
Hymenoptera	Megachilidae	<i>Osmia montana</i>	OSMO	0	0	1	0	2
Hymenoptera	Sphecidae	<i>Podalonia</i>	PODAL	0	0	2	0	2

## Appendix B.

We used Bayesian p-values to summarize the posterior predictive check for the goodness-of-fit of our models. We defined our test statistic  $\chi^2$  as:

$$\chi^2 = \frac{Y_j - (\lambda_j * \rho)^2}{\sqrt{\lambda_j * \rho + e}}$$

where  $Y_j$  are the counts by site  $j$ ,  $\lambda_j$  is our mean abundance,  $\rho$  is the overdispersion parameter, and  $e = 0.0001$ . This was summed over all observations to generate the posterior distribution of our observed dataset.

We created a hypothetical perfect dataset that followed the Poisson distribution with parameter  $\lambda_j * \rho$  statistic, with the posterior distribution and calculated the posterior distribution of this “expected” dataset using the equation above. Both are expected and observed  $\chi^2$  statistics are calculated in each run of the MCMC with the respective parameter estimates. The Bayesian p-value is the posterior probability of observing a more extreme value, given the data (Gelman et al. 1996, Kéry and Royle 2020).

Gelman, A., X.-L. Meng, and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. *Statistica Sinica*:733–760.

Kéry, M., and J. A. Royle. 2020. *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced Models*. Academic Press.

**Table B1.** Posterior means and standard deviations (SD) of coefficients related to habitat, fire and floral resources from negative binomial generalized linear mixed models (community models for *Bombus* and insects, regular models for butterflies and hummingbirds). Data were collected in upland and meadow habitat in the Sierra Nevada, California, in 2016 and 2017, following the 2014 King Fire. Full model results available in Tables B2-B5. Bold values have 95% Bayesian Credible Intervals that do not overlap zero and are considered significant. Code=species code used in figures.

Taxon	Code	Burn severity in meadow		Burn severity in upland		Burn severity <sup>2</sup> in upland		Habitat, upland		Floral abundance		Floral richness	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<b><i>Bombus</i> community</b>		-0.525	0.49	-0.206	0.603	-0.695	0.569	-2.121	0.701	-0.023	0.19	0.468	0.199
<i>Bombus bifarius</i>	BOBI	-1.340	0.969	-0.897	1.150	-1.070	1.093	-2.545	1.316	-0.086	0.285	0.280	0.328
<i>Bombus fervidus</i>	BOFE	-0.287	0.508	0.070	0.605	-0.519	0.704	-2.383	1.007	0.127	0.214	0.570	0.254
<i>Bombus flavifrons</i>	BOFL	-0.161	0.508	0.452	0.634	-0.089	0.780	-2.404	1.072	0.052	0.228	0.243	0.286
<i>Bombus insularis</i>	BOIN	-0.401	0.496	-0.222	0.671	-1.402	0.948	-2.132	0.844	-0.176	0.303	0.353	0.279
<i>Bombus mixtus</i>	BOMI	-1.547	0.814	-1.686	0.972	-0.550	0.768	-1.948	0.957	-0.110	0.288	0.595	0.271
<i>Bombus vandykei</i>	BOVA	0.362	0.463	0.582	0.433	-0.780	0.511	-1.466	0.812	-0.063	0.193	0.562	0.187
<i>Bombus vosnesenskii</i>	BOVO	-0.161	0.335	0.444	0.261	-0.581	0.362	-1.919	0.578	0.127	0.156	0.646	0.143
<b>Insect community</b>		-0.551	0.259	0.199	0.266	-0.628	0.319	-2.028	0.474	0.000	0.105	0.389	0.117
<i>Anastrangalia sanguinea</i>	ANSA	-0.745	0.480	-0.191	0.693	-0.776	0.593	-2.331	0.915	-0.060	0.251	0.268	0.272
<i>Anthophora urbana</i>	ANUR	-0.590	0.410	-0.308	0.495	-0.846	0.519	-1.343	0.796	0.094	0.201	0.366	0.22
<i>Apis mellifera</i>	APME	-0.389	0.382	0.541	0.34	-0.528	0.375	-1.159	0.703	0.141	0.114	0.664	0.189
<i>Bombyliidae 4</i>	Bomb4	-0.680	0.456	-0.183	0.624	-0.439	0.554	-1.591	0.839	0.048	0.233	0.441	0.249
<i>Bombyliidae 6</i>	Bomb6	-0.283	0.467	0.777	0.72	-0.499	0.558	-2.062	0.890	-0.018	0.252	0.37	0.268
<i>Calliopsis edwardsii</i>	CAED	-0.742	0.482	-0.103	0.698	-0.780	0.594	-2.435	0.967	0.018	0.226	0.322	0.269

**Table B1.** Posterior means and standard deviations (SD) of coefficients related to habitat, fire and floral resources from negative binomial generalized linear mixed models (community models for *Bombus* and insects, regular models for butterflies and hummingbirds). Data were collected in upland and meadow habitat in the Sierra Nevada, California, in 2016 and 2017, following the 2014 King Fire. Full model results available in Tables B2-B5. Bold values have 95% Bayesian Credible Intervals that do not overlap zero and are considered significant. Code=species code used in figures.

Taxon	Code	Burn severity in meadow		Burn severity in upland		Burn severity <sup>2</sup> in upland		Habitat, upland		Floral abundance		Floral richness	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Cerambycidae</i>	CERAM	-0.616	0.457	0.135	0.722	-0.790	0.612	-2.539	1.042	0.042	0.228	0.321	0.27
<i>Crabronidae 1</i>	CRAB1	-0.329	0.451	0.929	0.722	-0.349	0.562	-1.842	0.862	-0.076	0.262	0.357	0.271
<i>Geron</i>	GERON	-0.661	0.474	-0.219	0.759	-0.569	0.577	-1.984	0.933	-0.041	0.259	0.330	0.283
<i>Halictus confusus</i>	HACO	-0.410	0.403	-0.077	0.59	-0.766	0.526	-1.724	0.767	-0.065	0.237	0.493	0.24
<i>Halictidae</i>	HALI	-0.570	0.444	0.164	0.627	-0.312	0.567	-1.662	0.861	0.253	0.161	0.306	0.27
<i>Hylaeus episcopalis</i>	HYEP	-0.495	0.448	0.138	0.716	-0.816	0.607	-2.188	0.969	-0.064	0.266	0.330	0.286
<i>Lasioglossum anhypops</i>	LAAN	-0.769	0.491	-0.552	0.747	-0.428	0.563	-1.904	0.872	-0.117	0.261	0.284	0.27
<i>Lasioglossum Dialictus</i>	LADI	-0.516	0.388	0.664	0.454	-0.692	0.45	-1.362	0.677	0.02	0.201	0.501	0.203
<i>Lasioglossum olympiae</i>	LAOL	-0.663	0.451	0.126	0.688	-0.876	0.628	-2.822	1.094	0.019	0.213	0.277	0.252
<i>Lasioglossum 2</i>	LASI2	-0.650	0.466	-0.196	0.722	-0.601	0.566	-2.15	0.891	0.002	0.230	0.323	0.269
<i>Lepturobosca chrysocoma</i>	LECH	-0.607	0.462	0.15	0.724	-0.787	0.614	-2.528	1.05	-0.107	0.264	0.313	0.262
<i>Lygus spp</i>	LYGUS	-0.509	0.439	0.565	0.646	-0.492	0.542	-1.941	0.899	-0.013	0.234	0.288	0.263
<i>Megachile angularum</i>	MEAN	-0.435	0.432	0.717	0.609	-0.479	0.522	-1.355	0.866	-0.042	0.242	0.482	0.248
<i>Melissodes microsticta</i>	MEMI	-0.494	0.438	0.245	0.714	-0.794	0.612	-2.525	1.050	-0.012	0.247	0.416	0.269
<i>Mordella 1</i>	MORD1	-0.694	0.465	-0.541	0.729	-0.528	0.55	-1.951	0.917	-0.049	0.233	0.561	0.254
<i>Orphilus subnitidus</i>	ORSU	-0.613	0.441	0.216	0.614	-0.520	0.543	-1.933	0.844	-0.009	0.233	0.415	0.258
<i>Osmia coloradensis</i>	OSCO	-0.441	0.445	0.515	0.65	-0.485	0.542	-1.766	0.847	0.017	0.232	0.363	0.267

**Table B1.** Posterior means and standard deviations (SD) of coefficients related to habitat, fire and floral resources from negative binomial generalized linear mixed models (community models for *Bombus* and insects, regular models for butterflies and hummingbirds). Data were collected in upland and meadow habitat in the Sierra Nevada, California, in 2016 and 2017, following the 2014 King Fire. Full model results available in Tables B2-B5. Bold values have 95% Bayesian Credible Intervals that do not overlap zero and are considered significant. Code=species code used in figures.

Taxon	Code	Burn severity in meadow		Burn severity in upland		Burn severity <sup>2</sup> in upland		Habitat, upland		Floral abundance		Floral richness	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>Osmia montana</i>	OSMO	-0.609	0.458	0.086	0.698	-0.850	0.613	-2.146	0.902	0.078	0.227	0.430	0.267
<i>Podalonia</i>	PODAL	-0.247	0.457	0.989	0.718	-0.304	0.559	-1.89	0.847	-0.053	0.258	0.429	0.266
<i>Syrphidae 3</i>	SYR3	-0.618	0.426	0.221	0.594	-0.667	0.532	-1.799	0.764	-0.092	0.242	0.540	0.237
<i>Syrphidae 4</i>	SYR4	-0.526	0.441	0.601	0.68	-0.498	0.552	-2.251	0.881	0.066	0.231	0.329	0.262
<i>Tachinidae 1</i>	TACH1	-0.626	0.457	0.128	0.723	-0.795	0.611	-2.541	1.052	0.059	0.231	0.333	0.273
<i>Tachinidae 3</i>	TACH3	-0.591	0.457	0.144	0.726	-0.804	0.615	-2.567	1.055	0.072	0.221	0.416	0.254
<i>Xeromelecta californica</i>	XECA	-0.379	0.437	0.331	0.722	-0.792	0.607	-2.492	1.035	-0.100	0.265	0.434	0.271
<b>Butterfly</b>													
Hesperiidae		-0.464	0.719	0.435	0.852	NA	NA	-3.261	1.296	0.677	0.352	0.089	0.400
Lycaenidae		0.799	0.739	2.082	0.829	NA	NA	-2.297	1.124	0.712	0.517	0.369	0.381
Nymphalidae		0.159	0.420	0.576	0.418	NA	NA	-1.380	0.753	0.146	0.185	0.247	0.193
Pieridae		0.776	0.456	1.872	0.534	NA	NA	-2.710	0.839	0.146	0.193	-0.190	0.194
<b>Hummingbird</b>		0.917	0.410	0.833	0.445	-0.225	0.684	-1.899	0.971	0.218	0.107	0.375	0.160

**Table B2.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from bumble bee community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response	Covariate	Mean	SD	2.50%	97.50%	Rhat
beta	Community	Intercept	-3.016	1.093	-5.446	-1.090	1.062
beta	Community	DSS	-0.075	0.224	-0.522	0.375	1.003
beta	Community	Floral richness	0.468	0.199	0.060	0.852	1.007
beta	Community	Floral abundance	-0.023	0.190	-0.439	0.319	1.006
beta	Community	Year	-0.354	0.870	-2.124	1.392	1.012
beta	Community	Elevation (m)	0.208	0.374	-0.490	0.990	1.021
beta	Community	Burn severity, meadow	-0.525	0.490	-1.676	0.323	1.005
beta	Community	Habitat, upland	-2.121	0.701	-3.693	-0.885	1.001
beta	Community	Burn (Upland-Meadow)	0.319	0.489	-0.655	1.228	1.004
beta	Community	Burn severity <sup>2</sup> , upland	-0.695	0.569	-1.864	0.347	1.011
delta	BOBI	Intercept	-2.106	1.726	-6.172	0.748	1.011
delta	BOFE	Intercept	-1.324	1.489	-4.618	1.492	1.014
delta	BOFL	Intercept	-1.176	1.480	-4.361	1.512	1.016
delta	BOMI	Intercept	-0.336	1.333	-3.039	2.271	1.021
delta	BOVA	Intercept	1.355	1.200	-0.918	3.938	1.039
delta	BOVO	Intercept	4.239	1.125	2.295	6.788	1.063
delta	BOIN	Intercept	-2.121	1.509	-5.345	0.647	1.013
delta	BOBI	DSS	0.022	0.346	-0.672	0.724	1.000
delta	BOFE	DSS	-0.069	0.311	-0.714	0.536	1.000
delta	BOFL	DSS	0.465	0.343	-0.119	1.229	1.001
delta	BOMI	DSS	-0.302	0.336	-1.040	0.293	1.000
delta	BOVA	DSS	-0.084	0.277	-0.648	0.452	1.001
delta	BOVO	DSS	-0.051	0.247	-0.557	0.434	1.003
delta	BOIN	DSS	0.028	0.306	-0.575	0.649	1.001
delta	BOBI	Floral richness	-0.187	0.314	-0.875	0.383	1.000
delta	BOFE	Floral richness	0.102	0.273	-0.419	0.678	1.001
delta	BOFL	Floral richness	-0.225	0.287	-0.845	0.292	1.001
delta	BOMI	Floral richness	0.127	0.284	-0.400	0.735	1.001
delta	BOVA	Floral richness	0.094	0.238	-0.369	0.585	1.004
delta	BOVO	Floral richness	0.178	0.216	-0.223	0.630	1.005
delta	BOIN	Floral richness	-0.115	0.281	-0.705	0.420	1.001
delta	BOBI	Floral abundance	-0.063	0.279	-0.639	0.477	1.001
delta	BOFE	Floral abundance	0.150	0.247	-0.305	0.685	1.003
delta	BOFL	Floral abundance	0.075	0.250	-0.405	0.595	1.002
delta	BOMI	Floral abundance	-0.087	0.277	-0.680	0.429	1.000
delta	BOVA	Floral abundance	-0.040	0.227	-0.486	0.420	1.002



**Table B2.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from bumble bee community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	BOVO	Floral abundance	0.150	0.221	-0.247	0.640	1.005
delta	BOIN	Floral abundance	-0.153	0.288	-0.792	0.361	1.000
delta	BOBI	Year	-1.627	1.183	-4.140	0.540	1.004
delta	BOFE	Year	1.140	1.005	-0.797	3.225	1.008
delta	BOFL	Year	0.552	1.006	-1.429	2.622	1.005
delta	BOMI	Year	-1.728	1.254	-4.463	0.474	1.006
delta	BOVA	Year	-0.451	0.961	-2.383	1.472	1.008
delta	BOVO	Year	-1.199	0.912	-3.060	0.624	1.012
delta	BOIN	Year	3.292	1.317	1.056	6.265	1.004
delta	BOBI	Elevation (m)	0.782	0.718	-0.348	2.371	1.002
delta	BOFE	Elevation (m)	-0.487	0.595	-1.832	0.489	1.005
delta	BOFL	Elevation (m)	-0.002	0.505	-1.061	1.011	1.003
delta	BOMI	Elevation (m)	0.030	0.499	-0.929	1.097	1.006
delta	BOVA	Elevation (m)	0.148	0.449	-0.728	1.086	1.007
delta	BOVO	Elevation (m)	-0.073	0.408	-0.941	0.700	1.019
delta	BOIN	Elevation (m)	-0.367	0.500	-1.465	0.525	1.011
delta	BOBI	Burn severity, meadow	-0.815	0.902	-2.954	0.525	1.005
delta	BOFE	Burn severity, meadow	0.238	0.607	-0.855	1.593	1.003
delta	BOFL	Burn severity, meadow	0.364	0.622	-0.733	1.769	1.002
delta	BOMI	Burn severity, meadow	-1.022	0.773	-2.757	0.227	1.001
delta	BOVA	Burn severity, meadow	0.887	0.627	-0.147	2.323	1.003
delta	BOVO	Burn severity, meadow	0.364	0.535	-0.550	1.616	1.017
delta	BOIN	Burn severity, meadow	0.124	0.594	-0.995	1.418	1.002
delta	BOBI	Habitat, upland	-0.424	1.067	-3.127	1.130	1.002
delta	BOFE	Habitat, upland	-0.261	0.831	-2.256	1.239	1.001
delta	BOFL	Habitat, upland	-0.283	0.866	-2.375	1.190	1.003
delta	BOMI	Habitat, upland	0.173	0.830	-1.450	2.067	1.001
delta	BOVA	Habitat, upland	0.656	0.871	-0.597	2.842	1.002
delta	BOVO	Habitat, upland	0.202	0.684	-0.977	1.943	1.003
delta	BOIN	Habitat, upland	-0.011	0.766	-1.570	1.647	1.001
delta	BOBI	Burn (Upland-Meadow)	0.125	0.705	-1.182	1.712	1.001
delta	BOFE	Burn (Upland-Meadow)	0.039	0.570	-1.076	1.272	1.001
delta	BOFL	Burn (Upland-Meadow)	0.294	0.636	-0.749	1.806	1.002
delta	BOMI	Burn (Upland-Meadow)	-0.458	0.750	-2.261	0.634	1.001
delta	BOVA	Burn (Upland-Meadow)	-0.099	0.537	-1.196	0.960	1.002
delta	BOVO	Burn (Upland-Meadow)	0.286	0.500	-0.588	1.376	1.011

