Pyrodiversity begets plant–pollinator community diversity

LAUREN C. PONISIO[1], KATE WILKIN[1], LEITHEN K. M'GONIGLE[1,2], KELLY KULHANEK[1], LINDSAY COOK[1], ROBBIN THORP[3], TERRY GRISWOLD[4] and CLAIRE KREMEN[1]

[1]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720, USA, [2]Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA, [3]Department of Entomology and Nematology, University of California, Davis, Davis, CA 95616, USA, [4]Department of Biology, Utah State University, Logan, UT 84322, USA

Abstract

Fire has a major impact on the structure and function of many ecosystems globally. Pyrodiversity, the diversity of fires within a region (where diversity is based on fire characteristics such as extent, severity, and frequency), has been hypothesized to promote biodiversity, but changing climate and land management practices have eroded pyrodiversity. To assess whether changes in pyrodiversity will have impacts on ecological communities, we must first understand the mechanisms that might enable pyrodiversity to sustain biodiversity, and how such changes might interact with other disturbances such as drought. Focusing on plant–pollinator communities in mixed-conifer forest with frequent fire in Yosemite National Park, California, we examine how pyrodiversity, combined with drought intensity, influences those communities. We find that pyrodiversity is positively related to the richness of the pollinators, flowering plants, and plant–pollinator interactions. On average, a 5% increase in pyrodiversity led to the gain of approximately one pollinator and one flowering plant species and nearly two interactions. We also find that a diversity of fire characteristics contributes to the spatial heterogeneity (β-diversity) of plant and pollinator communities. Lastly, we find evidence that fire diversity buffers pollinator communities against the effects of drought-induced floral resource scarcity. Fire diversity is thus important for the maintenance of flowering plant and pollinator diversity and predicted shifts in fire regimes to include less pyrodiversity compounded with increasing drought occurrence will negatively influence the richness of these communities in this and other forested ecosystems. In addition, lower heterogeneity of fire severity may act to reduce spatial turnover of plant–pollinator communities. The heterogeneity of community composition is a primary determinant of the total species diversity present in a landscape, and thus, lower pyrodiversity may negatively affect the richness of plant–pollinator communities across large spatial scales.

Keywords: bees (Hymenoptera: Apoidea), community assembly, drought, environmental heterogeneity, fire regime, fire severity

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Introduction

Understanding the mechanisms underlying the maintenance of biodiversity in natural and human dominated systems is critical to conservation and restoration. One fundamental and widely supported theory of biodiversity in biogeography is the idea that diversity begets biodiversity (Hutchinson, 1959; MacArthur & MacArthur, 1961; Rosenzweig, 1995). The 'causal' diversity here might take the form of environmental heterogeneity which could promote coexistence by facilitating resource partitioning (MacArthur & MacArthur, 1961; MacArthur & Levins,

Correspondence: Lauren C. Ponisio, tel. +1 559 618 1303, fax +1 510-643 5438, e-mail: lponisio@berkeley.edu

1964), or it might correspond to some aspects of biodiversity promoting other components (Whittaker, 1972; Thompson, 2005) via interactions across trophic levels (Janz *et al.*, 2006). Disturbance diversity is also thought to promote biodiversity because shifting environmental conditions discourage dominance (i.e., the intermediate disturbance hypothesis: Connell, 1978; Huston, 1979; Martin & Sapsis, 1992). All of these mechanisms can also interact to enhance or suppress their individual effects (e.g., Rosenzweig, 1995; Collins *et al.*, 2007; Kane *et al.*, 2015).

Fire is a disturbance that has the potential to affect biodiversity patterns both directly and indirectly via interactions between biotic and environmental heterogeneity (Martin & Sapsis, 1992; Parr & Andersen, 2006; Collins *et al.*, 2007; Davies *et al.*, 2012; Maravalhas

& Vasconcelos, 2014; Kane *et al.*, 2015). A fire regime is characterized by the frequency, severity, patch size, extent, and season of fire. Fires regimes have landscape-scale consequences for fire patterns and biotic and abiotic diversity in space and time. All of these factors can be influenced by both biotic and abiotic diversity including topographic heterogeneity and forest structure (Collins *et al.*, 2007; Kane *et al.*, 2015). A landscape with a diverse fire history – high 'pyrodiversity' (Martin & Sapsis, 1992) – will be characterized by significant local variation in fire history whereby adjacent patches will not have identical fire histories. This variation can generate diversity in ecological niches across space and time, thereby allowing a greater number of species to coexist (Martin & Sapsis, 1992; Parr & Brockett, 1999; Burrows, 2008). In addition, if pyrodiversity increases biodiversity, this may in turn influence subsequent fires, creating a feedback that might beget additional diversity (Parr & Brockett, 1999; Burrows, 2008). For example, pyrodiversity can create a mosaic of different successional stages, allowing flora and fauna associated with those different stages to coexist. If areas with unique fire histories support unique communities, the diversity of fire histories through space contributes to the spatial heterogeneity of communities and the turnover of species, that is, *β*-diversity (Farnsworth *et al.*, 2014; Burkle *et al.*, 2015). Communities that are spatially heterogeneous in their composition support more regional diversity than areas with little species turnover (Farnsworth *et al.*, 2014).

Fire, however, also acts as an environmental filter by selecting for species that can tolerate disturbances (Cavender-Bares & Reich, 2012). Whether there is an opportunity for 'pyrodiversity to beget biodiversity' has, thus, been challenged by findings that some taxa do not respond to fine-scale variation in fire histories (Parr & Andersen, 2006; Andersen *et al.*, 2014; Farnsworth *et al.*, 2014). In addition, factors associated with land management, such as logging, grazing, and fire suppression and their interaction with the effects of climate change such as drier summers, have acted to decrease pyrodiversity by leading to larger, homogeneous, and higher severity burns (e.g., Dellasala *et al.*, 2004; Noss *et al.*, 2006; Miller, 2012; Moritz *et al.*, 2012). To assess whether changes in pyrodiversity will have impacts on ecological communities, we must first understand the mechanisms that might enable pyrodiversity to sustain biodiversity.

The preservation of species interactions is of particular concern because, through the mechanism of biodiversity begetting biodiversity, these interactions have the capacity to generate and maintain biodiversity (Thompson, 2005). Plant–pollinator interactions are particularly ubiquitous, with animal pollination positively influencing the reproduction of 87% of all flowering plant species (Ollerton *et al.*, 2011). Pollination systems, however, are under increasing anthropogenic threats from land-use change, habitat fragmentation, pesticide use, and invasions of non-native plants and animals (Kearns *et al.*, 1998; Potts *et al.*, 2010).

Although fire directly affects resources that are critical for sustaining pollinator populations, such as floral communities, our understanding of how pollinator communities assemble in response to fire is limited (Winfree *et al.*, 2009; Thom *et al.*, 2015). Past work has shown that secondary succession after fire can increase the abundance of floral resources which can, in turn, lead to higher diversity and abundance of bees (Potts *et al.*, 2001 2003a,b; Vulliamy *et al.*, 2006; Campbell *et al.*, 2007; Grundel *et al.*, 2010; Van Nuland *et al.*, 2013). Fire can also affect nest-site availability by increasing the abundance of key nesting resources, such as bare ground and cavities in dead wood (Potts *et al.*, 2005). Pyrodiversity may also play an important role in sustaining pollinator diversity because pollinators differ in their degree of direct susceptibility to fire (Cane & Neff, 2011). Few studies have, however, explored the effects of fire on pollinators in forested ecosystems where altered fire regimes may have the greatest impact. This lack is likely because fire regimes are so altered by human activities (Miller, 2012) that there are few landscapes where it is possible to study the interaction between natural fire patterns and wildlife communities.

In addition to understanding the direct effects of pyrodiversity on communities, we must also examine how pyrodiversity might interact with the types of disturbances that we expect to become more frequent in the future. Future climate projections predict in some regions droughts, of both long and short duration, to double and triple, respectively (Sheffield & Wood, 2008). Drought has far-reaching effects on forested ecosystems (Dale *et al.*, 2001) and affects pollinators by diminishing availability of pollen and nectar resources (Rashad & Parker, 1958; Iserbyt & Rasmont, 2012) and may also cause shifts in the composition of pollinator communities and even extinction (Ehrlich *et al.*, 1980; Minckley *et al.*, 2013). If drought interacts with fire history such that resources are differentially affected in different areas, pyrodiversity may be important to buffer the impacts of resource scarcity.

Here, we utilize a landscape with a restored fire regime in Yosemite National Park to test whether landscape diversity, in the form of environmental diversity or pyrodiversity, contributes to the maintenance of plant–pollinator biodiversity. We first determine whether pyrodiversity or the diversity of environmental conditions (solar radiation, water availability, and

soil condition) affects local flowering plant and pollinator richness. In addition, to test whether landscape diversity has the potential to maintain biodiversity through promoting species interactions, we examine the relationship between landscape diversity and the richness of plant–pollinator interactions. Next, we determine whether different fire characteristics, mainly fire severity, has the potential to contribute to regional plant–pollinator diversity through affecting community spatial heterogeneity. Lastly, we examine whether fire diversity buffers pollinator communities against drought-induced resource scarcity. Our study is the first to examine the potential of fire diversity to sustain the plant–pollinator biodiversity, as well the first to examine the response of species interactions to pyrodiversity.

Materials and methods

Study sites and collection methods

Our study is located in the Illilouette Creek Basin of Yosemite National Park, in the central Sierra Nevada of California. The basin is approximately 20 000 hectares and has never been harvested or grazed. The Illilouette is in the upper elevation mixed-conifer zone and is dominated by Jeffrey pine (*Pinus jeffreyi*), white fir (*Abies concolor*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta* var. *murrayana*), interspersed with meadows and shrublands. Based on tree-ring reconstructions, the historic fire regime predominantly consists of frequent fires, where the alteration of vegetation and soils, known as fire severity, is low to moderate (Collins & Stephens, 2010). Fire was suppressed from the late 1800s until the early 1970s, when Yosemite National Park adopted a 'let burn' management strategy. Lightning-ignited fires are allowed to run their course, restoring natural fire regimes to the basin and creating a patchwork of burns of varying severities and ages. Because of the unique fire management of the Illilouette Basin, it has a long history of research on the dynamics of frequent fires in forested ecosystems (Collins *et al.*, 2007; Collins & Stephens, 2007 2010; van Wagtendonk *et al.*, 2012). Importantly, studies have found that after only 30 years of allowing lightning-ignited fires to burn, the historic fire regime and forest structure have been largely restored to the basin (Collins & Stephens, 2007).

In 2013, we established 18 monitoring sites, each (50 m^2), across the Illilouette Basin. Monitoring sites were separated by an average of 4 km and a minimum of 500 m (greater than the foraging distance of most bees, Gathmann & Tscharntke, 2002). Sites were split between two fires, one that burned in 2001, and the other in 2004.

Within each fire perimeter, sites were chosen randomly by selecting coordinates from a 100 m grid (within 2 km of a trail), but stratified to include different burn severities of the most recent fire. The severity of a burn not only influences changes to soil chemistry and vegetation, but can also affect the plant community that develops (Turner *et al.*, 1999; Wang

& Kemball, 2005; Swanson *et al.*, 2010). We sampled across different fire severities so that we could explore the interaction between fire severity and plant/pollinator community assembly. Burn severity was classified according to the Relative difference Normalized Burn Ratio (RdNBR; Miller & Thode, 2007) at a (30 m)^2 resolution, and six predominantly high, five moderate, and seven low burn severity were selected (Fig. 1c). High-severity sites had open canopies due to high rates of tree mortality following the fire and high soil disturbance from the fire. Moderate-severity sites also had open canopies, but less tree mortality and soil disturbance. Low-severity sites had little soil disturbance or tree mortality.

We sampled pollinator communities between June and August in 2013 and 2014. Each year, sites were sampled four times. Sampling began earlier in 2014 to account for the timing of the snow melt. In each round of sampling, the order in which sites were sampled was randomized. Surveys were conducted under sunny conditions when the temperature was above 12 °C and wind speed was below 2.5 m s^{-1}. Flower visitors were netted for 1.5 h of active search time (the timer was paused while handling specimens). In addition, five sets of fluorescent blue, white, and fluorescent yellow pan traps (15 total) were set 12.5 m apart in two lines forming an 'X' for 4.5 h following established protocols (modified from LeBuhn *et al.*, 2003). Pans were placed in clusters of three with one pan of each color.

All insect flower visitors that touched the reproductive parts of the flower and insects that entered the pan traps were collected; however, here we focus only on bees, the most abundant and efficient pollinators in the system. Bee specimens were identified to species (or morpho-species for the genera *Hylaeus*, *Nomada*, and *Sphecodes* and *Lasioglossum* subgenus *Dialictus*). Expert taxonomist Jason Gibbs aided with assigning the morpho-species classifications to males and females.

Floral resources were also surveyed each time pollinators were sampled. To do this, each blooming plant species (excluding graminoids) in the monitoring site was recorded. We did not record plants that bloomed outside of the flight season of the pollinators (e.g., early season plants like *Arctostaphylos*) or night-blooming flowers because they are not as less likely to interact with the pollinator community we sampled. For each blooming species, an estimate of the number of inflorescences within the sampling area was also recorded (estimated on a log scale). To make an estimate, the site was divided into quadrants and the number of inflorescences of each species was counted, then summed for an estimate of the site.