**Table B2.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from bumble bee community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	BOIN	Burn (Upland-Meadow)	-0.140	0.602	-1.465	0.988	1.001
delta	BOBI	Burn severity <sup>2</sup> , upland	-0.375	0.996	-2.844	1.082	1.009
delta	BOFE	Burn severity <sup>2</sup> , upland	0.176	0.692	-1.131	1.731	1.003
delta	BOFL	Burn severity <sup>2</sup> , upland	0.606	0.789	-0.559	2.591	1.001
delta	BOMI	Burn severity <sup>2</sup> , upland	0.145	0.734	-1.314	1.764	1.003
delta	BOVA	Burn severity <sup>2</sup> , upland	-0.085	0.616	-1.381	1.155	1.012
delta	BOVO	Burn severity <sup>2</sup> , upland	0.114	0.572	-0.926	1.351	1.013
delta	BOIN	Burn severity <sup>2</sup> , upland	-0.707	0.905	-3.037	0.487	1.009
sigma	Community	Intercept	2.776	1.087	1.387	5.497	1.003
sigma	Community	DSS	0.436	0.203	0.187	0.945	1.001
sigma	Community	Floral richness	0.377	0.169	0.172	0.803	1.002
sigma	Community	Floral abundance	0.347	0.155	0.163	0.739	1.002
sigma	Community	Year	2.157	0.912	0.966	4.438	1.006
sigma	Community	Elevation (m)	0.680	0.389	0.215	1.661	1.005
sigma	Community	Burn severity, meadow	0.954	0.533	0.280	2.297	1.002
sigma	Community	Habitat, upland	0.863	0.650	0.220	2.575	1.003
sigma	Community	Burn (Upland-Meadow)	0.663	0.446	0.208	1.804	1.003
sigma	Community	Burn severity <sup>2</sup> , upland	0.818	0.613	0.218	2.428	1.015
sigma	BOBI	Model	1.701	1.363	0.067	5.160	1.002
sigma	BOFE	Model	2.354	1.083	0.737	4.922	1.001
sigma	BOFL	Model	2.587	0.984	1.119	4.945	1.004
sigma	BOMI	Model	1.998	1.068	0.349	4.573	1.019
sigma	BOVA	Model	1.434	0.541	0.546	2.673	1.001
sigma	BOVO	Model	1.063	0.268	0.613	1.662	1.000
sigma	BOIN	Model	1.091	0.787	0.043	2.966	1.003
BP, species	BOBI	Model	0.599	0.490	0.000	1.000	1.000
BP, species	BOFE	Model	0.379	0.485	0.000	1.000	1.000
BP, species	BOFL	Model	0.363	0.481	0.000	1.000	1.000
BP, species	BOMI	Model	0.369	0.482	0.000	1.000	1.000
BP, species	BOVA	Model	0.310	0.462	0.000	1.000	1.000
BP, species	BOVO	Model	0.500	0.500	0.000	1.000	1.000
BP, species	BOIN	Model	0.516	0.500	0.000	1.000	1.000
BP, community	Community	Model	0.353	0.478	0.000	1.000	1.000
r	Community	Model	0.312	0.041	0.240	0.401	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
beta	Community	Intercept	-4.061	0.353	-4.787	-3.416	1.002
beta	Community	DSS	-0.585	0.180	-0.948	-0.236	1.001
beta	Community	Floral richness	0.000	0.105	-0.223	0.192	1.000
beta	Community	Floral abundance	0.389	0.117	0.159	0.616	1.000
beta	Community	Elevation (m)	0.071	0.135	-0.197	0.333	1.000
beta	Community	Burn severity, meadow	-0.551	0.259	-1.075	-0.056	1.000
beta	Community	Habitat, upland	-2.028	0.474	-3.055	-1.186	1.002
beta	Community	Burn (Upland-Meadow)	0.749	0.344	0.081	1.432	1.001
beta	Community	Burn severity2, upland	-0.628	0.319	-1.261	-0.002	1.000
delta	ANSA	Intercept	-0.382	0.884	-2.322	1.183	1.004
delta	CERAM	Intercept	-0.525	0.828	-2.281	0.979	1.000
delta	LAAN	Intercept	-0.575	0.852	-2.418	0.949	1.000
delta	LAOL	Intercept	0.208	0.829	-1.608	1.695	1.001
delta	LECH	Intercept	-0.495	0.843	-2.324	1.016	1.001
delta	SYR3	Intercept	0.750	0.757	-0.846	2.136	1.002
delta	TACH3	Intercept	-0.547	0.853	-2.397	0.984	1.000
delta	ANUR	Intercept	1.504	0.828	-0.161	3.035	1.001
delta	APME	Intercept	2.740	0.862	0.803	4.283	1.005
delta	XECA	Intercept	0.091	0.788	-1.573	1.542	1.000
delta	LYGUS	Intercept	-0.223	0.883	-2.114	1.370	1.003
delta	ORSU	Intercept	-0.212	0.792	-1.897	1.247	1.003
delta	SYR4	Intercept	0.148	0.826	-1.673	1.623	1.003
delta	Bomb4	Intercept	-0.333	0.851	-2.188	1.184	1.000
delta	MEAN	Intercept	0.091	0.770	-1.530	1.529	1.002
delta	LADI	Intercept	1.989	0.711	0.422	3.276	1.002
delta	MEMI	Intercept	-0.034	0.794	-1.742	1.414	1.000
delta	HACO	Intercept	1.126	0.796	-0.534	2.581	1.002
delta	MORD1	Intercept	-0.348	0.880	-2.251	1.239	1.000
delta	LASI2	Intercept	-0.436	0.822	-2.183	1.068	1.001
delta	TACH1	Intercept	-0.143	0.803	-1.858	1.334	1.001
delta	CAED	Intercept	-0.209	0.930	-2.236	1.459	1.000
delta	HALI	Intercept	-0.403	0.857	-2.290	1.124	1.001

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	HYEP	Intercept	-0.656	0.976	-2.815	1.048	1.000
delta	CRAB1	Intercept	-0.364	0.852	-2.228	1.154	1.000
delta	OSMO	Intercept	-0.614	0.844	-2.425	0.922	1.000
delta	Bomb6	Intercept	-0.604	0.887	-2.552	0.960	1.001
delta	PODAL	Intercept	-0.168	0.783	-1.835	1.263	1.000
delta	OSCO	Intercept	-0.517	0.856	-2.366	1.025	1.001
delta	GERON	Intercept	-0.975	0.945	-3.053	0.649	1.000
delta	ANSA	DSS	-0.939	0.516	-2.049	-0.025	1.000
delta	CERAM	DSS	-0.684	0.522	-1.801	0.251	1.000
delta	LAAN	DSS	-0.536	0.506	-1.603	0.399	1.000
delta	LAOL	DSS	-0.880	0.467	-1.869	-0.043	1.000
delta	LECH	DSS	-0.565	0.513	-1.648	0.367	1.000
delta	SYR3	DSS	0.341	0.377	-0.384	1.102	1.000
delta	TACH3	DSS	-0.663	0.520	-1.766	0.284	1.000
delta	ANUR	DSS	0.818	0.336	0.183	1.498	1.001
delta	APME	DSS	0.504	0.278	-0.032	1.052	1.001
delta	XECA	DSS	0.916	0.519	-0.022	2.007	1.000
delta	LYGUS	DSS	-0.307	0.465	-1.264	0.569	1.000
delta	ORSU	DSS	-0.462	0.495	-1.495	0.453	1.000
delta	SYR4	DSS	-0.066	0.444	-0.956	0.789	1.000
delta	Bomb4	DSS	0.130	0.472	-0.800	1.067	1.000
delta	MEAN	DSS	0.339	0.451	-0.523	1.255	1.000
delta	LADI	DSS	0.086	0.314	-0.532	0.702	1.000
delta	MEMI	DSS	0.164	0.490	-0.794	1.144	1.000
delta	HACO	DSS	0.219	0.382	-0.530	0.980	1.000
delta	MORD1	DSS	-0.066	0.469	-1.009	0.839	1.000
delta	LASI2	DSS	-0.432	0.517	-1.517	0.520	1.000
delta	TACH1	DSS	0.052	0.492	-0.929	1.016	1.000
delta	CAED	DSS	-0.087	0.415	-0.917	0.717	1.000
delta	HALI	DSS	0.473	0.494	-0.459	1.484	1.000
delta	HYEP	DSS	0.769	0.570	-0.264	1.980	1.000
delta	CRAB1	DSS	0.545	0.505	-0.396	1.597	1.000
delta	OSMO	DSS	-0.602	0.542	-1.746	0.384	1.000
delta	Bomb6	DSS	0.021	0.527	-1.027	1.062	1.000
delta	PODAL	DSS	1.044	0.535	0.084	2.179	1.000
delta	OSCO	DSS	-0.345	0.514	-1.408	0.615	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	GERON	DSS	0.142	0.556	-0.942	1.260	1.000
delta	ANSA	Floral abundance	-0.060	0.228	-0.539	0.370	1.000
delta	CERAM	Floral abundance	0.042	0.215	-0.381	0.475	1.000
delta	LAAN	Floral abundance	-0.117	0.235	-0.630	0.308	1.000
delta	LAOL	Floral abundance	0.019	0.201	-0.375	0.426	1.000
delta	LECH	Floral abundance	-0.108	0.237	-0.620	0.326	1.000
delta	SYR3	Floral abundance	-0.092	0.221	-0.562	0.318	1.000
delta	TACH3	Floral abundance	0.072	0.212	-0.337	0.504	1.000
delta	ANUR	Floral abundance	0.094	0.199	-0.287	0.503	1.000
delta	APME	Floral abundance	0.141	0.142	-0.112	0.449	1.000
delta	XECA	Floral abundance	-0.100	0.239	-0.615	0.335	1.000
delta	LYGUS	Floral abundance	-0.013	0.217	-0.457	0.408	1.000
delta	ORSU	Floral abundance	-0.009	0.218	-0.454	0.417	1.000
delta	SYR4	Floral abundance	0.066	0.221	-0.368	0.514	1.000
delta	Bomb4	Floral abundance	0.047	0.221	-0.390	0.490	1.000
delta	MEAN	Floral abundance	-0.042	0.223	-0.510	0.378	1.000
delta	LADI	Floral abundance	0.020	0.192	-0.359	0.403	1.000
delta	MEMI	Floral abundance	-0.012	0.229	-0.480	0.433	1.000
delta	HACO	Floral abundance	-0.065	0.217	-0.521	0.343	1.000
delta	MORD1	Floral abundance	-0.049	0.214	-0.498	0.359	1.000
delta	LASI2	Floral abundance	0.002	0.215	-0.433	0.420	1.000
delta	TACH1	Floral abundance	0.059	0.219	-0.370	0.499	1.000
delta	CAED	Floral abundance	0.018	0.213	-0.410	0.438	1.000
delta	HALI	Floral abundance	0.253	0.179	-0.072	0.630	1.000
delta	HYEP	Floral abundance	-0.064	0.242	-0.574	0.394	1.000
delta	CRAB1	Floral abundance	-0.076	0.238	-0.582	0.367	1.000
delta	OSMO	Floral abundance	0.078	0.218	-0.345	0.523	1.000
delta	Bomb6	Floral abundance	-0.019	0.232	-0.493	0.430	1.000
delta	PODAL	Floral abundance	-0.053	0.235	-0.548	0.390	1.000
delta	OSCO	Floral abundance	0.017	0.217	-0.420	0.449	1.000
delta	GERON	Floral abundance	-0.041	0.237	-0.535	0.408	1.000
delta	ANSA	Floral richness	-0.121	0.251	-0.654	0.348	1.000
delta	CERAM	Floral richness	-0.068	0.249	-0.584	0.408	1.000
delta	LAAN	Floral richness	-0.106	0.248	-0.633	0.358	1.000
delta	LAOL	Floral richness	-0.112	0.233	-0.594	0.332	1.000
delta	LECH	Floral richness	-0.076	0.242	-0.575	0.391	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	SYR3	Floral richness	0.150	0.228	-0.272	0.629	1.000
delta	TACH3	Floral richness	0.027	0.238	-0.441	0.508	1.000
delta	ANUR	Floral richness	-0.023	0.209	-0.437	0.393	1.000
delta	APME	Floral richness	0.274	0.198	-0.084	0.691	1.000
delta	XECA	Floral richness	0.045	0.253	-0.448	0.564	1.000
delta	LYGUS	Floral richness	-0.101	0.243	-0.610	0.357	1.000
delta	ORSU	Floral richness	0.026	0.242	-0.447	0.515	1.000
delta	SYR4	Floral richness	-0.061	0.243	-0.561	0.407	1.000
delta	Bomb4	Floral richness	0.052	0.234	-0.404	0.531	1.000
delta	MEAN	Floral richness	0.093	0.235	-0.355	0.582	1.000
delta	LADI	Floral richness	0.112	0.200	-0.265	0.527	1.000
delta	MEMI	Floral richness	0.027	0.250	-0.465	0.534	1.000
delta	HACO	Floral richness	0.104	0.230	-0.331	0.585	1.000
delta	MORD1	Floral richness	0.172	0.244	-0.273	0.695	1.000
delta	LASI2	Floral richness	-0.066	0.248	-0.580	0.413	1.000
delta	TACH1	Floral richness	-0.056	0.252	-0.578	0.433	1.000
delta	CAED	Floral richness	-0.068	0.248	-0.578	0.410	1.000
delta	HALI	Floral richness	-0.083	0.249	-0.604	0.395	1.000
delta	HYEP	Floral richness	-0.059	0.263	-0.604	0.450	1.000
delta	CRAB1	Floral richness	-0.032	0.251	-0.543	0.463	1.000
delta	OSMO	Floral richness	0.041	0.250	-0.448	0.552	1.000
delta	Bomb6	Floral richness	-0.019	0.248	-0.519	0.474	1.000
delta	PODAL	Floral richness	0.040	0.249	-0.448	0.548	1.000
delta	OSCO	Floral richness	-0.026	0.247	-0.525	0.458	1.000
delta	GERON	Floral richness	-0.059	0.261	-0.599	0.444	1.000
delta	ANSA	Elevation (m)	-0.079	0.321	-0.742	0.546	1.000
delta	CERAM	Elevation (m)	-0.139	0.339	-0.868	0.492	1.000
delta	LAAN	Elevation (m)	0.024	0.319	-0.605	0.674	1.000
delta	LAOL	Elevation (m)	0.283	0.309	-0.275	0.944	1.000
delta	LECH	Elevation (m)	0.121	0.315	-0.476	0.782	1.000
delta	SYR3	Elevation (m)	0.145	0.280	-0.385	0.730	1.000
delta	TACH3	Elevation (m)	-0.033	0.316	-0.678	0.592	1.000
delta	ANUR	Elevation (m)	0.310	0.273	-0.185	0.884	1.001
delta	APME	Elevation (m)	-0.211	0.221	-0.658	0.215	1.000
delta	XECA	Elevation (m)	-0.212	0.337	-0.949	0.399	1.000
delta	LYGUS	Elevation (m)	-0.141	0.325	-0.830	0.472	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	ORSU	Elevation (m)	0.030	0.314	-0.588	0.668	1.000
delta	SYR4	Elevation (m)	0.260	0.303	-0.290	0.904	1.000
delta	Bomb4	Elevation (m)	0.000	0.316	-0.636	0.630	1.000
delta	MEAN	Elevation (m)	-0.024	0.309	-0.650	0.589	1.000
delta	LADI	Elevation (m)	0.005	0.240	-0.472	0.481	1.000
delta	MEMI	Elevation (m)	-0.092	0.321	-0.763	0.525	1.000
delta	HACO	Elevation (m)	-0.345	0.330	-1.056	0.246	1.001
delta	MORD1	Elevation (m)	0.193	0.323	-0.395	0.899	1.000
delta	LASI2	Elevation (m)	0.158	0.325	-0.450	0.848	1.000
delta	TACH1	Elevation (m)	0.094	0.325	-0.529	0.778	1.000
delta	CAED	Elevation (m)	0.354	0.356	-0.254	1.149	1.003
delta	HALI	Elevation (m)	0.098	0.320	-0.513	0.769	1.000
delta	HYEP	Elevation (m)	-0.012	0.341	-0.703	0.674	1.000
delta	CRAB1	Elevation (m)	-0.204	0.350	-0.970	0.432	1.000
delta	OSMO	Elevation (m)	-0.067	0.336	-0.766	0.587	1.000
delta	Bomb6	Elevation (m)	-0.164	0.351	-0.920	0.482	1.000
delta	PODAL	Elevation (m)	-0.204	0.344	-0.958	0.421	1.000
delta	OSCO	Elevation (m)	-0.027	0.330	-0.695	0.631	1.000
delta	GERON	Elevation (m)	-0.106	0.345	-0.837	0.552	1.000
delta	ANSA	Burn severity, meadow	-0.194	0.401	-1.102	0.519	1.000
delta	CERAM	Burn severity, meadow	-0.065	0.388	-0.879	0.697	1.000
delta	LAAN	Burn severity, meadow	-0.218	0.410	-1.159	0.491	1.000
delta	LAOL	Burn severity, meadow	-0.112	0.379	-0.939	0.602	1.000
delta	LECH	Burn severity, meadow	-0.056	0.390	-0.885	0.702	1.000
delta	SYR3	Burn severity, meadow	-0.067	0.358	-0.816	0.638	1.000
delta	TACH3	Burn severity, meadow	-0.040	0.387	-0.850	0.723	1.000
delta	ANUR	Burn severity, meadow	-0.039	0.343	-0.745	0.647	1.000
delta	APME	Burn severity, meadow	0.162	0.328	-0.446	0.864	1.001
delta	XECA	Burn severity, meadow	0.171	0.386	-0.526	1.030	1.000
delta	LYGUS	Burn severity, meadow	0.042	0.373	-0.696	0.822	1.000
delta	ORSU	Burn severity, meadow	-0.062	0.368	-0.842	0.655	1.000
delta	SYR4	Burn severity, meadow	0.025	0.374	-0.713	0.804	1.000
delta	Bomb4	Burn severity, meadow	-0.129	0.379	-0.953	0.578	1.000
delta	MEAN	Burn severity, meadow	0.115	0.372	-0.583	0.924	1.000
delta	LADI	Burn severity, meadow	0.035	0.332	-0.622	0.719	1.000
delta	MEMI	Burn severity, meadow	0.057	0.377	-0.680	0.852	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	HACO	Burn severity, meadow	0.141	0.352	-0.516	0.900	1.000
delta	MORD1	Burn severity, meadow	-0.144	0.389	-1.005	0.577	1.000
delta	LASI2	Burn severity, meadow	-0.099	0.391	-0.952	0.640	1.000
delta	TACH1	Burn severity, meadow	-0.075	0.385	-0.904	0.671	1.000
delta	CAED	Burn severity, meadow	-0.191	0.405	-1.112	0.526	1.000
delta	HALI	Burn severity, meadow	-0.019	0.375	-0.790	0.735	1.000
delta	HYEP	Burn severity, meadow	0.056	0.382	-0.696	0.862	1.000
delta	CRAB1	Burn severity, meadow	0.222	0.400	-0.474	1.131	1.000
delta	OSMO	Burn severity, meadow	-0.058	0.386	-0.878	0.693	1.000
delta	Bomb6	Burn severity, meadow	0.268	0.418	-0.436	1.244	1.000
delta	PODAL	Burn severity, meadow	0.304	0.414	-0.388	1.269	1.000
delta	OSCO	Burn severity, meadow	0.110	0.382	-0.611	0.940	1.000
delta	GERON	Burn severity, meadow	-0.110	0.400	-0.984	0.635	1.000
delta	ANSA	Habitat, upland	-0.303	0.782	-2.067	1.115	1.000
delta	CERAM	Habitat, upland	-0.511	0.881	-2.618	0.934	1.000
delta	LAAN	Habitat, upland	0.124	0.787	-1.473	1.792	1.000
delta	LAOL	Habitat, upland	-0.794	0.922	-3.017	0.570	1.000
delta	LECH	Habitat, upland	-0.500	0.885	-2.609	0.945	1.000
delta	SYR3	Habitat, upland	0.229	0.718	-1.128	1.803	1.000
delta	TACH3	Habitat, upland	-0.539	0.891	-2.670	0.888	1.001
delta	ANUR	Habitat, upland	0.685	0.825	-0.679	2.564	1.001
delta	APME	Habitat, upland	0.870	0.777	-0.365	2.626	1.001
delta	XECA	Habitat, upland	-0.464	0.878	-2.561	0.990	1.000
delta	LYGUS	Habitat, upland	0.087	0.806	-1.583	1.758	1.001
delta	ORSU	Habitat, upland	0.095	0.768	-1.456	1.728	1.001
delta	SYR4	Habitat, upland	-0.223	0.761	-1.907	1.219	1.000
delta	Bomb4	Habitat, upland	0.438	0.818	-0.996	2.309	1.001
delta	MEAN	Habitat, upland	0.673	0.869	-0.735	2.685	1.000
delta	LADI	Habitat, upland	0.666	0.721	-0.508	2.295	1.001
delta	MEMI	Habitat, upland	-0.497	0.892	-2.627	0.952	1.000
delta	HACO	Habitat, upland	0.304	0.742	-1.068	1.952	1.001
delta	MORD1	Habitat, upland	0.078	0.827	-1.621	1.801	1.000
delta	LASI2	Habitat, upland	-0.121	0.775	-1.804	1.399	1.000
delta	TACH1	Habitat, upland	-0.513	0.886	-2.629	0.938	1.000
delta	CAED	Habitat, upland	-0.407	0.819	-2.302	1.012	1.000
delta	HALI	Habitat, upland	0.366	0.818	-1.118	2.224	1.000