During our collection period, the Sierra Nevada experienced a drought that began in 2012 (Griffin & Anchukaitis, 2014). In 2013, the intensity of the drought in our study area was categorized as 'severe' (Griffin & Anchukaitis, 2014). In 2014, the drought conditions were upgraded to 'extreme' and 'exceptional' – the highest moisture deficit accumulation than any previous recorded span of years (Griffin & Anchukaitis, 2014). In the field, the difference between 2013 and 2014 was clear; water levels were lower in the streams and rivers throughout the season and there were few of the usual summer lightning storms. In addition, perennial plants like
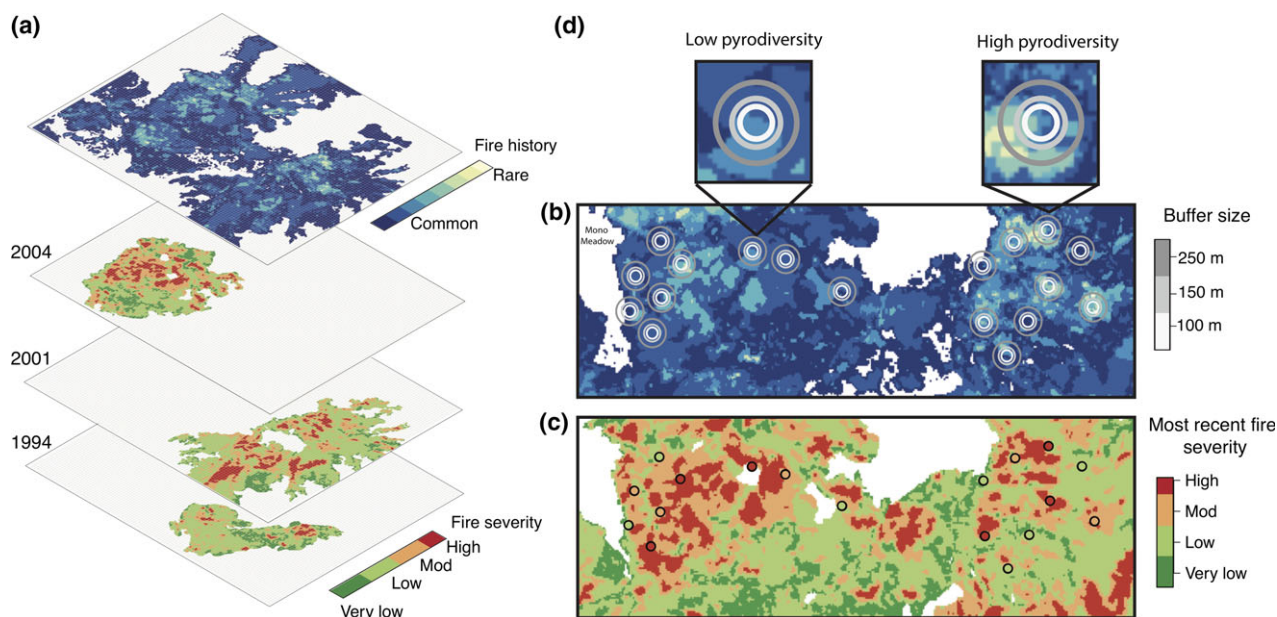
Fig. 1 Representation of the method used to estimate pyrodiversity. (a) Each raster cell is assigned a fire history classification based on the fires and severities it experienced (three representative fires depicted). (b) The diversity of fire histories, either weighted for the similarity of fire history or unweighted, is calculated within buffers 100−250 m around the monitoring sites. (c) The severity of the most recent fire is also included as a possible interaction with pyrodiversity. (d) An example of sites with relatively low and high pyrodiversity measured as the diversity of unique fire histories at different buffer sizes. In the low pyrodiversity example, the pyrodiversity was estimated as 0.2, 0.5, and 0.7 within the 100, 150, and 250 m buffers, respectively. In the high pyrodiversity example, the pyrodiversity was estimated as 0.7, 0.8, and 0.8 in buffers of increasing diameter. Within a buffer, the number of different fire history categories ranged from 1 to 23. Larger buffer sizes were not included because there was considerable overlap between buffers around different sites beyond that threshold. Smaller buffers were also not included because at scales smaller than 100 m most buffers only contained one fire history category (i.e., a pyrodiversity score of zero). Some buffers overlapped areas did not burn during the time period for which we have burn history data (i.e., Mono Meadow, large rocky outcrops, and fires that occurred before 1984). Those areas were assigned their own fire history category.

Ceanothus cordulatus experienced die back from exposure to freezing temperatures because of insufficient snow pack. Many plants that bloomed in 2013 did not in 2014 and many areas the blooming period was cut short. We therefore contrast the communities in 2013 and 2014 to determine the influence of drought intensity on flowering plant and pollinator communities. This test is not replicated in time and factors other than drought intensity changed. However, given the known effects of drought on plant and pollinator communities and the drastic decline in water availability between 2013 and 2014, we assume the majority of the shifts in the communities between these years were due to the increase in drought intensity.

Pyrodiversity

To estimate pyrodiversity, we developed a metric to quantify the diversity of the fire histories in relation to fire frequency, age, extent, and severity experienced in an area. We obtained fire history data of our study area, dating back to 1984, from Yosemite National Park and the United States Forest Service (Miller, 2012; van Wagtendonk *et al.*, 2012; Yosemite National Park, 2012). Each fire digitization contains rasterized values of burn severity (Miller & Thode, 2007). Fire season, another

component of fire history, was not directly considered. There was, however, little variability in fire season within any one fire, and most fires occurred in different months. Thus, season is indirectly included in the identity of each fire.

To estimate pyrodiversity, we evaluated the uniqueness of the fire history of each raster cell (30 m^2 resolution, Fig. 1a). We first created categories of fire severity within a fire (Miller, 2012). For each raster cell, we then used the sequence of fires and the severity of each of those fires to define unique fire histories. We identified 135 unique fire histories in the basin. We then considered two different ways of characterizing pyrodiversity as the diversity of unique fire histories either unweighted or weighted by their similarity. To calculate the unweighted pyrodiversity score, raster cells received different categories if they differed in any aspect of fire history; for example, if they were burned by the same fire but at different severities, or if they were burned by different fires, even if at the same severity. Pyrodiversity was then calculated as the Simpson's diversity of fire history categories (the compliment of the sum of the squared proportion of each fire history category) around a monitoring plot within 100−250 m buffers in increments of 50 m (Fig. 1, Tscharntke *et al.*, 2005). This allowed us to evaluate the scale at which pyrodiversity affected plant and pollinator communities most strongly.

To calculate the weighted pyrodiversity score, we transformed fire characteristics, mainly the year the fire occurred and severity, into traits for each pixel and then used a functional dispersion metric to calculate the diversity of fire 'traits' (see Appendix S1). The fire histories of each raster cell were thus weighted based on the similarity of fire traits. For example, a low-severity pixel in the same fire would be more similar to a moderate-severity pixel than to a high-severity pixel. Fire traits were also weighted by the number of years since the fire occurred to account for the variety of fire ages. Like the unweighted pyrodiversity, we calculated the weighted pyrodiversity score within different buffer sizes around the survey sites.

To determine the effect of pyrodiversity on flowering plant and pollinator communities and their interactions, we built generalized linear mixed models that reflected our biological hypotheses (Bates *et al.*, 2014). We included richness of bees, flowers, and interactions (the unique combination of bee and floral species observed interacting in netted samples) in each sample as response variables and pyrodiversity (either weighted or unweighted) as an explanatory variable. Because fire severity can have strong effects on the plant communities that develop after fire (Turner *et al.*, 1999; Wang & Kemball, 2005; Swanson *et al.*, 2010), we included an interaction between pyrodiversity and fire severity of the most recent fire to allow the response of the flowering plant and pollinator communities to pyrodiversity to depend on the most recent fire's severity. Because the sites were split between fires that burned only 3 years apart, we did not have sufficient variation in the time since the most recent fire to include it as an explanatory variable.

To test whether the effect of pyrodiversity on plant and pollinator communities is mediated by drought intensity, we also included an interaction between year, which is interpreted as primarily reflecting a shift in drought intensity, pyrodiversity, and fire severity. A significant negative interaction between pyrodiversity and year would indicate that the response of flowering plants, bees, and their interactions to pyrodiversity was eroded by increasing drought intensity. In addition, a significant interaction between year, pyrodiversity, and the severity of the most recent fire would indicate that the response of communities to shifts in climate varies depending on the fire severity of the area.