**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	HYEP	Habitat, upland	-0.159	0.848	-2.038	1.481	1.000
delta	CRAB1	Habitat, upland	0.187	0.794	-1.354	1.921	1.000
delta	OSMO	Habitat, upland	-0.118	0.785	-1.833	1.409	1.000
delta	Bomb6	Habitat, upland	-0.034	0.788	-1.700	1.567	1.000
delta	PODAL	Habitat, upland	0.138	0.772	-1.383	1.787	1.000
delta	OSCO	Habitat, upland	0.262	0.791	-1.233	2.009	1.000
delta	GERON	Habitat, upland	0.044	0.834	-1.687	1.780	1.000
delta	ANSA	Burn (Upland-Meadow)	-0.196	0.592	-1.525	0.901	1.000
delta	CERAM	Burn (Upland-Meadow)	0.001	0.603	-1.232	1.256	1.000
delta	LAAN	Burn (Upland-Meadow)	-0.532	0.672	-2.141	0.514	1.000
delta	LAOL	Burn (Upland-Meadow)	0.040	0.586	-1.144	1.265	1.000
delta	LECH	Burn (Upland-Meadow)	0.008	0.608	-1.243	1.271	1.000
delta	SYR3	Burn (Upland-Meadow)	0.089	0.532	-0.956	1.223	1.000
delta	TACH3	Burn (Upland-Meadow)	-0.015	0.611	-1.281	1.238	1.000
delta	ANUR	Burn (Upland-Meadow)	-0.467	0.510	-1.593	0.413	1.000
delta	APME	Burn (Upland-Meadow)	0.180	0.413	-0.606	1.055	1.001
delta	XECA	Burn (Upland-Meadow)	-0.039	0.610	-1.328	1.186	1.000
delta	LYGUS	Burn (Upland-Meadow)	0.325	0.585	-0.707	1.641	1.000
delta	ORSU	Burn (Upland-Meadow)	0.080	0.544	-0.986	1.233	1.000
delta	SYR4	Burn (Upland-Meadow)	0.377	0.614	-0.664	1.810	1.000
delta	Bomb4	Burn (Upland-Meadow)	-0.253	0.559	-1.499	0.761	1.000
delta	MEAN	Burn (Upland-Meadow)	0.403	0.569	-0.555	1.692	1.000
delta	LADI	Burn (Upland-Meadow)	0.430	0.487	-0.413	1.504	1.000
delta	MEMI	Burn (Upland-Meadow)	-0.010	0.606	-1.273	1.236	1.000
delta	HACO	Burn (Upland-Meadow)	-0.417	0.568	-1.700	0.554	1.000
delta	MORD1	Burn (Upland-Meadow)	-0.596	0.678	-2.226	0.453	1.000
delta	LASI2	Burn (Upland-Meadow)	-0.295	0.624	-1.731	0.796	1.000
delta	TACH1	Burn (Upland-Meadow)	0.005	0.607	-1.253	1.257	1.000
delta	CAED	Burn (Upland-Meadow)	-0.110	0.587	-1.380	1.021	1.000
delta	HALI	Burn (Upland-Meadow)	-0.016	0.549	-1.135	1.113	1.000
delta	HYEP	Burn (Upland-Meadow)	-0.117	0.611	-1.445	1.073	1.000
delta	CRAB1	Burn (Upland-Meadow)	0.509	0.649	-0.528	2.053	1.000
delta	OSMO	Burn (Upland-Meadow)	-0.054	0.591	-1.297	1.129	1.000
delta	Bomb6	Burn (Upland-Meadow)	0.311	0.621	-0.763	1.746	1.000
delta	PODAL	Burn (Upland-Meadow)	0.486	0.642	-0.542	2.013	1.000
delta	OSCO	Burn (Upland-Meadow)	0.206	0.570	-0.851	1.479	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	GERON	Burn (Upland-Meadow)	-0.307	0.649	-1.824	0.819	1.000
delta	ANSA	Burn severity2, upland	-0.148	0.500	-1.282	0.763	1.000
delta	CERAM	Burn severity2, upland	-0.162	0.517	-1.344	0.764	1.000
delta	LAAN	Burn severity2, upland	0.200	0.498	-0.692	1.345	1.000
delta	LAOL	Burn severity2, upland	-0.248	0.532	-1.506	0.647	1.000
delta	LECH	Burn severity2, upland	-0.160	0.518	-1.348	0.769	1.000
delta	SYR3	Burn severity2, upland	-0.039	0.453	-0.999	0.863	1.000
delta	TACH3	Burn severity2, upland	-0.176	0.521	-1.383	0.749	1.001
delta	ANUR	Burn severity2, upland	-0.218	0.453	-1.244	0.583	1.001
delta	APME	Burn severity2, upland	0.099	0.368	-0.615	0.874	1.001
delta	XECA	Burn severity2, upland	-0.164	0.513	-1.341	0.761	1.000
delta	LYGUS	Burn severity2, upland	0.135	0.471	-0.752	1.169	1.000
delta	ORSU	Burn severity2, upland	0.107	0.470	-0.799	1.135	1.000
delta	SYR4	Burn severity2, upland	0.130	0.471	-0.754	1.174	1.000
delta	Bomb4	Burn severity2, upland	0.189	0.492	-0.694	1.327	1.000
delta	MEAN	Burn severity2, upland	0.148	0.457	-0.706	1.160	1.000
delta	LADI	Burn severity2, upland	-0.065	0.392	-0.884	0.708	1.000
delta	MEMI	Burn severity2, upland	-0.166	0.519	-1.359	0.761	1.000
delta	HACO	Burn severity2, upland	-0.139	0.452	-1.146	0.695	1.000
delta	MORD1	Burn severity2, upland	0.100	0.482	-0.832	1.151	1.000
delta	LASI2	Burn severity2, upland	0.026	0.484	-0.959	1.038	1.000
delta	TACH1	Burn severity2, upland	-0.167	0.514	-1.348	0.758	1.000
delta	CAED	Burn severity2, upland	-0.152	0.501	-1.287	0.762	1.000
delta	HALI	Burn severity2, upland	0.316	0.513	-0.535	1.539	1.001
delta	HYEP	Burn severity2, upland	-0.189	0.516	-1.384	0.715	1.000
delta	CRAB1	Burn severity2, upland	0.278	0.498	-0.572	1.452	1.000
delta	OSMO	Burn severity2, upland	-0.223	0.520	-1.453	0.662	1.000
delta	Bomb6	Burn severity2, upland	0.129	0.480	-0.774	1.200	1.000
delta	PODAL	Burn severity2, upland	0.324	0.498	-0.510	1.492	1.000
delta	OSCO	Burn severity2, upland	0.143	0.474	-0.741	1.197	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
delta	GERON	Burn severity2, upland	0.058	0.498	-0.927	1.130	1.000
sigma	Community	Intercept	1.176	0.307	0.606	1.833	1.002
sigma	Community	DSS	0.720	0.184	0.404	1.123	1.000
sigma	Community	Burn severity, meadow	0.244	0.069	0.142	0.407	1.000
sigma	Community	Elevation (m)	0.270	0.076	0.154	0.446	1.000
sigma	Community	Burn (Upland-Meadow)	0.365	0.116	0.184	0.631	1.002
sigma	Community	Burn severity2, upland	0.396	0.156	0.180	0.773	1.000
sigma	Community	Habitat, upland	0.855	0.416	0.256	1.831	1.001
sigma	Community	Floral abundance	0.627	0.279	0.224	1.280	1.001
sigma	Community	Floral richness	0.490	0.226	0.194	1.051	1.001
sigma	ANSA	Model	1.415	1.083	0.067	4.087	1.005
sigma	CERAM	Model	0.808	0.695	0.033	2.598	1.003
sigma	LAAN	Model	1.232	0.998	0.037	3.731	1.001
sigma	LAOL	Model	0.983	0.844	0.030	3.114	1.003
sigma	LECH	Model	0.962	0.823	0.029	3.031	1.002
sigma	SYR3	Model	0.989	0.782	0.043	2.903	1.005
sigma	TACH3	Model	0.958	0.822	0.036	3.061	1.002
sigma	ANUR	Model	1.862	0.895	0.542	4.035	1.001
sigma	APME	Model	1.585	0.627	0.677	3.124	1.003
sigma	XECA	Model	1.066	0.847	0.048	3.152	1.002
sigma	LYGUS	Model	2.034	1.156	0.264	4.807	1.003
sigma	ORSU	Model	1.094	0.902	0.057	3.324	1.019
sigma	SYR4	Model	1.063	0.880	0.035	3.307	1.006
sigma	Bomb4	Model	1.455	1.044	0.083	3.960	1.002
sigma	MEAN	Model	1.193	0.972	0.046	3.688	1.010
sigma	LADI	Model	0.747	0.618	0.037	2.341	1.004
sigma	MEMI	Model	1.015	0.843	0.042	3.147	1.001
sigma	HACO	Model	1.510	1.013	0.055	3.865	1.007
sigma	MORD1	Model	2.128	1.128	0.369	4.807	1.000
sigma	LASI2	Model	1.081	0.888	0.044	3.307	1.009
sigma	TACH1	Model	1.110	0.886	0.050	3.320	1.004
sigma	CAED	Model	2.013	1.159	0.206	4.776	1.003
sigma	HALI	Model	1.584	1.106	0.075	4.187	1.005
sigma	HYEP	Model	2.589	1.396	0.329	5.914	1.003
sigma	CRAB1	Model	1.409	1.116	0.064	4.152	1.007
sigma	OSMO	Model	1.101	0.897	0.048	3.380	1.001

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
sigma	Bomb6	Model	1.336	1.073	0.054	3.987	1.002
sigma	PODAL	Model	1.126	0.899	0.046	3.343	1.000
sigma	OSCO	Model	1.320	1.008	0.056	3.712	1.002
sigma	GERON	Model	1.580	1.259	0.049	4.692	1.001
BP, species	ANSA	Model	0.559	0.497	0.000	1.000	1.000
BP, species	CERAM	Model	0.629	0.483	0.000	1.000	1.000
BP, species	LAAN	Model	0.434	0.496	0.000	1.000	1.000
BP, species	LAOL	Model	0.606	0.489	0.000	1.000	1.000
BP, species	LECH	Model	0.601	0.490	0.000	1.000	1.000
BP, species	SYR3	Model	0.350	0.477	0.000	1.000	1.000
BP, species	TACH3	Model	0.640	0.480	0.000	1.000	1.000
BP, species	ANUR	Model	0.389	0.487	0.000	1.000	1.000
BP, species	APME	Model	0.403	0.491	0.000	1.000	1.000
BP, species	XECA	Model	0.435	0.496	0.000	1.000	1.000
BP, species	LYGUS	Model	0.385	0.487	0.000	1.000	1.000
BP, species	ORSU	Model	0.391	0.488	0.000	1.000	1.000
BP, species	SYR4	Model	0.377	0.485	0.000	1.000	1.000
BP, species	Bomb4	Model	0.294	0.456	0.000	1.000	1.000
BP, species	MEAN	Model	0.315	0.464	0.000	1.000	1.000
BP, species	LADI	Model	0.347	0.476	0.000	1.000	1.000
BP, species	MEMI	Model	0.411	0.492	0.000	1.000	1.000
BP, species	HACO	Model	0.353	0.478	0.000	1.000	1.000
BP, species	MORD1	Model	0.443	0.497	0.000	1.000	1.000
BP, species	LASI2	Model	0.399	0.490	0.000	1.000	1.000
BP, species	TACH1	Model	0.456	0.498	0.000	1.000	1.000
BP, species	CAED	Model	0.504	0.500	0.000	1.000	1.000
BP, species	HALI	Model	0.297	0.457	0.000	1.000	1.000
BP, species	HYEP	Model	0.477	0.499	0.000	1.000	1.000
BP, species	CRAB1	Model	0.362	0.481	0.000	1.000	1.000
BP, species	OSMO	Model	0.578	0.494	0.000	1.000	1.000
BP, species	Bomb6	Model	0.362	0.480	0.000	1.000	1.000
BP, species	PODAL	Model	0.418	0.493	0.000	1.000	1.000
BP, species	OSCO	Model	0.345	0.476	0.000	1.000	1.000
BP, species	GERON	Model	0.374	0.484	0.000	1.000	1.000
BP, community	Community	Model	0.243	0.429	0.000	1.000	1.000

**Table B3.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from insect community negative binomial generalized linear mixed model. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. Beta shows the community-level response to the covariate, delta indicates the deviation of the species from the community response. Values reported in text for species-level response were derived from actual MCMC chains. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt. See Table A3 for species code interpretation.

Parameter	Response variable	Covariate	Mean	SD	2.50%	97.50%	Rhat
r	Community	Model	0.308	0.069	0.203	0.469	1.014

**Table B4.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from butterfly negative binomial generalized linear mixed models (separate model fit for each family). Data were collected in 2016 in the Sierra Nevada, California, following the 2014 King Fire. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt.

Taxa	Parameter	Mean	SD	2.50%	97.50%	Rhat
Pieridae	Intercept	-0.086	0.525	-1.194	0.941	1.004
Pieridae	DSS	-1.007	0.212	-1.437	-0.602	1.000
Pieridae	Floral richness	-0.190	0.194	-0.566	0.198	1.001
Pieridae	Floral abundance	0.146	0.193	-0.230	0.529	1.001
Pieridae	Elevation (m)	-0.514	0.409	-1.383	0.263	1.001
Pieridae	Burn severity in meadow	0.776	0.456	-0.146	1.658	1.004
Pieridae	Habitat, upland	-2.710	0.839	-4.501	-1.148	1.004
Pieridae	Burn (Upland-Meadow)	1.105	0.721	-0.231	2.608	1.003
Pieridae	sigma	1.068	0.430	0.415	2.092	1.002
Pieridae	BP	0.406	0.491	0.000	1.000	1.000
Pieridae	r	0.586	0.149	0.349	0.930	1.000
Hesperiidae	Intercept	-1.981	0.685	-3.429	-0.717	1.009
Hesperiidae	DSS	-0.958	0.494	-2.062	-0.128	1.001
Hesperiidae	Floral richness	0.089	0.400	-0.702	0.893	1.001
Hesperiidae	Floral abundance	0.677	0.352	0.036	1.421	1.001
Hesperiidae	Elevation (m)	-1.122	0.603	-2.338	0.055	1.004
Hesperiidae	Burn severity in meadow	-0.464	0.719	-1.635	1.346	1.002
Hesperiidae	Habitat, upland	-3.261	1.296	-6.208	-1.163	1.006
Hesperiidae	Burn (Upland-Meadow)	0.890	1.208	-1.930	3.033	1.000
Hesperiidae	sigma	0.823	0.979	0.022	3.517	1.004
Hesperiidae	BP	0.356	0.479	0.000	1.000	1.001
Hesperiidae	r	1.288	8.094	0.111	1.931	1.128
Nymphalidae	Intercept	-0.434	0.535	-1.471	0.627	1.001
Nymphalidae	DSS	-0.283	0.175	-0.631	0.060	1.000
Nymphalidae	Floral richness	0.247	0.193	-0.120	0.636	1.001
Nymphalidae	Floral abundance	0.146	0.185	-0.207	0.522	1.000

**Table B4.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from butterfly negative binomial generalized linear mixed models (separate model fit for each family). Data were collected in 2016 in the Sierra Nevada, California, following the 2014 King Fire. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt.

Taxa	Parameter	Mean	SD	2.50%	97.50%	Rhat
Nymphalidae	Elevation (m)	-0.995	0.403	-1.850	-0.251	1.002
Nymphalidae	Burn severity in meadow	0.159	0.420	-0.686	0.982	1.003
Nymphalidae	Habitat (Upland-Meadow)	-1.380	0.753	-2.914	0.037	1.001
Nymphalidae	Burn (Upland-Meadow)	0.417	0.586	-0.765	1.562	1.002
Nymphalidae	sigma	1.024	0.377	0.476	1.943	1.001
Nymphalidae	BP	0.378	0.485	0.000	1.000	1.000
Nymphalidae	r	0.535	0.153	0.303	0.898	1.001
Lycaeniidae	Intercept	-1.438	0.626	-2.668	-0.221	1.001
Lycaeniidae	DSS	0.076	0.406	-0.727	0.864	1.000
Lycaeniidae	Floral richness	0.369	0.381	-0.356	1.148	1.000
Lycaeniidae	Floral abundance	0.712	0.517	-0.210	1.832	1.001
Lycaeniidae	Elevation (m)	-1.353	0.635	-2.735	-0.246	1.001
Lycaeniidae	Burn severity in meadow	0.799	0.739	-0.709	2.249	1.001
Lycaeniidae	Habitat (Upland-Meadow)	-2.297	1.124	-4.750	-0.375	1.003
Lycaeniidae	Burn (Upland-Meadow)	1.323	1.128	-0.661	3.810	1.001
Lycaeniidae	sigma	0.677	0.645	0.026	2.379	1.002
Lycaeniidae	BP	0.420	0.494	0.000	1.000	1.000
Lycaeniidae	r	0.128	0.027	0.101	0.198	1.002

**Table B5.** Posterior means, standard deviations (SD) and lower (2.50%) and upper (97.50%) limits of 95% Bayesian Credible Interval and convergence statistic (Rhat; <1.1 indicates convergence) of parameters from hummingbird negative binomial generalized linear mixed models. Data were collected in 2016 and 2017 in the Sierra Nevada, California, following the 2014 King Fire. sigma = standard deviation of random effect of site, BP=Bayesian p-value, r=negative binomial dispersion parameter, DSS=days since snowmelt.

	Mean	SD	2.50%	97.50%	Rhat
Intercept	-1.940	0.525	-3.069	-0.973	1.001
DSS	-0.843	0.234	-1.322	-0.403	1.001
Floral richness	0.375	0.160	0.071	0.704	1.003
Floral abundance	0.218	0.107	-0.001	0.425	1.001
Elevation (m)	-0.041	0.320	-0.660	0.614	1.001
Year	-0.735	0.412	-1.607	0.016	1.004
Burn severity in meadow	0.917	0.410	0.123	1.753	1.002
Habitat, upland	-1.899	0.971	-4.031	-0.188	1.010

Burn (Upland-Meadow)	-0.093	0.605	-1.237	1.162	1.001
Burn severity <sup>2</sup> in upland	-0.225	0.684	-1.540	1.148	1.002
sigma	0.921	0.465	0.147	1.968	1.017
BP	0.304	0.460	0.000	1.000	1.002
r	19.824	27.661	0.459	92.567	1.025

### **Chapter 3. Alpha and beta diversity of pollinators following megafire in upland and meadow habitats of the Sierra Nevada, California**

#### **Abstract**

In many regions of the world, fire regimes are changing in response to land use change, management, and climate change. One particular concern is that these changes are homogenizing regions that were historically pyrodiverse, with cascading effects for communities inhabiting these regions and the ecosystem services they provide. Pollinators provide important ecosystem services and in the dry forests of the western United States, depend on open habitat created or maintained by fire. How the increasingly occurring large and high-severity wildfires in this ecosystem affect pollinator diversity remains unknown. We investigated the impact of burn severity in upland (i.e., dry forest) and meadow habitat on pollinator diversity in a mid-elevation coniferous forest in the Sierra Nevada, California. We compared alpha and beta diversity derived from pollinator counts for burn-habitat classes of green (unburned) upland, moderate-severity upland, and high-severity upland and for green and high-severity meadow. We found that alpha and beta diversity were similar among all classes at the broader scale, but when metrics were modelled at the scale of the sampling plot, burn severity had negative impacts on richness in meadow habitat. Diversity was higher in meadows than uplands, regardless of burn severity. Community composition differed among green and high-severity meadow, and green and high-severity upland. As expected, pollinator species richness was positively associated with richness of floral resources, but not necessarily floral abundance. Diverse pollinator communities may provide redundancy and resilience to disturbance. High-severity fire in meadows had negative impacts on pollinator diversity, with possible cascading negative impacts on pollination services. Because pollinator diversity is more sensitive to the negative impacts of high-severity fire in



meadows, this habitat should be the focus of conservation measures given the high diversity of species it supports.

## **Introduction**

Understanding deviations from natural disturbance regimes affect biodiversity is a key challenge in the Anthropocene. Loss of biodiversity may lead to loss or degradation of ecosystem services and functions (Loreau et al. 2001, Cardinale et al. 2012). Worldwide, fire is the dominant source of disturbance that impacts the distribution and composition of species (Bond and Keeley 2005, Bond et al. 2005, He et al. 2019). Fires can impact nutrient cycling, soil decomposition rates, microclimates, and primary productivity; the magnitude of these effects depends on local conditions and fire regimes (Raison et al. 2009), as well as fire severity (i.e., the effect of fire on ecosystem properties). In many regions of the world, fire regimes are changing in response to land use change, management, and climate change (Flannigan et al. 2009, Pausas and Fernández-Muñoz 2012, Pausas and Keeley 2014). One particular concern is that these changes are homogenizing regions that were historically pyrodiverse (Hessburg et al. 2005, Lydersen et al. 2013, Merschel et al. 2014).

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 (Martin and Sapsis 1992, Ponisio et al. 2016, Jones and Tingley 2021), allowing more species to coexist. 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 through competitive advantages (Grime 1977, Tilman 1994, Burkle et al. 2015). As such, fire may not only increase species richness, but also increase species evenness by disrupting the dominance of highly competitive species (Connell 1978,

Cadotte 2007). When fires in historically pyrodiverse regions are regularly suppressed, lack of disturbance may lead to dominance by late-successional species, reducing both the number of species and their relative abundances at local scales, i.e., alpha diversity ( $\alpha$ ), and also the diversity of subcommunities within the larger region, i.e., beta diversity ( $\beta$ ).

The mixed-conifer forest of the Sierra Nevada is an ideal system to study how changes to the fire regime affect biodiversity. In this region, frequent and variable severity fire created a pyrodiverse landscape that shaped community structure and composition for thousands of years (Skinner et al. 1996). Historically, fires in the mid-elevation, mixed coniferous forests burned every 5-25 years. In addition to lightning, indigenous Nisenan, Washoe, and Maidu peoples started fires to manage forests, woodlands, and meadows (Anderson and Moratto 1996, Lake et al. 2017, Klimaszewski-Patterson et al. 2018). Burning at low-to-moderate severity, these fires were largely restricted to the forest floor with limited loss of trees (Beaty and Taylor 2008, Collins and Stephens 2010, Steel et al. 2015), and only small patches of high-severity, stand-replacing fire determined by local fuel conditions (Coppoletta et al. 2016), climate (Taylor and Beaty 2005, Westerling et al. 2006), and topography (Beaty and Taylor 2001). The result of this fire activity was three-fold: first, it regularly removed fuels (predominately shrubs and smaller trees) that could move a fire from the surface to the canopy (Parks et al. 2015, Ritter et al. 2020); second, it created a heterogeneous patchwork of uneven-aged and uneven-density stands (Perry et al. 2011, Bowman et al. 2016); and third, it prevented encroachment of meadows by woody species (Lepofsky et al. 2003, Norman and Taylor 2005a, Boisramé et al. 2017a).

In this system, extensive fire suppression and logging have resulted in contemporary forests with high levels of ground fuels (large and small woody debris), and densely packed even-aged stands of young trees that are less resilient to fire due to competition for resources,

pests and diseases (Donovan and Brown 2007). Many mid-elevation fire-suppressed meadows have been encroached by woody species reducing their overall size (DeBenedetti and Parsons 1979, Vale 1981, Norman and Taylor 2005b) and water storage capacity (Fletcher et al. 2014, Boisramé et al. 2017b, 2017a), and increasing fuel loads (Briggs et al. 2005), with subsequent consequences for soil organic matter when fires occur. Combined with warming climatic conditions and reduced winter snowpack, Sierra Nevada forests and meadows now experience increasingly long, hot and dry fire seasons (Westerling et al. 2006, Mote et al. 2005, Mote 2006). Consequently, ten of the largest and nine of the most destructive wildfires in California's recorded history have occurred in the last 10 years (California Department of Forestry and Fire Protection 2022). These so-called "megafires" burn outside the historic range of variation in size, severity, and frequency (Williams 2013, Stephens et al. 2014), resulting in a system with an altered fire regime. Because the historic fire regimes likely acted as a selective force for adaptive traits, these dramatic changes are expected to have major ecosystem consequences (Bond and Keeley 2005, Keeley et al. 2011, Pausas and Parr 2018). For example, today's fires often create large high-severity patches (i.e., patches with high rates of vegetation mortality) that are primarily colonized by early successional or disturbance-tolerant species (Safford and Stevens 2017, Cassell et al. 2019). These processes may lead to reductions in both  $\alpha$  and  $\beta$  diversity, due to large, stand-replacing fire creating homogenous habitat conditions (Hessburg et al. 2005, Perry et al. 2011, Cassell et al. 2019).

The response of pollinator communities to changed fire regimes are of particular interest, given their important role in plant reproduction for both crops and wild plants (Klein et al. 2007, Ollerton et al. 2011). Increasing pollinator diversity is associated with higher fruit and seed set (Carvalho et al. 2010, Albrecht et al. 2012, Ollerton 2017). Due to their mobility, rapid

response, and dependence on understory species that are sensitive to disturbance, pollinators are important indicators of ecosystem resilience (Kevan 1999, Potts et al. 2003, Carbone et al. 2019). In forested habitat, pollinators typically rely on gaps in the canopy and on meadows where understory species dominate (Loffland et al. 2017, Matonis and Binkley 2018). Whereas meadows are spatially and temporally more reliable habitat for pollinators (Potts et al. 2003, Rodríguez and Kouki 2017, Carbone et al. 2019), canopy gaps produced and maintained by fire can serve as ephemeral but important habitat (Matonis and Binkley 2018). Pollinator response to fire in forest is generally positive due to the increase in floral resources and nest sites after fire (Brown et al. 2017, Carbone et al. 2019), particularly in fire-suppressed upland habitat which tends to lack understory complexity. However, pollinator response may be mediated by the severity of the disturbance. Pollinator abundance has been shown to respond positively to fires burning with moderate severity for some guilds (Lazarina et al. 2019) and the habitat heterogeneity produced by fire may increase pollinator diversity (Ponisio et al. 2016, Rodríguez and Kouki 2017). Fires burning at high severity, however, may limit pollinator diversity if source populations are destroyed (Cane and Neff 2011, Brown et al. 2017), floral resources are slow to recover (Potts et al. 2003), or colonization is limited to disturbance-tolerant or highly mobile species (Brown et al. 2017, Pausas 2019). Meadow habitat may be particularly sensitive to high-severity fires that can damage or destroy seed sources and organic soil matter (DeBenedetti and Parsons 1979, Ratliff 1985).