When considering floral species richness as our response, we included a linear and quadratic day of the year term to allow for a seasonal phenology in flower blooming. We also included a random effect of site in this and all subsequent models. We assumed negative binomial error for pollinator models, and Poisson error for floral models. To facilitate interpretation of coefficients, all continuous variables were scaled by subtracting the mean and dividing by the standard deviation.

Simulations of the null hypothesis (no effect of the explanatory variables) suggested that the models had an inflated type I error rate, approximately equal to 0.1 with a nominal P-value of 0.05 (Ives, 2015); therefore, we used parametric bootstrapping to quantify support for a model that includes pyrodiversity, an interaction between pyrodiversity and fire severity, and an interaction between pyrodiversity, fire severity, and drought intensity in the models (Booth, 1995). All statistical analyses were conducted in R version 3.2 (R Core Team, 2014).

Environmental heterogeneity

We hypothesized that plant–pollinator communities would likely respond to solar radiation, water availability, and soil conditions. We therefore considered the effect of the following three measures of environmental heterogeneity (see Appendix S1 for details): heat load (i.e., McCune's solar radiation, an estimate of solar radiation taking latitude, slope and aspect into account, McCune & Keon, 2002) and topographic compound index (an estimate of the balance between water accumulation and drainage, Evans *et al.*, 2014).

As we did for our metric of pyrodiversity, we calculated the diversity of environmental conditions in buffers of different sizes and used this estimate as a metric of environmental heterogeneity for each variable (see Appendix S1). We considered weighted environmental heterogeneity only because the variables are not naturally categorical. We also could not create a composite metric across all environmental variables because there were too many unique combinations of variables to yield meaningful measures of diversity.

To examine the effect of environmental heterogeneity on flowering plant and pollinator communities, we followed the same approach as we did when examining the influence of pyrodiversity. With bee, floral or interaction richness as response variables, each environmental heterogeneity measure, along with terms for interactions between that environmental variable and severity of the most recent fire as well as drought intensity were included as explanatory variables. Parametric bootstraps were used to determine the support for including the environmental heterogeneity and the interaction between environmental heterogeneity, drought, and fire severity in the model.

β-diversity

Pyrodiversity may also influence the regional diversity of an area by affecting the spatial heterogeneity of communities. If areas that experienced different fire characteristics support distinct communities, this will lead to species turnover (β-diversity). Similarly, communities with similar fire characteristics may share many species, leading to less spatial heterogeneity between those communities. We investigated the flowering plant, pollinator, and interaction β-diversity between communities with different fire characteristics and compared that to the β-diversity between sites with similar fire characteristics. Because of its strong effects on site conditions, we focused on the severity of the most recent fire to group communities by fire similarity.

We first calculated the pairwise dissimilarity in plants, pollinators, and interactions between site pairs across all sites and within each fire severity classification (calculated using

the Jaccard index of dissimilarity, a proxy for species turnover through space. We also standardized turnover estimates to account for differences in the richness between sites (see Appendix S2 for details).

For the community dissimilarity across and within fire severity classifications, we regressed pairwise community dissimilarity against geographic distance using linear mixed models (Bates *et al.*, 2014; Kuznetsova *et al.*, 2014). A positive relationship between community dissimilarity and geographic distance would suggest that communities were spatially structured such that communities that are closer together share more species than communities that are farther apart.

Additionally, in the model of dissimilarities within a fire severity classification, we included an interaction between pairwise site distances and the fire severity of the site-pair to allow the different site types to have different rates of turnover through space. A significant interaction with the severity of the most recent fire and the geographic distance between communities would indicate that the rate of species turnover was influenced by fire severity.

Lastly, if the positive relationship between geographic distance and community dissimilarity is stronger between all sites than between sites of the same fire severity, this would be evidence shared fire severity between sites increases the similarity of these communities. Thus, a diversity of fire characteristics would contribute positively to the dissimilarity between sites and subsequently β-diversity.

Resource availability and use

We next investigated whether fire diversity has the potential to buffer against drought-induced resource scarcity. We first asked whether the floral resources in areas with contrasting fire characteristics responded differently to drought. We again focused on severity of the most recent fire to contrast the fire characteristics of an area. We used the total number of inflorescences of each plant species as a proxy for floral resource availability.

To determine whether fire severity influenced the effect of drought on resource availability, we asked whether floral resources depended on the interaction between severity of the most recent burn and year, assuming that the resource differences between years are primarily attributable to the shift in drought intensity. We also included a linear and quadratic term for day of the year to account for floral phenologies. The measurements of floral abundance were taken at the level of flowering plant species, so we included a random effect of plant species to account for differences in the number of inflorescences across species. We log-transformed floral abundance and assumed a Gaussian error distribution. A negative effect of year would indicate that floral resources were decreased in a more extreme drought year, and an interaction with fire severity would indicate that that magnitude of the effect of drought was influenced by fire characteristics.

Fire severity may also buffer against the effects of resource scarcity by influencing the way pollinator resource use is altered by drought. Limited floral resources might cause pollinators to visit less preferred resources or shift the pollinator community composition to favor generalists. If different fire severity areas are differentially affected by drought, however, some areas may be able to maintain a more stable level of interaction specialization through shifts in resource availability. We therefore first determined whether bee community specialization differed between years to look for an effect of drought intensity, and whether there was evidence for an interaction effect between year and the severity of the most recent fire.

To investigate this, we created plant–pollinator interaction networks for each survey day. We then calculated community-level specialization (H2, Blüthgen *et al.*, 2006). This specialization metric measures the deviation of the observed interaction frequency between plants and pollinators from a null expectation where all partners interact in proportion to their abundances (Blüthgen *et al.*, 2006). To standardize the metric across communities with different numbers of species and abundance distributions, we also corrected the specialization estimates using the expected specialization of randomly assembled communities with the same species richness, species' abundances, and interactions per species (Blüthgen *et al.*, 2006; Vázquez *et al.*, 2007). To detect changes in specialization across years, we used the community-level specialization scores as the response variable in a linear mixed model that included a term for the interaction between fire severity and year. A negative effect of year would suggest that pollinators were more generalized in a more extreme drought year, and an interaction with fire severity would indicate that the shift in foraging behavior was influenced by fire characteristics.

Fire severity might also affect pollinator resource use and its interaction with drought by influencing the spatial distribution of pollinators in relation to their floral hosts. If pollinator communities track floral resources, differences in floral community composition between sites should lead to corresponding differences in pollinator communities. Fire severity may also interact with this process if, for example, only high-severity areas support plants that primarily attract the specialized pollinators that are most likely to track the distribution of their floral hosts. Thus, high- severity pollinator community composition would be most strongly correlated with floral host composition. Drought might enhance or diminish this pattern in areas with specific fire severities, depending on its effect on pollinator community specialization.

To investigate this hypothesis, we tested for an interaction between year and fire severity on patterns of pollinators tracking specific floral resources across space. We correlated the floral community dissimilarities to analogous dissimilarities for the pollinator communities using Mantel tests, analyzing each year separately. We did this within and across communities in different burn severities to determine whether pollinators tracked resources differently depending on the severity of the most recent fire. We used an abundance-based measure to estimate the dissimilarity of plant and pollinator communities (Chao *et al.*, 2005).