Here, we investigated how fire affects pollinator diversity in mid-elevation fire suppressed coniferous forest, 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 King Fire (Sierra Nevada, California) three years post-fire in upland and meadow habitat that experienced

different burn severities. We predicted that fire effects on pollinator diversity would depend on burn severity and habitat type. More specifically,

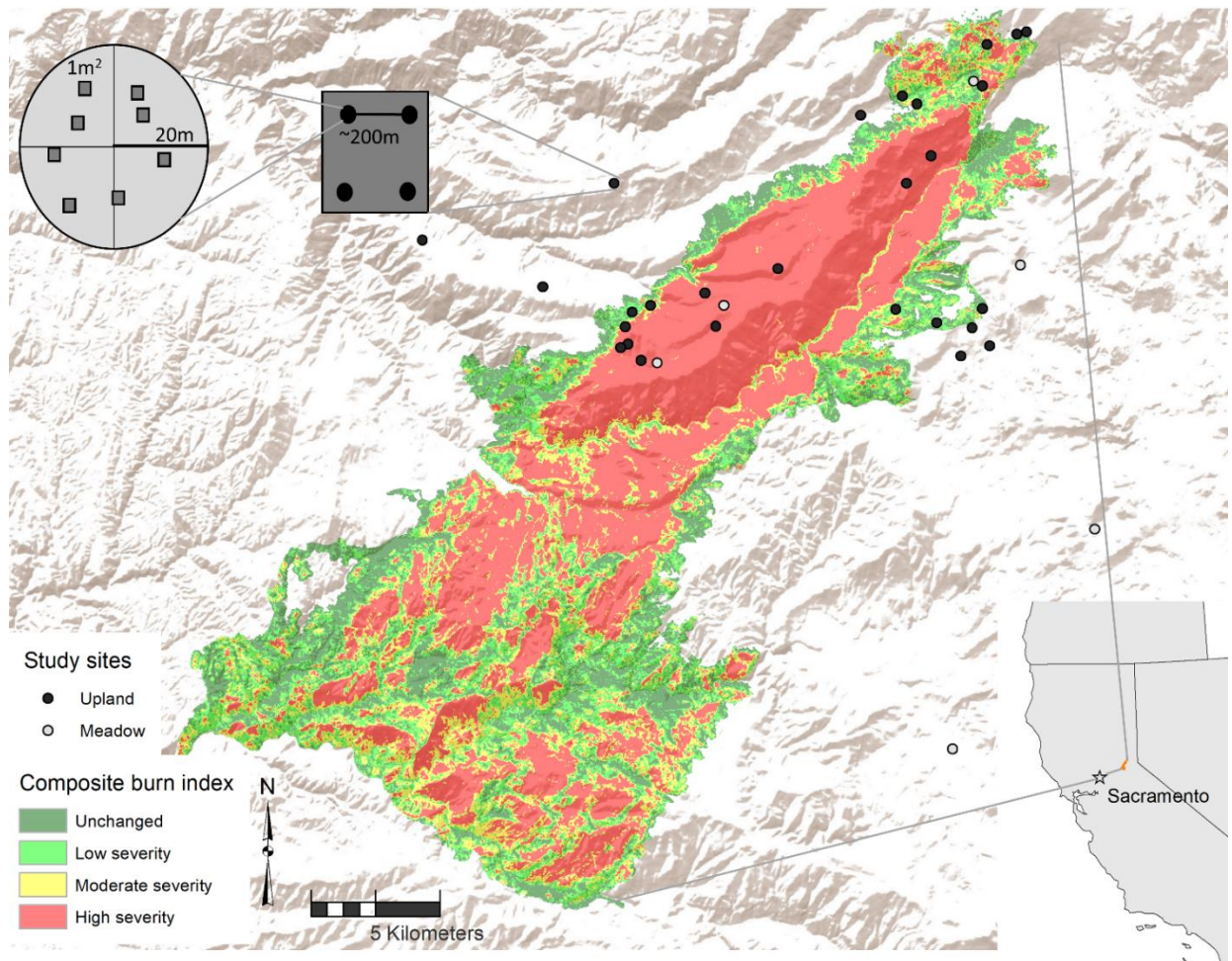
1. In uplands, pollinator  $\alpha$  and  $\beta$  will be highest in moderate-severity habitat due to increased habitat heterogeneity.
2. We expect both fire-suppressed and high-severity habitats to be homogenized. Thus, green and burned habitats will be similar in  $\alpha$  and  $\beta$  diversities, for both uplands and meadows.
3. Community composition will differ among green and burned habitats. In upland habitat, this pattern will be stronger among green and high-severity burned habitat, with moderate-severity habitat sharing species with the other burn categories.
4. Pollinator  $\alpha$  and  $\beta$  will increase with increasing floral richness and abundance. Because meadows have higher floral abundance and richness and provide other important resources, we expect them to have higher pollinator diversity than uplands.

## **Methods**

### Study Area

Our 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 (Fig. 1). The fire's size, rate of spread and large swaths of tree mortality led to its classification as a "megafire" (Stephens et al. 2014). 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 characterized by wet, cool winters with most precipitation falling as snow and dry, warm summers with little precipitation. Prior to the King Fire, the forest was largely composed of dense stands of relatively young white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus*

*lambertiana*), Douglas fir (*Pseudotsuga menziseii*) and incense cedar (*Calocedrus decurrens*). 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 and wasps (Hymenoptera: Apocrita), flies (Diptera), beetles (Coleoptera), and hummingbirds (Trochilidae).



**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 organized within sites. Pollinators were surveyed within each 20m-radius circular plot, plants with open flowers were surveyed in eight randomly located 1m<sup>2</sup> quadrats within each plot.

### Sampling design

To minimize differences in pollinator communities due to elevation, we restricted our sampling sites to lower montane forest and meadow communities (between ~1300 and 1800m above sea level). Sites were assigned to upland forest or meadow habitat using ArcGIS. Each site was located in patches of a given burn severity determined based on the US Forest Service King Fire Rapid Assessment of Vegetation Condition after Wildfire (RAVG) (USDA Forest Service 2014) composite burn index. The composite burn index is a discrete standardized vegetation severity rating that incorporates the mortality to all of the vegetation layers from the forest floor to the upper canopy. We used it to locate sites in green (unchanged), moderate (mix of surface fire and more severe fire with some mortality of the dominant vegetation), and high-severity (dominant vegetation has high-to-complete mortality) fire (Fig. 1). Sites were ground-truthed to verify habitat and burn severity classes and to ensure that sites were fairly homogenous across the sampling area. We excluded private lands, areas slated 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). 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 (Fig. 1). Plots were separated by at least 100m (average distance = 198m). Plot size and layout followed Loffland (2017) to allow comparison with other studies on *Bombus* populations in the Sierra Nevada. Because meadow habitat was limited within the fire footprint, we were only able to sample six meadow sites, with three high-severity sites and three unburned sites. Plot location varied in meadows due to meadow size and configuration such that each meadow site had three or four plots per site, arranged in a more linear orientation for a total of 22 meadow plots. Meadow sites further differed from upland sites in that they were visited three times per season, versus twice in

upland, due to their longer flowering period. For this study we summarized data across visits such that each plot only contributed one data point.

#### Burn severity metrics

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

#### Flower-visitor surveys

At each plot during each visit, two observers used a 40-mm sized insect net to capture all *Bombus* species in two consecutive 16-minute fixed area surveys and all other insect species visiting flowers in one separate 16-minute fixed area surveys. 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 and Johnson 2005, UC Davis Bohart Museum). Surveys were completed from June to September 2017, during daylight hours (between 8am to 5pm) when weather conditions supported insect activity: temperatures were  $> 2^{\circ}\text{C}$ , wind speeds were below 25 mph ( $\leq 6$  on the Beaufort scale), with no precipitation. For each plot, pollinator abundance of each species or morphospecies was summed across all visits. We compared



diversity of pollinators in burn-habitat classes using several metrics described below, all derived from total plot-level abundances.

#### Floral abundance and richness

We sampled floral abundance and richness to account for importance of floral resources to pollinators. We evaluated floral abundance and richness in eight 1-m<sup>2</sup> quadrats in each plot (Fig. 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 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. Because pollinators were rarely or never observed visiting some plant species, we only included the subset of 30 plants that were frequently visited (>10 visits) by pollinators (Appendix Table A1). Floral abundance was defined as the number of inflorescences with open flowers on frequently visited species in each plot, averaged over all visits. Floral richness was the number of frequently visited species with open flowers found in all quadrats of a plot, averaged over all visits.

#### Analysis

##### *Sampling effort*

For diverse taxa, such as insects, the more individuals sampled, the more species will be detected, and thus differences in sampling effort can introduce bias when comparing communities. To combat this bias, we attempted to equalize effort when collecting data through the use of timed surveys. Despite this, we found large differences in the number of individuals detected in each burn habitat-class (Table 1), suggesting that there are true ecological differences in the abundance of pollinator species in these classes. We chose not to rarefy samples to a standardized sample size of individuals in order to preserve and better understand these

ecological differences. Instead, we addressed this potential bias by adjusting our estimates of  $\alpha$  to incorporate unobserved species, where the number of unobserved species is based on the discovery rate of new species in the observed data (Chao and Jost 2015). This type of method tends to be robust to differences in data structure (many or few rare species) and sample size (Beck and Schwanghart 2010). For  $\beta$ , we selected an abundance-based metric because they tend to be more robust to differences in sample sizes (Beck et al. 2013). Further, we calculated that metric using a logarithmic transformation of abundance to “heavyweight” our  $\beta$  to rare species (Melo 2021). This approach is shown to reduce the influence of the most common species, which are likely to be generalist (and therefore, ubiquitous) and shared among communities, and thus less informative when attempting to differentiate communities (Cao et al. 2001, Melo 2021). The methods we selected for  $\alpha$  and  $\beta$  also do not discard any data, unlike rarefaction, allowing us to compare communities that differ in number of pollinators while minimizing the influence of sampling bias (McMurdie and Holmes 2014, Chao and Jost 2015, Melo 2021).

### *Alpha diversity*

We used Hill’s numbers to provide a measure of  $\alpha$  for each burn-habitat class. Hill’s numbers are a family of  $\alpha$  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 ( $D$ ) 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 (Jost 2006, 2007, Chao et al. 2014). 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 used the Diversity function in the SpadeR package (version 0.1.1., Chao et al. 2016) in R to estimate Hill's diversities for each burn-habitat class. This function uses the slope of the sample-size based species accumulation curve to generate the rate of new species discovery and uses these rates to correct diversity estimates (Chao and Jost 2015). We plotted the corrected diversity profiles of each burn-habitat class and obtained bootstrapped 95% confidence intervals for estimates of richness, Shannon and Simpson diversity. We considered estimates for a given diversity measure as significantly different if the intervals were non-overlapping.

### *Beta diversity*

Beta diversity is the variation in composition among subunits within a larger community and in the simplest definition is the ratio of the local  $\alpha$  to regional  $\gamma$  diversities (Whittaker 1960, Jost 2007). High  $\beta$  indicates that a subunit has few shared species, making it unique within the larger community. Low  $\beta$  indicates that most species are shared across different subunits, and may be a sign of homogenization. One commonly-used metric of  $\beta$  is to transform the

community matrix into a dissimilarity matrix, then locate the spatial median, the point in multidimensional space that minimizes the sum of the distances of all of the subunits of a community (Anderson et al. 2006, Qian 2009, Legendre and De Cáceres 2013). We calculated  $\beta$  based on the Bray-Curtis dissimilarity index applied to our log-transformed abundance-based community matrix (Odum 1950, Bray and Curtis 1957, Legendre and Legendre 2012), using the `vegdist` function in the `vegan` package (version 2.5-7, Oksanen et al. 2020). Because this index is based on the proportion of species that are shared among subcommunities, plots with zero species detections were dropped from this analysis. We considered both class-level  $\beta$ , the mean distance of all plots from their respective burn-habitat spatial median, and plot-level  $\beta$ , the distance of each plot from its respective burn-habitat spatial median; we calculated both with the `betadisper` function in `vegan`. Finally, we used the `permutest` function in `vegan` to compare class-level  $\beta$  and adjusted for multiple comparisons with the false discovery rate. Permutations were run 999 times. Analysis of plot-level  $\beta$  is described in the following section.

The location of the multivariate median of the community matrix is a measure of community composition. We tested if subcommunities differed significantly in their composition among burn-habitat classes with permutational multivariate analysis of variance (PERMANOVA), using the `adonis` function in `vegan`. PERMANOVA assumes that variance within burn-habitat classes (i.e., mean distance to spatial median) are homogeneous, which we tested with the `betadisper` function as described above. The overall test found significant differences in variances ( $F_{4,70}=3.073$ ,  $p$ -value=0.032) and pairwise differences were significant among green upland and high-severity meadow habitat, therefore, we decided to analyze meadows and upland habitat separately (Table 2). Variances were homogenous among meadow classes ( $F_{1,17}=0.288$ ,  $p$ -value=0.621). The overall test of variance found significant differences

among upland classes ( $F_{2,53}=4.061$ ,  $p=0.035$ ), but pairwise differences were not significant (all  $p$ -value  $>0.05$ , Appendix Table A2) indicating that any significant differences found by PERMANOVA are due to variation among (not within) subcommunities. Permutations were run 999 times.

### *Drivers of pollinator diversity*

In order to determine the factors that influence pollinator diversity, we modeled plot-level estimates of species richness (observed counts of unique number of species per plot) and plot-level  $\beta$  (i.e., the distance of each plot to the spatial median of its respective burn-habitat class as described above) as functions of burn severity, habitat type, and floral resources. We used the GLMMadaptive package (version 0.8-2, Rizopoulos 2020) to build generalized linear mixed models (GLMM) for each diversity metric with mean floral abundance and richness, continuous burn severity (RdNBR), habitat type (upland or meadow), and an interaction term for burn severity and habitat as the main effects, and site as the random effect to account for spatial autocorrelation of plots within a site. In upland sites we also considered a quadratic term for burn severity to account for potential non-linear responses that have been observed for understory plants in this region (Richter et al. 2019). This term was not included for meadow habitat because burn severity values were largely bimodal indicating that meadows were either unburned, or burned at high severity.

We tested for collinearity among predictor variables and found that correlations among all continuous covariates were  $\leq 0.68$  and variance inflation factors were  $\leq 2$  (Appendix Table A3). Because floral resource variables were correlated with the habitat type, we standardized the mean floral abundance and richness with the mean and standard deviation for its respective habitat type (Appendix Fig. A1). Thus, the baseline difference in floral resources among meadow

and upland habitat is included in the categorical habitat covariate, and the mean richness and mean abundance covariates capture additional variability within each habitat (i.e., they describe the deviation from the habitat-level mean). All other continuous covariates were scaled and centered using the overall means and standard deviations. Model fit was evaluated with the Dharma package (version 0.4.3, Hartig 2021) and GLMMadaptive wrapper (Rizopoulos 2022; Appendix Fig. A2-A3). Species richness was modelled with a hurdle model, which first models the binomial probability that the response variable is zero (i.e., no pollinators occur at a plot), and then applies a GLMM with the zero-truncated Poisson distribution to describe the non-zero data (Pinheiro and Bates 1995). 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 that are otherwise unaccounted for in the truncated model (Rizopoulos 2020). Hence, we interpret the coefficients qualitatively as significantly positive or negative, rather than as absolute values of change in richness. Plot-level  $\beta$  was modelled with a GLMM with residuals following the beta distribution. Coefficient estimates were rescaled to determine how each burn and habitat variable and their interaction affected the response variable relative to its green control (i.e., rather than the default of comparing all burn-habitat classes against a single reference category, we compared high-severity meadow to green meadow, and high- and moderate-severity upland to green upland), and how the number of days since snowmelt affected the response variable in each burn-habitat class (i.e., rather than looking at how different the slope was in each burn-habitat category from that in a single reference category, we derived the actual slope in each burn-habitat class). We calculated standard errors and 95% Wald confidence intervals for each rescaled coefficient using the `deltamethod` function in the `msm` package

## 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), nine true bugs (n=20), two butterflies (n=5), and one neuropteran morphospecies (n=1) (full list in 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 green meadow (Table 1). For upland habitat, moderate-severity habitat had the most species and individuals observed (48 species, n=149), followed by high-severity upland habitat (35 species, n=113), and green upland habitat (28 species, n=54). Fifty-two out of 130 plots did not have any pollinator species detected (Table 1).

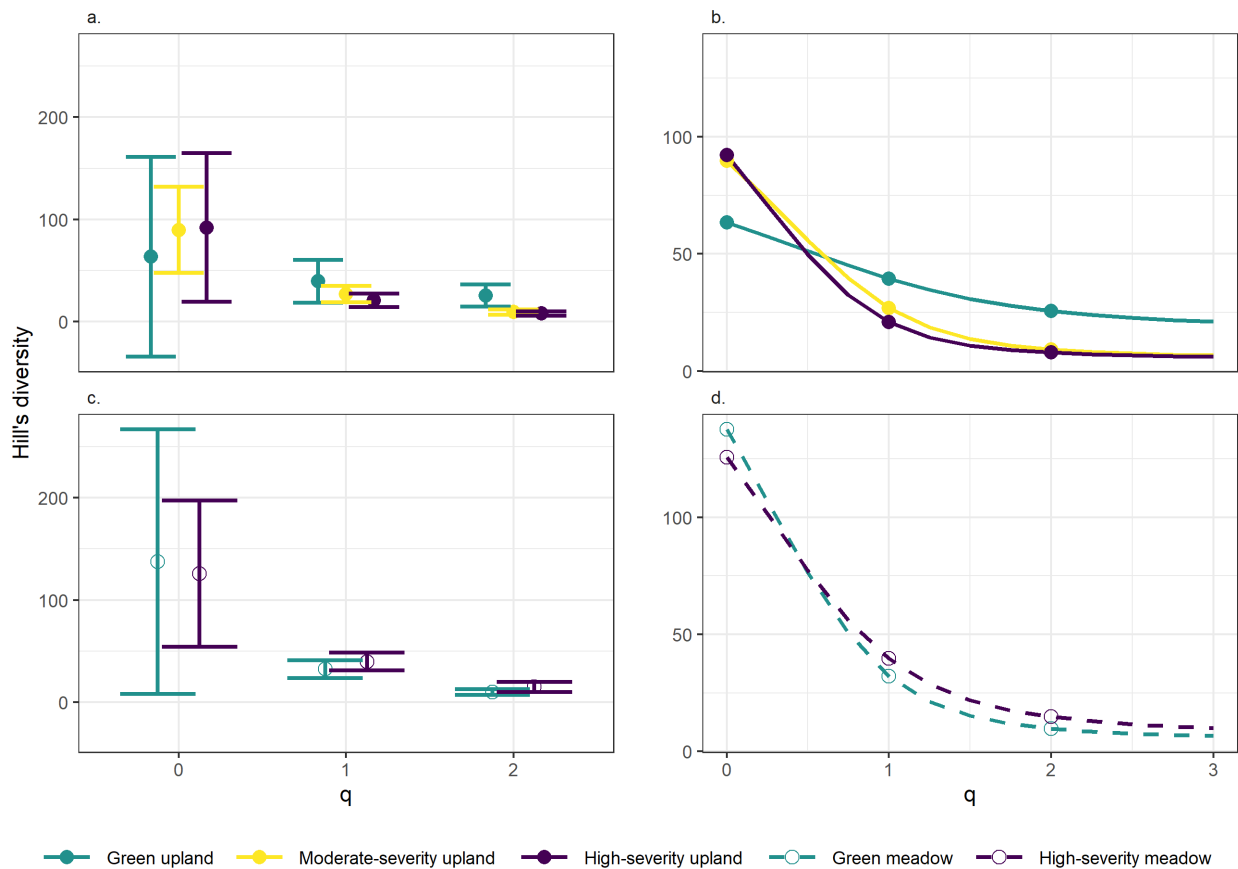
Table 1. Total abundance (N), total pollinator richness, plot-level mean and standard deviation (SD) of pollinator richness, and number of plots sampled by burn-habitat classes in green, moderate- and high-severity upland and green and high-severity meadows in the Sierra Nevada, California in 2017, following the 2014 King Fire.

Burn-habitat class	N	Total richness	Mean richness	SD	Plots surveyed	Plots without pollinators
Green upland	54	28	1.028	1.732	36	22
Moderate-severity upland	149	48	2.361	2.520	36	12
High-severity upland	113	35	1.750	2.557	36	18
Green meadow	186	57	8.455	7.202	11	2
High-severity meadow	178	58	8.727	7.072	11	1

### Alpha diversity

At the class level, pollinator species richness did not differ significantly across burn-habitat classes. As predicted, species richness (i.e.,  $D$  at  $q=0$ ) was slightly higher in meadow habitat than in upland habitat, and slightly higher in green meadows compared to high-severity meadows. Burned upland habitat tended to have higher richness than green upland habitat, although these differences were not significant (Fig. 2).

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. High-severity and unburned meadows were indeed similar (no significant differences), although burned meadows tended to be more even (Fig. 2). In upland habitats, however, fire resulted in less even communities.



**Figure 2.** Alpha diversity of pollinators in different burn-habitat classes in a post-fire forest in the Sierra Nevada, California, three years after the 2014 King Fire. Estimates of species richness ( $q=0$ ), Shannon diversity ( $q=1$ ), and Simpson diversity ( $q=2$ ) for each burn-habitat class in a) upland and c) meadow habitats with bootstrapped 95% confidence intervals. Estimates with non-overlapping confidence intervals are considered significantly different. Diversity profiles for each burn-habitat class in b) upland and d) meadow habitat where the importance of abundance for diversity increases with increasing values of  $q$ .



Differences in diversity indices were significant when comparing green upland habitat to both moderate and high-severity upland habitat (Simpson diversity), indicating that communities in green upland habitats were more even.

Beta diversity

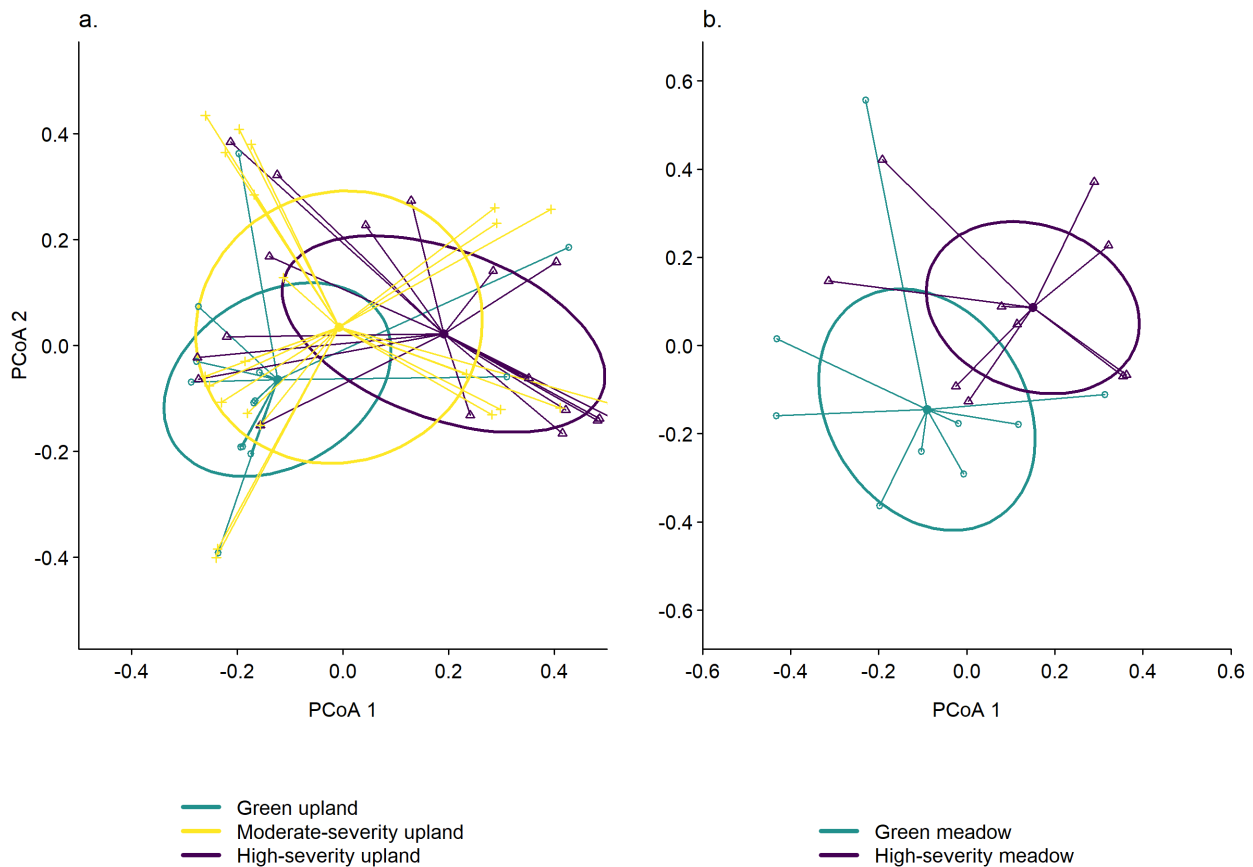
The overall permutational test indicated that class-level  $\beta$  differed significantly among the burn-habitat classes, however when we corrected for multiple comparisons only the difference between green upland and high-severity meadow habitat was significant at  $\alpha=0.05$  (Table 2, Fig. 3). We expected green upland habitat to be highly homogenized, with highly similar subcommunities found throughout this habitat type, however, we found that green upland plots had the highest class-level  $\beta$ , followed by moderate-severity upland, green meadow, high-severity upland, and high-severity meadow.

**Table 2.** Pollinator class-level  $\beta$  diversity by burn-habitat class for green, moderate-, and high-severity upland and green and high-severity meadows of the Sierra Nevada, California, in 2017, following the 2014 King Fire.  $\beta$  is the mean distance of all sampling plots in a class to its spatial median of the Bray-Curtis dissimilarity matrix. P-values are adjusted for multiple comparisons with false discovery rate; bold values are significant at  $\alpha=0.05$ .

Burn-habitat class	Class-level $\beta$	P-values for pairwise comparisons			
		Green upland	Moderate-severity upland	High-severity upland	Green meadow
Green upland	0.662				
Moderate-severity upland	0.634	0.377			
High-severity upland	0.561	0.070	0.126		
Green meadow	0.571	0.063	0.195	0.881	
High-severity meadow	0.538	<b>0.040</b>	0.063	0.757	0.723

Although both  $\alpha$  and  $\beta$  were similar across the burn-habitat classes (Fig. 2, Table 2), as we predicted, the composition of communities differed significantly by burn severity for both upland ( $F_{2,53}= 1.75$ , p-value= 0.016,  $R^2=0.062$ ) and meadow ( $F_{1,17}=1.68$ , p-value=0.044,  $R^2=0.090$ ) habitats (Fig. 3). Further, for upland habitat, composition differed most between green

and high-severity habitat (adjusted p-value=0.024), whereas differences between moderate-severity on one side, and unburned and high-severity habitat on the other side were non-significant (adjusted p-values of 0.325 and 0.065, respectively), corroborating our expectations. However, burn severity class only explained about 6% and 9% of variation in community composition for upland and meadow habitats, respectively. Large differences in variances among meadow and upland communities precluded comparisons between these habitats.



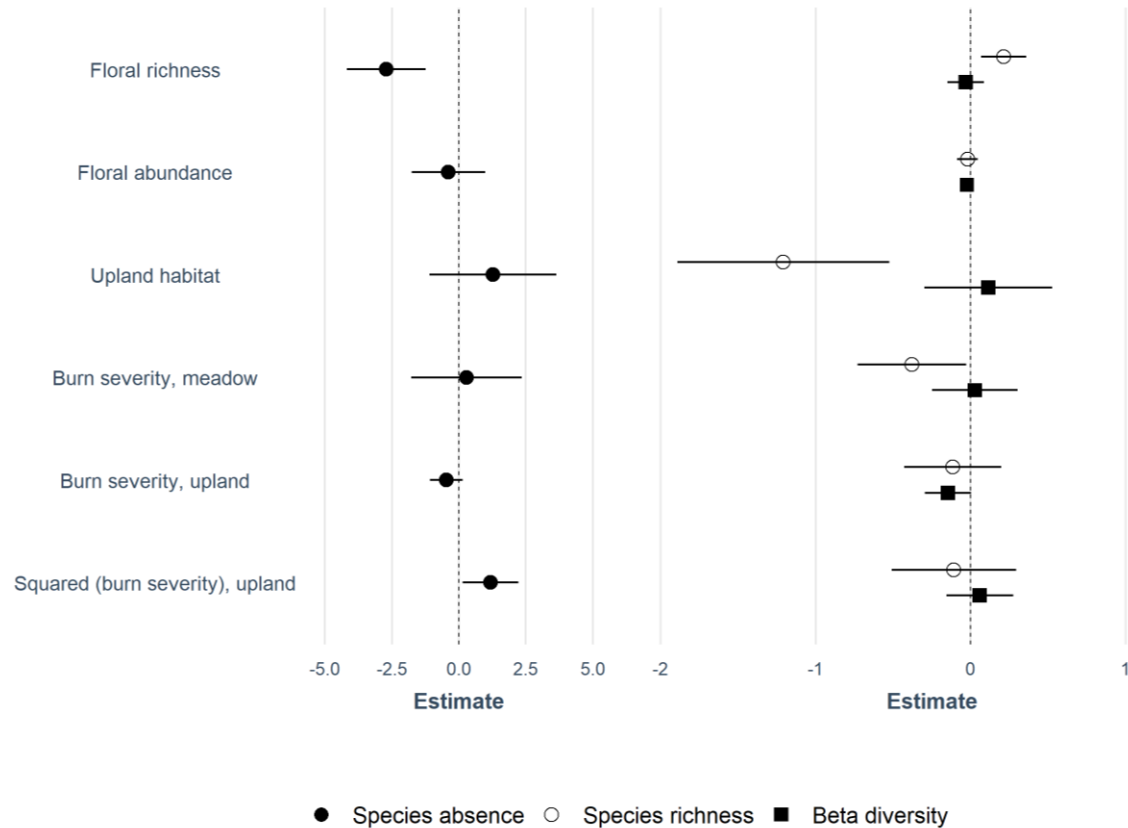
**Figure 3.** Beta diversity ( $\beta$ ) of pollinators in a) upland and b) meadow habitat in the Sierra Nevada, California, three years after the 2014 King Fire. Each sampling plot (hollow point) is located in space based on the abundance-based community matrix, the spatial median (larger, solid point) is the point in multidimensional space where the sum of the distances from all the plots of a burn-habitat class is minimized, and the ellipse encompasses one standard deviation. The class-level  $\beta$  is the mean distance across plots from the spatial median for each class, whereas the community composition of each class is represented by the locations of the spatial medians. Note the difference in axis scales between plots.

### Drivers of pollinator diversity

Overall, we found that habitat type and floral resources were the most influential predictors of pollinator diversity, and that habitat mediated the response of pollinators to burn severity, with upland habitat having significantly lower pollinator richness than meadow habitat (Fig. 4, Appendix C). In meadow habitat, burn severity had a negative influence on pollinator species richness, whereas in upland habitat there was no significant influence of the linear or the quadratic burn severity term, although both were negative. Floral richness was also an important predictor of pollinator richness; as floral richness increased relative to their habitat-level mean, pollinator species richness also increased (Poisson submodel, Fig. 4). Moreover, plots with higher floral richness were less likely to have zero species (binomial submodel; Fig. 4). Additionally, the quadratic burn severity term was positively associated with the probability of zero species, indicating that upland habitat at the extremes of the burn severity gradient were more likely to have zero species, whereas moderate-severity burned plots were more likely to have at least one species detected. Plot-level  $\beta$  (the distance of each plot to its burn-habitat class spatial median) did not respond significantly to any covariates (Fig. 4).