Results

Over 2 years and across 18 sites, we collected 7626 bee specimens comprising 162 species or morphospecies

across 32 genera. We observed pollinator visitation on 71 flowering plant species. We observed 1213 unique plant–pollinator interactions (10.5% of potential interactions). Over one thousand specimens were collected in each of the genera *Bombus*, *Lasioglossum*, and *Hylaeus*. The most species-rich genera were *Osmia* (36 species), *Andrena* (19 species), *Lasioglossum* (12 species or morphospecies), and *Megachile* (12 species). Approximately 20% of the bee species were observed only once, and approximately 40% of species were collected fewer than five times, rates that are consistent with what is found in other, even longer term studies (e.g., Olesen *et al.*, 2008; Petanidou *et al.*, 2008; M'Gonigle *et al.*, 2015). In addition, in a 4-year survey across all of Yosemite National Park, T. Griswold and colleagues collected around 520 bee species and morphospecies, and in our survey, we collected 30% of those species. All plant and pollinator species were native except the European honey bee, *Apis mellifera*, which was common throughout the basin. Around 800 (11%) of collected specimens were honey bees.

Pyrodiversity

Pyrodiversity, both weighted and unweighted by the similarity of fire histories, positively affected floral, pollinator, and interaction richness, although the strength of the effect depended on the scale at which pyrodiversity was calculated (Figs 2 and S2). The effect size of both metrics of pyrodiversity peaked within 150 m of the monitoring area (Tables 1 and S1). Within this buffer, the unweighted diversity of fire histories ranged from 0.25 to 0.85 and weighted diversity from 0.03 to 0.13 (both with hypothetical ranges from 0 to 1). In addition, unweighted pyrodiversity at a 150 m scale explained significant variation in the plant, pollinator, and interaction richness. Weighted pyrodiversity interacted with the severity of the most recent fire and, for pollinators and plant–pollinator interactions, pyrodiversity also interacted with drought intensity (Table 1). Weighted pyrodiversity showed similar trends, although the significance was marginal (Table S1). Because the trends were similar but unweighted pyrodiversity showed a stronger effect, we focus on the response of communities to unweighted pyrodiversity.

In areas where the most recent fire was low or moderate in severity, pyrodiversity had a positive effect on bee, floral, and interaction richness (Table 2; Fig. 2). This translates into a mean gain of ~54–58 bee species (~35% of the observed bees), 8–14 flowering species (~20% of flowering plants), and 24–43 interactions (~4% of interactions) between areas with the minimum and maximum observed pyrodiversity. In

areas where the most recent fire was high in severity, however, floral, pollinator, and interaction richness did not respond to pyrodiversity (Table 2; Fig. 2).

High-severity areas, however, had higher plant, pollinator and interaction richness than low-severity areas at mean levels of pyrodiversity (i.e., at pyrodiversity = 0, Fig. 2, estimate ± bootstrapped standard error of the estimate of the difference between low- and high-severity sites bee richness, 2.171 ± 0.17; plant richness, 0.440 ± 0.21; interaction richness, 0.532 ± 0.28). This corresponds to an average of 5 more pollinator and plant species and nine more interactions in high-severity sites than in low-severity sites. Moderate-severity sites also had higher pollinator and floral richness than low-severity sites (bee richness, 1.545 ± 0.18; plant richness, 0.300 ± 0.22). In moderate-severity sites, there was an average of four more plant and pollinator species than in low-severity sites.

There was a significant effect of year on bee and interaction richness, suggesting a negative effect of drought (estimate for the difference between 2013 and 2014 ± standard error of the estimate, bee richness: −0.330 ± 0.09; interaction richness: −0.625 ± 0.09). This resulted in 3, 3, and 7 fewer bee species and 6, 6, and 8 fewer interactions in low, moderate, and high-severity sites, respectively. The decline in interaction richness in moderate-severity sites was buffered in these sites where the difference between years was less pronounced (estimate for interaction between moderate-severity site and year ± standard error of the estimate, 0.315 ± 0.12).

In contrast, floral richness in low- and moderate-severity sites was not significantly reduced in the more extreme drought year, but it was in high-severity sites (estimate of the decline in floral richness, −0.28 ± 0.14, Fig. 2). Species richness in high-severity areas declined by an average of three flowering species.

Response of bee and interaction richness to pyrodiversity was weaker in the more intense drought year, and the magnitude of the difference was higher in areas where severity of the last burn was low or moderate (Table 1; compare the slope of moderate and low in 2013 vs. 2014, Table 2; compare first and second panels, Fig. 2). The interaction of year and the relationship between floral richness and pyrodiversity were not significant (Table 1; Fig. 2).

Environmental heterogeneity

Plant and pollinator communities did not respond to the measures of environmental heterogeneity we considered at any scale, except there was a negative relationship between bee and interaction richness and heat
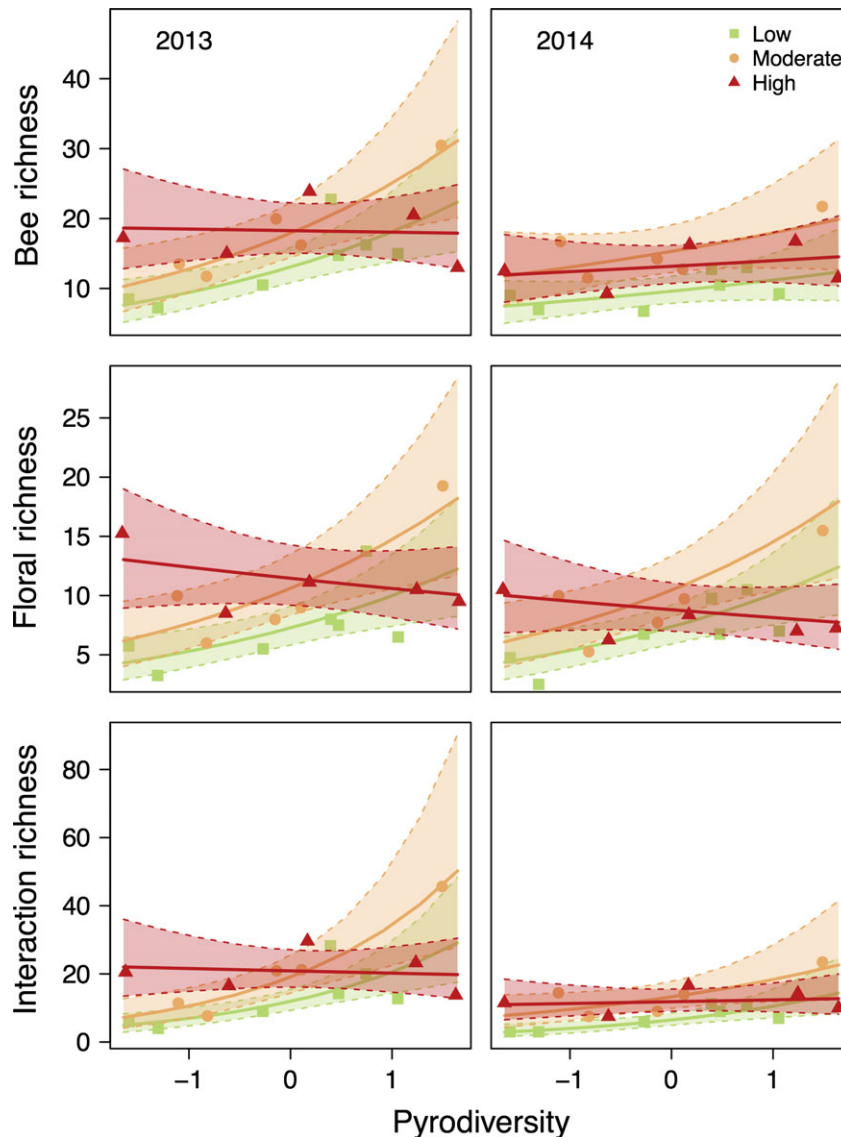
Fig. 2 The response of bee, floral, and interaction richness to pyrodiversity. The color of the curves and points correspond to low, moderate, and high severity of the most recent fire classifications. The columns depict trends in 2013 and 2014, severe and extreme/exceptional drought years, respectively. The solid line indicates the mean slope estimate, and the dashed lines are the 95% confidence intervals around the estimate. Points represent the richness of plants, pollinators, or interactions averaged across the study season. The pyrodiversity axis is scaled so that zero represents the mean pyrodiversity.

load diversity at a buffer size of 200m and 250m (Tables S2 and S3; Fig. S3).