### **Discussion**

The greatest impacts of fire on pollinator communities occurred at smaller scales on species richness, and at larger scales on community composition. We found that the response of pollinator communities to fire in mid-elevation coniferous forest depended on habitat type, and differed among different aspects of diversity.



**Figure 4.** Factors influencing pollinator diversity in meadow and upland habitat of the Sierra Nevada, three years after the 2014 King Fire, from generalized linear mixed models (GLMM). Species richness (Poisson-binomial hurdle model) and plot-level beta diversity (GLMM with beta distribution) were modeled as functions of burn severity, habitat type (with meadow as reference category), and floral resources. The left-hand plot shows how the covariates affected the probability of a plot having 0 species (binomial submodel for species richness). The right-hand plot shows the responses of species richness (>0 species observed, Poisson submodel for species richness) and plot-level beta diversity to the covariates. Coefficients are considered significant when 95% confidence intervals do not overlap 0.

Although fire did not significantly affect richness of pollinator communities in meadow or upland habitat at the burn-habitat class-level, at the plot-level fire significantly reduced richness in meadow habitat, suggesting that there are some negative impacts of high-severity fire on species in this habitat. The last century of fire suppression allowed the build-up of woody fuels in meadows that can lead to hotter fires with longer residence time than would be typical of a meadow. This may negatively impact soils, destroying organic matter, volatilizing nutrients, increasing leaching and erosion, and changing soil microbe communities (reviewed in Certini

2005). High-severity fire may also reduce viability or abundance of seed banks (Abella et al. 2009, Esque et al. 2010, Lipoma et al. 2018). In this system, we did not find significant differences in floral richness or abundance in burned relative to green meadows (Chapter 1). This suggests that negative effects of fire on pollinators in this habitat were not mediated by changes in flowering resources. Pollinator communities may have been directly impacted by fire if pollinators or nesting sites were destroyed by fast-moving, high-severity fire in meadows (Williams et al. 2010, Brown et al. 2017). Pollinator abundance was also lower in burned meadows, suggesting that source populations may have been impacted (Chapter 2). However, the fact that class-level analysis did not find significant negative impacts on diversity suggests that small-scale (i.e., plot level) losses in diversity may be compensated for by the increased habitat heterogeneity in burned meadows (i.e., on the class level) that created pollinator communities with different compositions. This is supported by similar changes in floral composition observed among burned and green meadows (Chapter 1).

Owing to the increase in foraging and nesting resources for pollinators post-fire, we expected an increase in richness in burned upland habitat, with a peak at intermediate severity. The only significant evidence supporting this hypothesis was the low probability of a complete absence of pollinators in moderate-severity upland habitat (Fig. 5, binomial species richness submodel). Additionally, contrary to our expectations, we found that pollinator communities in green upland habitat tended to be more even than in burned upland habitat. This indicates that fire in upland habitat tended to reset pollinator successional dynamics favoring the establishment of “rarer” or disturbance-prone species. This effect may be temporary, and an increase in evenness may occur as more competitive species are able to re-establish (Yeboah et al. 2016).

Both fire suppression and high-severity fire may have homogenizing effects on habitats and communities (Hessburg et al. 2005, Merschel et al. 2014, Cassell et al. 2019). We expected these homogenizing effects to be reflected in lower class-level  $\beta$  in both green and high-severity habitats relative to moderate-severity habitat, however, heterogeneity in subcommunities was similar across burn classes in each habitat. One possible explanation is that all habitats in our study were fire-suppressed before the King Fire occurred. This may have limited the amount of variability in source populations and regional diversity. Our GLMM analysis corroborated that fire was not an important driver of plot-level  $\beta$ ; neither were floral resources. Other factors that influence  $\beta$  may include local and regional factors, such as history, microclimate, or propagule availability (Ricklefs 1987, Foster and Dickson 2004, Ohler et al. 2020), or factors related to the pollinators themselves, such as life history traits (Williams et al. 2010) or dispersal ability (Qian 2009).

Contrary to our expectations that the dense and homogeneous stands of unburned, upland forest would have low  $\alpha$  and  $\beta$  diversity, we observed the highest class-level  $\beta$  in green upland. This may be due to the overall lower plot-level species richness in this habitat (Table 1). Many plots in green upland habitat did not share any species, resulting in high  $\beta$  with lower overall richness. This pattern has been observed in other systems, where the most unique subcommunities have low  $\alpha$  (Landeiro et al. 2018, Dubois et al. 2020). We also observed higher floral  $\beta$  and many plots without any open flowers in green upland habitat, suggesting that floral resources in this habitat are spatially aggregated, whereas floral resources were more diverse and evenly distributed in burned and meadow habitats (Chapter 1). Pollinator diversity seems to follow a similar pattern, with more homogenized subcommunities where there are many

resources and less speciose, but unique, subcommunities in green uplands where resources are patchy.

As expected, floral richness was important to pollinator diversity and was positively associated with pollinator species richness, a pattern observed in many other studies (Ponisio et al. 2016, Rodríguez and Kouki 2017, Lazarina et al. 2019). 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 contain plant species that specialists require during different stages of their life history (Loreau et al. 2001, Cardinale et al. 2012). In addition, multiple species provide resources at different points in time, as plants flower asynchronously, supporting pollinators that emerge at different times, or are long-lived (Ebeling et al. 2008, Kral-O'Brien et al. 2021).

In addition to  $\alpha$  and  $\beta$ ,  $\gamma$ , or regional diversity, is also important. We found that community composition in green and high-severity habitats differed significantly, although the variation explained by our model was low. Community composition may in fact be driven by many other variables, at both local and regional scales. For example, we found (as expected) that moderate-severity upland habitat tended to share species with both green and high-severity upland habitat. 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. Habitat patchiness may allow for coexistence of species that differ in their ability to colonize or compete, whereas one would expect high-severity habitat to be dominated by disturbance-tolerant colonizers and green upland to be dominated by good competitors (Grime 1977, Tilman 1994, Cadotte 2007). Teasing apart the

effects of distance to green habitat and burn severity was not possible with this fire (and many megafires 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.

We found that post-fire mid-elevation coniferous forests hosted a diverse pollinator community. Diverse pollinator communities tend to provide more pollination services, particularly in natural systems, where diversity provides redundancy, insurance, and resilience to disturbance (Ricklefs 1987, Loreau et al. 2001, Senapathi et al. 2015). In turn, 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 (Hessburg et al. 2005, Mote 2006, Westerling et al. 2006, Fernandes et al. 2016, Lydersen et al. 2017). The build-up of fuels in many of these habitats also increases the likelihood of high-severity fire (Pausas and Fernández-Muñoz 2012, Coppoletta et al. 2016, Lydersen et al. 2017). High-severity fire is likely to have negative impacts on pollinator diversity, particularly in meadows. The negative effects in upland habitat are less pronounced, 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 (Chapters 1 and 2). Managing negative effects of high-severity fire on pollinators may include protecting meadows from high-severity fire so they may provide refugia for pollinators, decreasing the patch-size of high-severity fire through active management, and conserving and creating patchiness within green forests that support diverse understory communities.



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## Appendices

### Appendix A.

Table A1. Species or morphospecies of plants that had least 10 visits by any pollinator sampled in the Sierra Nevada, California, two and three years after the 2014 King Fire.

ScientificName	Family	Visits
<i>Perideridia parishii</i>	Apiaceae	11
<i>Cirsium andersonii</i>	Asteraceae	11
<i>Cirsium vulgare</i>	Asteraceae	198
<i>Erigeron</i> species	Asteraceae	26
<i>Eriophyllum lanatum</i>	Asteraceae	17
<i>Helenium bigelovii</i>	Asteraceae	21
<i>Oreostemma alpigenum</i> var. <i>andersonii</i>	Asteraceae	15
<i>Rudbeckia occidentalis</i>	Asteraceae	10
<i>Senecio triangularis</i>	Asteraceae	23
<i>Solidago canadensis</i>	Asteraceae	19
<i>Solidago elongata</i>	Asteraceae	13
<i>Symphyotrichum spathulatum</i> var. <i>spathulatum</i>	Asteraceae	122
<i>Eriodictyon lobbii</i>	Boraginaceae	50
<i>Phacelia hastata</i>	Boraginaceae	13
<i>Phacelia</i> species	Boraginaceae	30
<i>Asyneuma prenanthoides</i>	Campanulaceae	43
<i>Cuscuta californica</i>	Convolvulaceae	50
<i>Lupinus latifolius</i> var. <i>columbianus</i>	Fabaceae	13
<i>Lupinus</i> species	Fabaceae	70
<i>Trifolium pratense</i>	Fabaceae	44
<i>Hypericum perforatum</i>	Hypericaceae	19
<i>Hypericum scouleri</i>	Hypericaceae	11
<i>Monardella odoratissima</i>	Lamiaceae	14
<i>Sidalcea glaucescens</i>	Malvaceae	18
<i>Veratrum californicum</i>	Melanthiaceae	21
<i>Mimulus guttatus</i>	Phrymaceae	17
<i>Mimulus moschatus</i>	Phrymaceae	16
<i>Bistorta bistortoides</i>	Polygonaceae	25
<i>Drymacallis glandulosa</i>	Rosaceae	13
<i>Horkelia fusca</i>	Rosaceae	51

Table A2. Differences in class-level  $\beta$  (homogeneity of multivariate dispersions) for green, moderate- and high-severity upland habitat in the Sierra Nevada, California, three years after the 2014 King Fire. P-values for pairwise comparisons are adjusted with false discovery rate; bold values are significant at  $\alpha = 0.05$ . DF = degrees of freedom, SS = sum of squares.

Upland class-level $\beta$							
	DF	SS	Mean SS	F	p-value	Pairwise comparison	p-value
Groups	2	0.091	0.045	4.061	0.035	GreenUpland-HighUpland	0.06
Residuals	53	0.591	0.011			GreenUpland-ModerateUpland	0.247
						HighUpland-ModerateUpland	0.12

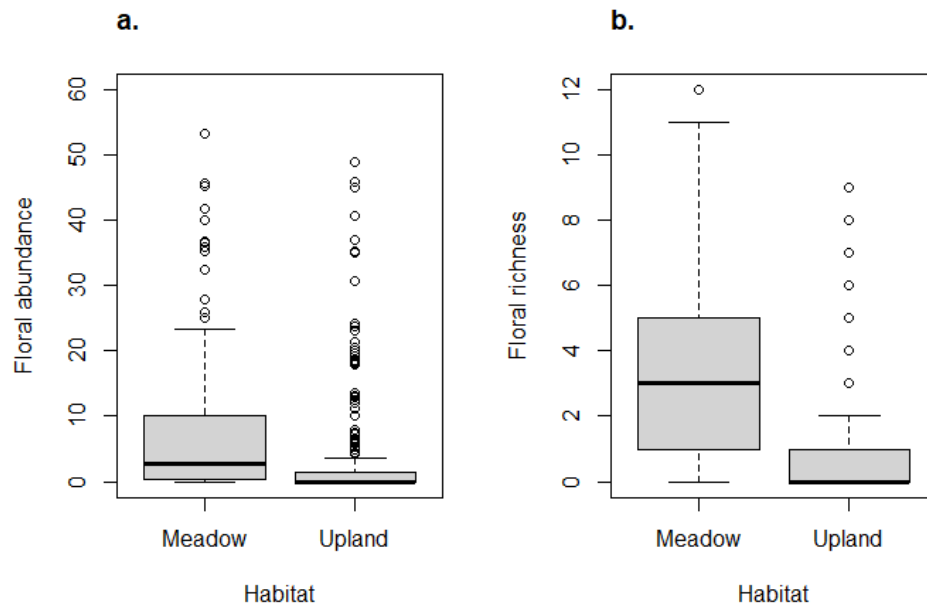
PERMANOVA is analogous to univariate ANOVA, and as such, assumes that variances within groups are homogeneous. We tested this assumption by comparing the multivariate dispersion of each burn-habitat class with the betadisper function in vegan (Oksanen et al. 2020). None of the post-hoc pairwise comparisons (adjusted with false discovery rate) were significant, indicating that variances among groups did not differ significantly. The adonis function in vegan finds the sum of squares distance from each plot to its respective burn-habitat spatial median and by repeating over many permutations, tests for significance with pseudo F-ratios. We used the false discovery rate method (Benjamini and Hochberg 1995, Benjamini and Yekutieli 2001) to adjust p-values for multiple comparisons in the pairwise.perm.manova function from the RVAideMemoire package (version 0.9-80, Hervé 2021).

Table A3. Tests for correlations among predictor variables used to model pollinator diversity, with Pearson's correlation and variance inflation factor (VIF), stratified by upland and meadow habitat. Floral data was collected three years after the 2014 King Fire, Sierra Nevada, California; burn severity was determined from remote sensed data.

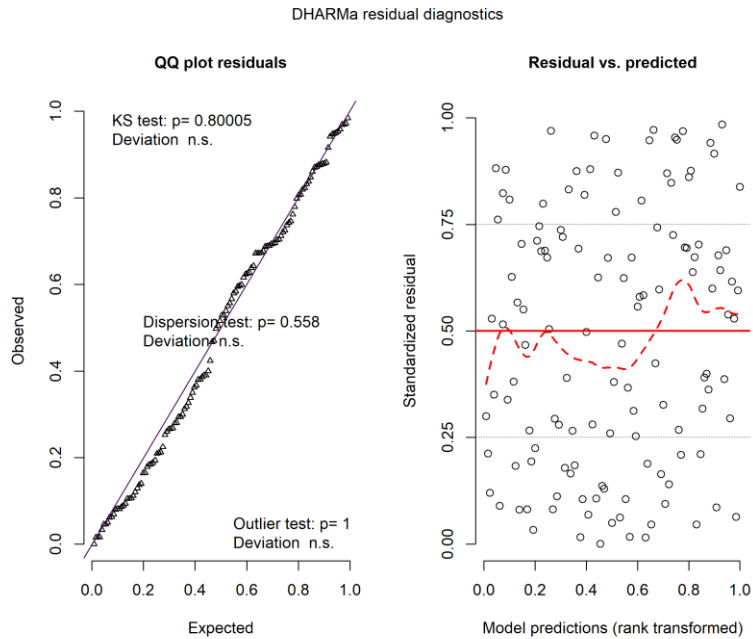
Upland				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.013		Burn severity	1.019
Floral richness	0.128	0.454	Floral abundance	1.264
			Floral richness	1.284

Table A3. Tests for correlations among predictor variables used to model pollinator diversity, with Pearson's correlation and variance inflation factor (VIF), stratified by upland and meadow habitat. Floral data was collected three years after the 2014 King Fire, Sierra Nevada, California; burn severity was determined from remote sensed data.

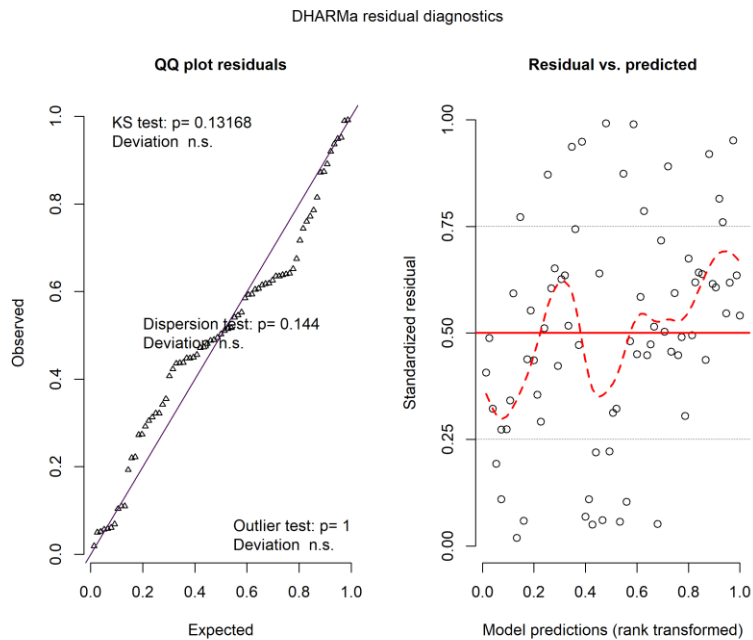
<b>Meadow</b>				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.203		Burn severity	1.092
Floral richness	0.290	0.676	Floral abundance	1.842
			Floral richness	1.928
<b>All</b>				
Pearson correlations	Burn severity	Floral abundance	Variables	VIF
Floral abundance	0.024		Burn severity	1.293
Floral richness	0.163	0.397	Floral abundance	1.190
			Floral richness	1.221



**Figure A1.** Correlation between meadow and upland habitats and a. floral abundance and b. floral richness in the Sierra Nevada, California, two and three years after the King Fire.



**Figure A2.** Residual plot for generalized linear mixed model (Poisson-binomial hurdle) for species richness of pollinators in the Sierra Nevada, California three years after the 2014 King Fire.



**Figure A3.** Residual plot for generalized linear mixed model (beta distribution) for class-level beta diversity of pollinators in the Sierra Nevada, California three years after the 2014 King Fire.

Appendix B.

**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, three years after the 2014 King Fire.

Order	Family	Morphospecies	GU	MU	HU	GM	HM	Total
Coleoptera	Anthribidae	<i>Anthribidae 1</i>	0	0	1	0	0	1
Coleoptera	Buprestidae	<i>Phaenops 1</i>	2	0	0	0	1	3
Coleoptera	Cerambycidae	<i>Anastrangalia laetifica</i>	0	0	0	0	1	1
Coleoptera	Cerambycidae	<i>Anastrangalia sanguinea</i>	0	1	0	2	4	7
Coleoptera	Cerambycidae	Cerambycidae 1	0	0	0	1	2	3
Coleoptera	Cerambycidae	<i>Lepturobosca chrysocoma</i>	0	0	0	3	0	3
Coleoptera	Cerambycidae	<i>Stenostrophia tribalteata</i>	0	0	0	0	3	3
Coleoptera	Chrysomelidae	Chrysomelidae 1	0	0	0	0	1	1
Coleoptera	Chrysomelidae	<i>Diabrotica undecimpunctata</i>	0	0	0	1	1	2
Coleoptera	Cleridae	<i>Trichodes ornatus</i>	0	0	1	0	1	2
Coleoptera	Coccinellidae	<i>Hippodamia convergens</i>	0	0	0	3	0	3
Coleoptera	Curculionidae	Curculionidae 1	0	1	0	0	0	1
Coleoptera	Dermestidae	<i>Orphilus subnitidus</i>	0	2	0	1	1	4
Coleoptera	Melyridae	Melyridae 1	1	0	1	0	0	2
Coleoptera	Mordellidae	<i>Mordella 1</i>	0	4	0	1	1	6
Coleoptera	Scarabaeidae	<i>Hoplia 1</i>	0	0	0	1	5	6
Diptera	Bombyliidae	Bombyliidae 1	1	0	0	0	0	1
Diptera	Bombyliidae	Bombyliidae 2	1	2	0	0	0	3
Diptera	Bombyliidae	Bombyliidae 3	1	1	0	0	0	2
Diptera	Bombyliidae	Bombyliidae 4	1	2	0	1	0	4
Diptera	Bombyliidae	Bombyliidae 5	0	0	0	1	1	2
Diptera	Bombyliidae	Bombyliidae 6	0	0	3	0	1	4
Diptera	Bombyliidae	<i>Geron 1</i>	2	3	0	0	0	5
Diptera	Conopidae	Conopidae 1	0	1	0	0	0	1
Diptera	Heleomyzidae	Heleomyzidae 1	0	0	0	0	1	1
Diptera	Heleomyzidae	Heleomyzidae 2	0	0	0	0	1	1
Diptera	Muscidae	<i>Lucilia 1</i>	0	0	0	1	1	2
Diptera	Muscidae	Muscidae 1	0	0	0	0	1	1
Diptera	Muscidae	Muscidae 2	0	0	0	1	0	1
Diptera	Sarcophagidae	Sarcophagidae 1	0	0	0	2	0	2
Diptera	Sarcophagidae	Sarcophagidae 2	0	0	0	1	0	1
Diptera	Sarcophagidae	Sarcophagidae 3	0	0	0	0	1	1
Diptera	Syrphidae	Syrphidae 1	0	0	0	1	0	1
Diptera	Syrphidae	Syrphidae 2	0	0	0	2	0	2
Diptera	Syrphidae	Syrphidae 3	0	2	1	5	1	9
Diptera	Syrphidae	Syrphidae 4	0	0	1	5	0	6
Diptera	Tachinidae	<i>Gymnosoma</i>	0	0	1	0	0	1
Diptera	Tachinidae	Tachinidae 1	0	0	0	1	2	3
Diptera	Tachinidae	Tachinidae 2	0	3	0	0	0	3

**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, three years after the 2014 King Fire.

Order	Family	Morphospecies	GU	MU	HU	GM	HM	Total
Diptera	Tachinidae	Tachinidae 3	0	0	0	2	2	4
Diptera	Tachinidae	Tachinidae 4	0	0	1	0	0	1
Diptera	Tachinidae	Tachinidae 5	0	0	1	1	0	2
Diptera	Tephritidae	Tephritidae	0	1	0	0	0	1
Hemiptera	Aphididae	Aphididae 1	0	0	0	1	0	1
Hemiptera	Berytidae	Berytidae 1	2	0	0	0	0	2
Hemiptera	Lygaeidae	<i>Neacoryphus bicrucis</i>	0	1	0	0	2	3
Hemiptera	Miridae	<i>Deraeocoris</i>	0	1	0	0	0	1
Hemiptera	Miridae	<i>Lygus shulli</i>	0	2	0	0	0	2
Hemiptera	Miridae	<i>Lygus spp</i>	0	1	3	1	1	6
Hemiptera	Reduviidae	<i>Apiomerus</i>	0	1	0	0	0	1
Hemiptera	Rhopalidae	Rhopalidae 1	1	0	0	0	2	3
Hymenoptera	Andrenidae	<i>Andrena 1</i>	1	0	0	0	0	1
Hymenoptera	Andrenidae	<i>Andrena 2</i>	0	2	0	0	0	2
Hymenoptera	Andrenidae	<i>Calliopsis edwardsii</i>	0	1	0	7	1	9
Hymenoptera	Apidae	<i>Anthophora urbana</i>	5	11	0	7	6	29
Hymenoptera	Apidae	<i>Apis mellifera</i>	4	39	31	24	11	109
Hymenoptera	Apidae	<i>Bombus bifarius</i>	0	0	0	2	0	2
Hymenoptera	Apidae	<i>Bombus fernaldae</i>	1	0	0	0	0	1
Hymenoptera	Apidae	<i>Bombus fervidus</i>	1	0	1	3	20	25
Hymenoptera	Apidae	<i>Bombus flavifrons</i>	0	1	0	5	6	12
Hymenoptera	Apidae	<i>Bombus insularis</i>	1	1	1	4	8	15
Hymenoptera	Apidae	<i>Bombus melanopygus</i>	1	0	0	0	0	1
Hymenoptera	Apidae	<i>Bombus mixtus</i>	4	1	0	0	0	5
Hymenoptera	Apidae	<i>Bombus vandykei</i>	1	6	7	1	10	25
Hymenoptera	Apidae	<i>Bombus vosnesenskii</i>	7	27	22	52	37	145
Hymenoptera	Apidae	<i>Diadasia bituberculata</i>	0	0	1	0	0	1
Hymenoptera	Apidae	<i>Melissodes microsticta</i>	0	0	0	2	1	3
Hymenoptera	Apidae	<i>Xeromelecta californica</i>	1	0	0	1	3	5
Hymenoptera	Apidae	<i>Xylocopa californica</i>	0	1	0	0	0	1
Hymenoptera	Chrysididae	Chrysididae 1	0	0	0	0	1	1
Hymenoptera	Collectidae	<i>Hylaeus episcopalis</i>	1	0	0	0	2	3
Hymenoptera	Collectidae	<i>Hylaeus modestus</i>	0	0	0	1	0	1
Hymenoptera	Collectidae	<i>Hylaeus spp</i>	0	1	0	0	0	1
Hymenoptera	Crabronidae	Crabronidae 5	0	0	0	1	0	1
Hymenoptera	Crabronidae	Crabronidae 1	0	0	2	0	1	3
Hymenoptera	Crabronidae	Crabronidae 2	0	0	0	1	0	1
Hymenoptera	Crabronidae	Crabronidae 3	0	0	0	1	0	1
Hymenoptera	Crabronidae	Crabronidae 4	0	0	0	0	1	1
Hymenoptera	Formicidae	<i>Formica 1</i>	0	0	0	1	0	1
Hymenoptera	Formicidae	<i>Formica argentea</i>	0	1	0	0	0	1

**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, three years after the 2014 King Fire.

Order	Family	Morphospecies	GU	MU	HU	GM	HM	Total
Hymenoptera	Formicidae	Formicidae 1	3	1	0	0	0	4
Hymenoptera	Halictidae	Halictidae 1	0	2	1	1	0	4
Hymenoptera	Halictidae	<i>Halictus confusus</i>	3	3	0	1	5	12
Hymenoptera	Halictidae	<i>Halictus farinosus</i>	0	0	0	2	0	2
Hymenoptera	Halictidae	<i>Lasioglossum 1</i>	0	0	0	1	0	1
Hymenoptera	Halictidae	<i>Lasioglossum 2</i>	0	1	0	1	1	3
Hymenoptera	Halictidae	<i>Lasioglossum 3</i>	0	0	1	0	1	2
Hymenoptera	Halictidae	<i>Lasioglossum anhypops</i>	0	2	0	1	0	3
Hymenoptera	Halictidae	<i>Lasioglossum Dialictus</i>	3	4	13	8	3	31
Hymenoptera	Halictidae	<i>Lasioglossum olympiae</i>	0	0	0	8	4	12
Hymenoptera	Halictidae	<i>Lasioglossum trizonatum</i>	0	1	0	1	0	2
Hymenoptera	Halictidae	<i>Sphecodes 1</i>	0	0	1	0	0	1
Hymenoptera	Halictidae	<i>Sphecodes 2</i>	0	0	0	0	1	1
Hymenoptera	Halictidae	<i>Sphecodes 3</i>	0	2	0	0	0	2
Hymenoptera	Ichneumonidae	Ichneumonidae 1	0	0	0	0	1	1
Hymenoptera	Megachilidae	<i>Anthidium mormonum</i>	0	1	0	0	0	1
Hymenoptera	Megachilidae	<i>Anthidium utahensis</i>	0	0	1	0	0	1
Hymenoptera	Megachilidae	<i>Ashmeadiella cactorum</i>	0	0	0	1	0	1
Hymenoptera	Megachilidae	<i>Ashmeadiella timberlakei</i>	0	1	0	0	0	1
Hymenoptera	Megachilidae	<i>Coelioxys rufitarsis</i>	0	0	0	1	0	1
Hymenoptera	Megachilidae	<i>Dianthidium ulkei ulkei</i>	1	0	0	1	0	2
Hymenoptera	Megachilidae	<i>Dufourea versatilis rufiventris</i>	0	0	2	0	0	2
Hymenoptera	Megachilidae	<i>Heriades cressoni</i>	0	0	0	0	1	1
Hymenoptera	Megachilidae	<i>Megachile angelarum</i>	0	2	2	1	0	5
Hymenoptera	Megachilidae	<i>Megachile apicalis</i>	0	0	1	0	1	2
Hymenoptera	Megachilidae	<i>Megachile fidelis</i>	0	0	1	0	1	2
Hymenoptera	Megachilidae	<i>Megachile gentilis</i>	0	0	0	1	0	1
Hymenoptera	Megachilidae	<i>Megachile perihirta</i>	0	0	0	1	1	2
Hymenoptera	Megachilidae	<i>Osmia albolateralis</i>	0	1	0	0	0	1
Hymenoptera	Megachilidae	<i>Osmia coloradensis</i>	0	1	1	0	1	3
Hymenoptera	Megachilidae	<i>Osmia densa</i>	0	1	0	0	2	3
Hymenoptera	Megachilidae	<i>Osmia indepressa</i>	0	0	1	0	0	1
Hymenoptera	Megachilidae	<i>Osmia integra</i>	0	1	0	0	0	1
Hymenoptera	Megachilidae	<i>Osmia laeta</i>	0	1	0	0	0	1
Hymenoptera	Megachilidae	<i>Osmia montana</i>	0	0	1	0	2	3
Hymenoptera	Megachilidae	<i>Osmia tristella</i>	0	1	1	0	0	2
Hymenoptera	Megachilidae	<i>Stelis laticincta</i>	0	1	1	0	0	2
Hymenoptera	Sphecidae	<i>Podalonia</i>	0	0	2	0	2	4
Hymenoptera	Tenthredinidae	Tenthredinidae 1	0	0	0	0	1	1
Hymenoptera	Vespidae	<i>Eumenes 1</i>	1	0	0	0	0	1
Hymenoptera	Vespidae	Vespidae 1	1	0	0	0	0	1

**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, three years after the 2014 King Fire.

Order	Family	Morphospecies	GU	MU	HU	GM	HM	Total
Hymenoptera	Vespidae	Vespidae 3	0	0	0	2	0	2
Hymenoptera	Vespidae	Vespidae 4	0	0	0	0	1	1
Lepidoptera	Coleophoridae	Coleophoridae 1	2	0	0	0	0	2
Lepidoptera	Pyralidae	Pyralidae 1	0	0	2	0	1	3
Neuroptera	Chysopidae	Chysopidae 1	0	1	0	0	0	1



Appendix C.

**Table C1.** Drivers of pollinator diversity in green, moderate, and high-severity upland and green and high-severity meadows of the Sierra Nevada of California, three years after the 2014 King Fire. Results for generalized linear mixed models for pollinator richness (Poisson-binomial hurdle) and beta diversity (beta), where meadow is the reference category. SE = standard error, SD = standard deviation, CI = lower and upper 95% confidence interval limits. Bold p-values are significant at  $\alpha = 0.05$ .

Response variable:	Species absence			
Model:	Binomial submodel for plots with 0 species observed			
Covariates	Estimate	SE	z.value	p-value
Intercept	-4.281	1.478	-2.897	0.004
<b>Floral richness</b>	<b>-2.659</b>	<b>0.767</b>	<b>-3.468</b>	<b>0.001</b>
Floral abundance	-1.166	1.863	-0.626	0.531
Habitat, upland	2.020	1.307	1.546	0.122
Burn severity, meadow	0.285	1.011	0.282	0.778
Burn severity, (upland-meadow)	-0.747	1.054	-0.709	0.478
<b>Burn severity<sup>2</sup>, upland</b>	<b>1.172</b>	<b>0.531</b>	<b>2.208</b>	<b>0.027</b>
Response variable:	Species richness		Random effect of site	
Model:	Poisson-hurdle submodel		SD:	0.523
Covariates	Estimate	SE	z.value	p-value
Intercept	2.092	0.236	8.865	< .001
<b>Floral richness</b>	<b>0.216</b>	<b>0.074</b>	<b>2.905</b>	<b>0.004</b>
Floral abundance	-0.059	0.086	-0.682	0.495
<b>Habitat, upland</b>	<b>-1.161</b>	<b>0.335</b>	<b>-3.465</b>	<b>0.001</b>
<b>Burn severity, meadow</b>	<b>-0.385</b>	<b>0.176</b>	<b>-2.185</b>	<b>0.029</b>
Burn severity (upland- meadow)	0.270	0.237	1.139	0.255
Burn severity <sup>2</sup> , upland	-0.107	0.204	-0.521	0.602
Response variable:	$\beta$ diversity		Random effect of site	
Model:	Beta mixed model		SD:	0.294
Covariates	Estimate	SE	z.value	p-value
Intercept	0.347	0.156	2.227	0.026
Floral richness	-0.033	0.060	-0.551	0.582
Floral abundance	-0.024	0.023	-1.070	0.285
Habitat, upland	0.114	0.211	0.539	0.590
Burn severity in meadow	0.027	0.141	0.193	0.847
Burn severity (upland-meadow)	-0.174	0.160	-1.092	0.275
Burn <sup>2</sup> in upland	0.058	0.110	0.530	0.596