β-diversity

The dissimilarity between flowering plant communities across the landscape was positively related to the distance between sites (estimate of the slope of dissimilarity with distance across all sites, 0.06 ± 0.026, *P*-value = 0.02, Fig. 3). In addition, the rate of turnover of floral communities depended on the severity of the fire they experienced (Fig. 3). The dissimilarity

between floral communities in high-severity sites did not respond to the distance between sites, whereas the dissimilarity between communities in low and moderate burn sites increased with distance at the same rate (estimate of the slope of dissimilarity with distance in low- and moderate-severity areas: 0.18 ± 0.055, *P*-value = 0.002, Fig. 3). The floral community dissimilarity at the mean geographic distance between sites was not significantly affected by burn severity, although the dissimilarity of higher severity sites was higher at the smaller geographic distance between sites.

Table 1 The support for including pyrodiversity of unique fire histories and its interaction with fire severity and drought intensity. χ^2 values represent the ratio of the likelihoods of the model with and without the variable of interest. *P*-values are calculated via 1000 parametric bootstrap iterations. They represent the probability of observing a χ^2 value more extreme than the observed value when data are simulated from the model without the variable of interest. Symbols denote significance, with ′ and * indicating 0.1 and 0.05, respectively. Significant terms are bolded

	Buffer radius	No interaction		Severity interaction		Severity, drought interaction	
		χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value
Bee richness	100	3.984	0.084′	6.818	0.193	12.765	0.122
	150	**5.905**	0.030*	10.074	0.072′	**17.044**	0.034*
	200	4.402	0.065′	7.517	0.163	12.467	0.140
	250	1.932	0.217	3.528	0.496	8.786	0.298
Floral richness	100	2.06	0.222	6.91	0.186	9.341	0.280
	150	3.969	0.104	**13.213**	0.025*	13.84	0.064′
	200	3.101	0.123	8.269	0.132	8.442	0.318
	250	0.923	0.406	2.662	0.602	2.697	0.901
Interaction richness	100	3.996	0.081′	6.877	0.170	15.009	0.067′
	150	**5.897**	0.047*	10.187	0.080	**19.52**	0.020*
	200	4.393	0.058′	7.563	0.161	14.427	0.078′
	250	1.940	0.248	3.582	0.487	10.903	0.179

Table 2 The estimate and standard error of the slope of bee , floral, and interaction richness against pyrodiversity. Terms where the 95% confidence interval around the parameter estimate did not overlap zero (indicated in bold) were inferred to explain significant variation in floral, bee or interaction richness (using the parametric bootstrap). Standard errors of the parameter estimates are calculated as the standard deviation of the parametric bootstrap estimates of the coefficient of interest (Booth, 1995)

	Buffer radius	Year	Low	Mod	High
Bee richness	100	2013	0.22 ± 0.122	0.408 ± 0.18	0.021 ± 0.105
	150	2013	**0.326 ± 0.125**	**0.337 ± 0.148**	−0.012 ± 0.115
	200	2013	0.196 ± 0.094	0.439 ± 0.188	−0.026 ± 0.141
	250	2013	0.144 ± 0.093	0.411 ± 0.219	−0.043 ± 0.138
	100	2014	0.044 ± 0.124	0.238 ± 0.176	0.076 ± 0.110
	150	2014	0.152 ± 0.127	0.16 ± 0.155	0.06 ± 0.113
	200	2014	0.086 ± 0.102	0.238 ± 0.192	0.066 ± 0.138
	250	2014	0.054 ± 0.099	0.132 ± 0.217	0.043 ± 0.141
Floral richness	100	2013	0.095 ± 0.133	0.457 ± 0.201	−0.001 ± 0.122
	150	2013	**0.317 ± 0.137**	**0.329 ± 0.173**	−0.078 ± 0.125
	200	2013	0.161 ± 0.110	0.45 ± 0.210	−0.054 ± 0.152
	250	2013	0.102 ± 0.110	0.294 ± 0.249	−0.057 ± 0.158
Interaction richness	100	2013	0.318 ± 0.185	0.769 ± 0.291	0.003 ± 0.183
	150	2013	**0.543 ± 0.201**	**0.59 ± 0.245**	−0.033 ± 0.174
	200	2013	0.318 ± 0.159	0.821 ± 0.3	−0.054 ± 0.216
	250	2013	0.224 ± 0.148	0.806 ± 0.357	−0.076 ± 0.239
	100	2014	0.272 ± 0.207	0.444 ± 0.296	0.084 ± 0.174
	150	2014	**0.485 ± 0.209**	0.325 ± 0.235	0.045 ± 0.179
	200	2014	0.307 ± 0.164	0.406 ± 0.309	0.059 ± 0.218
	250	2014	0.229 ± 0.155	0.18 ± 0.357	0.038 ± 0.226

The relationship between floral community dissimilarity and distance was weaker across all sites than the relationship within moderate and low-severity sites. In addition, at the mean distance between sites, the dissimilarity of floral communities between all sites was similar to the dissimilarity between sites that experienced the same fire severity (estimate of the dissimilarity across all sites vs. within the same fire severity, 0.47 ± 0.026 vs. 0.470 ± 0.054). Therefore, floral species turnover between sites across dif-
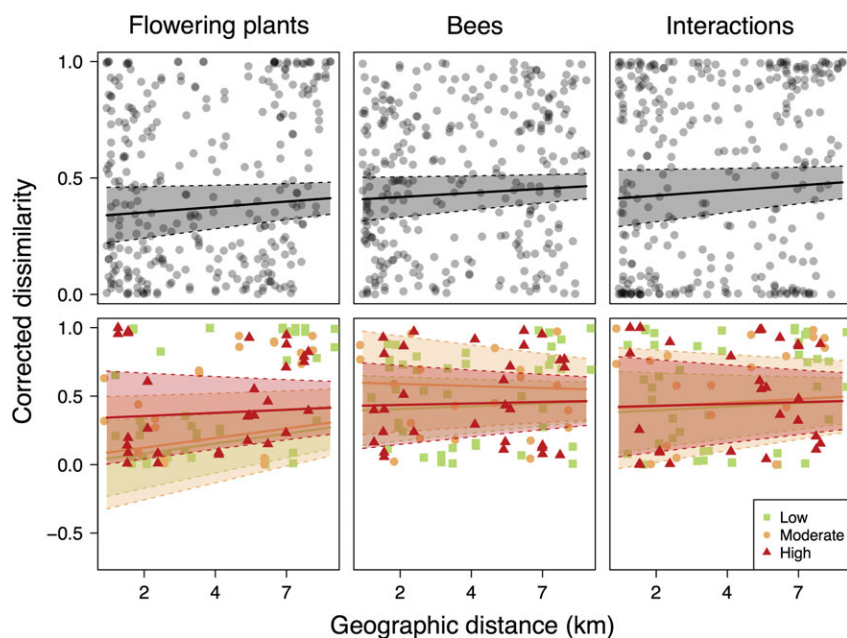
Fig. 3 The floral, bee, and interaction composition turnover across all sites (top panels) and within a fire severity classification (bottom panels). Points represent the pairwise dissimilarity of communities (corrected for differences in species richness). The solid line indicates the mean slope estimate, and the dashed lines are the 95% confidence intervals around the estimate.
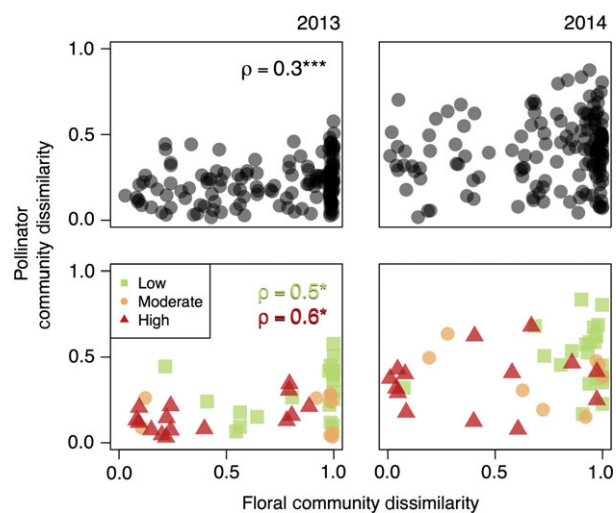
Fig. 4 The effect of the more recent fire severity an area experienced and drought intensity on resource use of pollinators across different fire severities (top panels) and between plant and pollinator communities at sites with similar fire histories (bottom panel). ρ corresponds to the Mantel statistic. Symbols denote significance, with * and *** indicating 0.05 and 0.001, respectively.

ferent fire severities is not stronger, on average, than the turnover between sites that experience similar fire histories.

In contrast to the floral communities, bees and interactions were only structured geographically across all sites (estimate of the slope of distance and bee commu-

nity dissimilarity: 0.046 ± 0.020, *P*-value = 0.03; interaction dissimilarity 0.053 ± 0.026, *P*-value = 0.03; Fig. 3).

Resource availability and use

Fire severity affected both availability of floral resources and their diminishment in response to increasing drought intensity. High-severity burn areas had higher floral abundance than low-severity areas (estimate $\pm$ standard error of the difference between high- and low-severity sites in log floral abundance, 2.920 ± 1.42, *P*-value = 0.05, Fig. S4), but flower abundance declined more strongly than in low- and moderate-severity sites in the extreme drought year (estimate of the decline in floral abundance, -7.60 ± 0.90, *P*-value $= 10^{-16}$, Fig. S4). Moderate- and low-severity sites also declined in flower abundance between years (-3.74 ± 0.96, *P*-value $= 10^{-5}$, Fig. S4). Pollinators were significantly more generalized in the more extreme drought year (estimate of the difference in specialization between 2013 and 2014, -0.45 ± 0.21, *P*-value = 0.004, Fig. S5), although fire severity did not influence this shift.

In addition, drought also disrupted the spatial correspondence between the composition of pollinator and floral communities. Like specialization, however, fire severity did not influence this change. In 2013, across the study landscape, the dissimilarity of pollinator commu-
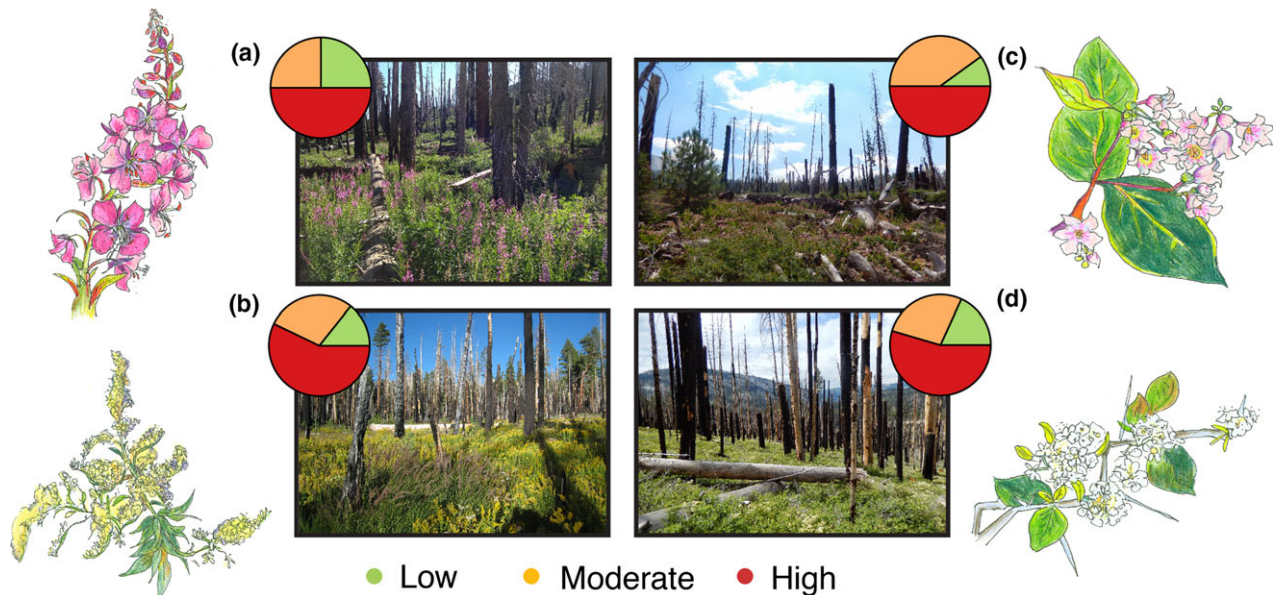
Fig. 5 The proportion of sites with disturbance specialists (a) *Epilobium angustifloium circumvagum* (fireweed), (b) *Solidago canadensis elongata* (goldenrod), (c) *Apocynum androsaemifolium* (dogbane), and (d) *Ceanothus cordulatus* (mountain whitethorn). *S. canadensis elongata* and *C. cordulatus* are nitrogen fixers. Photographs (a), (b), (d) by L. Ponisio and (c) by S. Stephens. Botanical illustrations by T. Norwood.

nities was significantly correlated with the plant community (ρ = 0.3, *P*-value = 0.009, Fig. 4), suggesting that pollinators track their floral hosts. Additionally, in high- and low-severity sites, the dissimilarity of plant and pollinator communities was significantly correlated (high: ρ = 0.6, *P*-value = 0.02, low: ρ = 0.5, *P*-value = 0.05, Fig. 4). These relationships disappeared in 2014. The dissimilarity of bee communities in areas with moderate-severity burns was not significantly correlated with the dissimilarity of flowering plants in either year.

Discussion

We have shown that fire diversity contributes to the maintenance of flowering plant and pollinator biodiversity. Plant–pollinator communities in low- and moderate-severity burn areas with the maximum observed pyrodiversity (as measured by the diversity of fire histories around a site) had 34% more pollinator species, 33% more flowering plant species, and 14% more interactions, on average, than areas with the minimum pyrodiversity. The turnover of pollinators and species interactions between areas with different fire characteristics was also greater than within areas that experienced the same most recent fire severity, suggesting fire characteristic diversity is important for maintaining the spatial heterogeneity of pollinator community composition and plant–pollinator interactions. Lastly, fire severity interacted with drought such

that floral resources were differentially affected depending on the severity of the most recent fire, suggesting that the diversity of fire characteristics may buffer the impacts of resource scarcity.

Importantly, however, the severity of the most recent fire interacted with the response of plant–pollinator communities to fire diversity. Flowering plants, pollinators, and their interactions in low- and moderate-severity burns responded positively to pyrodiversity, whereas communities in high-severity burns did not. Similarly, flowering plant communities in low- and moderate-severity sites were spatially structured (i.e., species turnover between sites increased with the geographic distance between them) while the floral communities at high-severity sites were not. High-severity fires, by definition, strongly affect biotic and abiotic soil conditions and, importantly, often volatilize soil nitrogen (Hart *et al.*, 2005; Hamman *et al.*, 2008; Johnson *et al.*, 2008). This may act as a biotic filter, limiting which plant species can establish and persist after a high-severity fire. If only a subset of plant species are able to colonize or germinate after a high-severity fire, the community that forms will depend less sensitively on landscape context and, hence, will be less affected by the surrounding pyrodiversity. A limited successful species pool would also constrain the spatial turnover of species. For example, in our study, the communities that characterize high-severity patches are often early successional species such as nitrogen fixers and other

disturbance specialists (Coladonato, 1993; Aleksoff, 1999; Groen, 2005, Fig. 5).

In contrast to high-severity sites, low-severity sites were characterized by a greater number of late succession species, while moderate-severity sites were characterized by a mix of early and late colonizers (Fig. 5). By altering the biotic and abiotic soil and canopy structure around these sites (Hart *et al.*, 2005; Hamman *et al.*, 2008; Johnson *et al.*, 2008), a mosaic of fire histories may create a diversity of ecological niches at local and landscape scales. Unlike in high-severity sites, after a fire, a diversity of source populations could subsequently colonize and persist. Together, these mechanisms would allow species of different successional stages to coexist, thus facilitating the establishment of species-rich floral communities. The response of the bee communities to pyrodiversity mirrored the response of the flowers. This is likely a result of plant–pollinator interactions and suggests that pyrodiversity has the capacity to generate and maintain biodiversity via interactions across trophic levels (Potts *et al.*, 2003b; Thompson, 2005; Janz *et al.*, 2006).

Bees may also benefit from the greater diversity of nesting resources that may be found in sites with greater pyrodiversity. In low- and moderate-severity sites, the strongest responses to pyrodiversity were in genera of species with diverse nesting habits, particularly *Osmia* and *Bombus* (Fig. S6, Cane *et al.*, 2007). A diverse fire history may thus increase heterogeneity among nesting resources and thus allow species with different preferences to coexist. In addition, in some genera there is evidence that floral preferences mediate the response of species to pyrodiversity. For example, *Andrena* species richness was generally positively related to pyrodiversity, though with some variability (Fig. S6). Nine of the 19 *Andrena* species were collected visiting primarily *Ceanothus cordulatus* (Fig. 5), and the sites with high pyrodiversity but low *Andrena* species richness did not have blooming *C. cordulatus*. Thus, although bee richness may respond to diversity of fire histories in an area, the reaction of specialized species will depend on the presence of their floral hosts.

Interestingly, at a local scale, high-severity burn areas had higher richness and abundance of flowers, which translated into more species-rich pollinator communities and interactions. Canopies opened by fire will often support more floral resources which in turn attract more pollinators (Campbell *et al.*, 2007; Grundel *et al.*, 2010; Van Nuland *et al.*, 2013). Focusing only on a local scale, therefore, would overlook the potential for high-severity fires to homogenize communities over larger scales by decreasing the spatial structure of floral communities. It is thus important to consider the effect of pyrodiversity at multiple spatial scales (Farnsworth *et al.*, 2014).

Drought also interacted with the effect of pyrodiversity on plant–pollinator communities by weakening the response of bees and plant–pollinator interactions to pyrodiversity. This is possibly because a lower level of overall resource availability across the landscape caused pollinators to shift their resource use. Specifically, the increase in drought intensity led to changes in pollinator community composition and foraging behavior such that interaction networks were less specialized and pollinators no longer tracked plant communities. The effect of pyrodiversity on pollinator communities is, therefore, context dependent, and the capacity for pyrodiversity to maintain diverse pollinator communities may diminish with increasing drought occurrence.

In contrast to pollinators, the effect of pyrodiversity on floral community richness did not depend on drought intensity. Floral species richness was most negatively affected by drought in the high-severity sites and, prior to the shift in drought intensity, floral richness at those sites was not related to pyrodiversity. Thus, there is no expectation that increasing drought intensity would alter the response of floral richness to pyrodiversity. It is unclear, however, whether drought might, over longer time scales, mediate pyrodiversity's ability to sustain floral diversity.

We found limited evidence that environmental heterogeneity directly affected plant and pollinator communities, and in fact, the only significant relationship we observed (that between bee and interaction richness and heat load) was negative. This may be because pollinators might respond positively to certain levels of solar radiation and negatively to others such that a diversity of conditions could negatively affect bees and subsequently interaction richness. Environmental heterogeneity is known to contribute to pyrodiversity (Collins *et al.*, 2007; Kane *et al.*, 2015), and thus, fire may provide a link between the diversity of abiotic conditions and the maintenance of biodiversity.

In the future, fires in this region are predicted to shift from primarily low/moderate to high severity. Historically in the Sierra Nevada, high-severity patches comprised less than 5% of fires and high-severity patches were also smaller (Collins *et al.*, 2007). In the 2013 Rim Fire, over 20% of a nearly 260 000 acre burn was classified as high severity (Lydersen *et al.*, 2014). Based on our findings, lower heterogeneity of fire severity may act to reduce spatial turnover in plant–pollinator communities. The heterogeneity of community composition is a primary determinant of the total species diversity present in a landscape, and thus, lower pyrodiversity may negatively affect the richness of plant–pollinator communities across large spatial scales (Burkle *et al.*, 2015).

On average, every 5% increase in pyrodiversity within 150 m of a site (a 0.05 unit increase in Simpson's diversity) gained approximately one pollinator and flowering plant species and almost two interactions. Thus, predicted shifts in fire regimes to include less pyrodiversity compounded with increasing drought occurrence will negatively influence the richness of plant and pollinator communities in this and other forested ecosystems. Some managers only allow fires to burn under mild (prescribed fire) or extreme (wildfire) conditions. We provide further evidence that pyrodiversity contributes to biodiversity and therefore managers should place more significance on burning under a wider range of fire conditions. Wildland Fire Use programs that restore fire regimes, such as those implemented in the Illilouette Basin, are integral for promoting both pyrodiversity and biodiversity. Additionally, the combination of Wildland Fire Use and prescribed fires with varied burn conditions will prevent homogenizing mega-fires such as the Rim Fire. These management strategies are already recommended, and our results affirm that their usage should continue and hopefully also expand.

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Author contributions

LCP, CK and KW designed the study, LCP, LKM, KW, KK, LC, and CK collected data, LCP, TG and RT identified the specimens, LCP analyzed output data. LCP wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article: