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Drivers of understory plant communities in Sierra Nevada mixed conifer forests with pyrodiversity

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Abstract

Background: Fire suppression in western North America increased and homogenized overstory cover in conifer forests, which likely affected understory plant communities. We sought to characterize understory plant communities and their drivers using plot-based observations from two contemporary reference sites in the Sierra Nevada, USA. These sites had long-established natural fire programs, which have resulted in restored natural fire regimes. In this study, we investigated how pyrodiversity—the diversity of fire size, severity, season, and frequency—and other environment factors influenced species composition and cover of forest understory plant communities.

Results: Understory plant communities were influenced by a combination of environmental, plot-scale recent fire history, and plot-neighborhood pyrodiversity within 50 m. Canopy cover was inversely proportional to understory plant cover, Simpson's diversity, and evenness. Species richness was strongly influenced by the interaction of plot-based fire experience and plot-neighborhood pyrodiversity within 50 m.

Conclusions: Pyrodiversity appears to contribute both directly and indirectly to diverse understory plant communities in Sierra Nevada mixed conifer forests. The indirect influence is mediated through variability in tree canopy cover, which is partially related to variation in fire severity, while direct influence is an interaction between local and neighborhood fire activity.

Keywords: Biodiversity, Frequent fire, Restoration, Sierra Nevada

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Resumen

Antecedentes: La supresión de incendios en el oeste de Norteamérica incrementó y homogeneizó la cobertura de los doseles en bosques de coníferas, lo cual afectó particularmente las comunidades del sotobosque. Buscamos caracterizar las comunidades vegetales del sotobosque y sus controladores usando observaciones en parcelas de dos sitios de referencia contemporáneos en Sierra Nevada, EEUU. En estos sitios se habían establecido programas de incendios naturales que resultaron en la restauración de regímenes naturales de fuegos. En este estudio, investigamos como la piro-diversidad—diversidad en el tamaño de los incendios, severidad, estación de fuego, y frecuencia de ocurrencia—y otros factores ambientales influencian la composición de especies y la cobertura de las comunidades vegetales del sotobosque.

Resultados: Las comunidades de plantas del sotobosque fueron influenciadas por una combinación de factores ambientales, historia de fuegos recientes a escala de parcelas, y la piro-diversidad de plantas en la vecindad de parcelas dentro de los 50 m. La cobertura del dosel fue inversamente proporcional a la cobertura del sotobosque. La diversidad y equitatividad, y la riqueza de especies medidas mediante el índice de Simpson fueron fuertemente influenciadas por la interacción de las parcelas experimentales y por la piro-diversidad de las parcelas vecinas dentro de los 50 m.

Conclusiones: La piro-diversidad parece contribuir tanto directa como indirectamente a la diversidad del sotobosque en las comunidades de plantas en bosques mixtos de coníferas de la Sierra Nevada. La influencia indirecta es mediada a través de la variabilidad en la cobertura del dosel arbóreo, que es parcialmente relacionada con la variación en la severidad el fuego, mientras que la influencia directa es debida a una interacción entre la actividad del fuego local y de su vecindad.

Introduction

Historical western USA dry mixed conifer forests likely supported diverse understory communities that were altered by fire suppression (Tilman and Lehman 2001). Frequent fire burning with complex spatial patterns of intensity and fuel consumption was a keystone ecological process that recycled nutrients, altered community composition and assembly, and selected for fire-resilient species (Bond and Keeley 2005). Specific pathways for fire suppression to influence plant communities include changes in light and moisture on the forest floor, reduction of nutrient cycling, and lack of mineral soil to promote seedling survival (Battles et al. 2001; North et al. 2005).

Historical forest reconstructions reflect fire dynamics through the past several hundred years and how forests responded to changing environments and climates (Swetnam 1993) (Hessburg et al. 2005), and human uses (Taylor et al. 2016). Long-fire-suppressed forests have been homogenized and densified, creating uncharacteristically continuous canopy tree layers (Larson and Churchill 2012; Lydersen et al. 2013; Boisramé et al. 2016; Lydersen and Collins 2018). These forests also have more shade-tolerant trees and denser canopies, which together block light to the forest floor and increase competition for water and nutrients (Kilgore 1973; Minnich et al. 1995; Bouldin 1999). The combination of many years since fire and additional trees also dramatically increases litter accumulation on the forest floor, which may enhance moisture, physically block understory plants, or both (Parsons and DeBenedetti 1979; North et al. 2005). While we understand fire suppression's influence on trees, we have limited information about possible changes to understory communities.

Modern forest understories are a major component of overall forest diversity (Fites 1993; Shevock 1996), yet we lack robust reference information on forest understories. Studies have described historical (Anderson and Carpenter 1991; Smith and Anderson 1992; Brunelle and Anderson 2003) and modern era (Potter 1998) understory plant communities and have investigated the effects of fire suppression (North et al. 2005), fire severity and wildfire (Stevens et al. 2015; Richter et al. 2019), timber management (Battles et al. 2001; Korb et al. 2007), forest restoration and fuel hazard reduction (Collins et al. 2007a; Collins et al. 2007b; Wayman and North 2007), and climate change (Hurteau and North 2008). Together, these studies suggest that light and moisture are important for understory plant communities and that non-native plants are uncommon. It is well established that fire history, especially time since fire and most recent fire severity, influences plant communities within a plot (plot-scale; Turner et al. 1999; Wang and Kemball 2005; Swanson et al. 2010). Some studies seek to understand the role of fire in understories, but they have limited applicability because they typically study prescribed fires that are only monitored for a few years (Huisinga et al. 2005; Collins et al. 2007b; Hurteau and North 2008), or single wildfires (Richter et al. 2019). In the Sierra Nevada mixed conifer forests, low to moderate fire severity effects are known to promote diversity within and between plots (Richter et al. 2019), while high-severity fires do not (e.g., the intermediate disturbance hypothesis; Connell 1978). More recent work observed an increase in landscape heterogeneity in areas with long-reintroduced fire, including dramatic increases of sparse meadows, dense meadows, and shrubs (Boisramé et al. 2017); these changes may influence local- and landscape-level diversity (Harner and Harper 1976; Huston 1994). As a result, there is a research gap in understanding the dynamics and drivers of mixed conifer forest understories with restored natural fire regimes and how fire surrounding the plot at the neighborhood scale (within 250 m of a plot) influences the plant understory.

There are few places to study forests with relatively intact or natural fire regimes because most forests in the western USA have been logged, grazed, and fire suppressed. On some federal lands designated as wilderness, they are unlogged, had limited grazing, and lighting-strike fires were allowed to burn beginning in the late 1960s or later (van Wagtendonk 2007). An example of this management is on the North Rim of Grand Canyon National Park where a few mixed conifer and ponderosa pine (*Pinus ponderosa* Douglas ex Lawson & C. Lawson) understory studies found that plant richness had a negative relationship with time since fire and increasing tree cover (Laughlin et al. 2004; Laughlin et al. 2005). While other areas in the northern and southern US Rocky Mountains with long-established natural fire programs have been studied (Rollins et al. 2002; Holden et al. 2009; Parks et al. 2015), specific focus on understory plant communities is lacking.

One of the difficult aspects of characterizing species responses across landscapes with intact fire regimes is the complexity associated with varying fire extent, frequency, seasonality, and severity over time, collectively known as pyrodiversity. Martin and Sapsis (1992) explored the concept of pyrodiversity and hypothesized that pyrodiversity across a given landscape increases biodiversity. This hypothesis was based on the idea that fire creates unique niches in space and time and alters competition and resource availability; this increase in environmental heterogeneity increases the number of species that can coexist (Martin and Sapsis 1992; Bond and Keeley 2005). The biodiversity fostered by pyrodiversity may in turn also make future fires more diverse by altering fuels and increase future biodiversity. However, few studies specifically addressed the pyrodiversity neighborhood-scale hypothesis with understory plants due to the rarity of having detailed vegetation data from landscapes with sufficient fire activity and accompanying information on fire occurrence and effects over time (Kelly and Brotons 2017). Recent work in a Sierra Nevada wilderness area with a long-established natural fire program developed an approach to resolve the complexities associated with fire occurrence and effects over time using a metric of pyrodiversity (Ponisio et al. 2016). Importantly, Ponisio et al. (2016) demonstrated that plot-scale fire severity and great diversity of plot-neighborhood fire experiences foster more species, specifically that pyrodiversity promotes diversity across taxa through trophic interactions for plants and pollinators.

In this study, we sought to characterize understory plant communities and their drivers using plot-based observations from two contemporary reference sites with long-established natural fire programs (Collins et al. 2007a; Collins et al. 2007b). Despite having similar timing in the adoption of these programs (early 1970s), one of the sites experienced more fire activity and, as a result, experienced greater overall change in landscape-level vegetation patterns (Boisramé et al. 2017; Stevens et al. 2020). The strength of this study is the extent of the data through time and space: two frequent-fire landscapes and multiple measurements over 15 years from forest inventory plots including intensive understory sampling. This is one of the first studies to consider the long-term effect of fire experienced on a plot and pyrodiverse fire experienced in the plots' neighborhood on the entire plant community including trees, shrubs, and herbaceous plants. We broadly asked, how does plot-based and plot-neighborhood fire experiences and the environment influence understory plant communities across spatial and temporal scales? Specifically, our goals were to:

(1) Describe plant communities that develop in frequent-fire upper-elevation mixed conifer forests.

(2) Determine if pyrodiversity influences understory plant species richness and diversity, and if so, determine the spatial plot-neighborhood scale at which pyrodiversity might be important.

(3) Understand the most important environmental and fire variables that influence plant communities through space and time at the plot scale.

Methods

Study site

Our reference sites for mixed conifer forests in the Sierra Nevada are within US National Park Service wilderness areas, including Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, hereafter referred to as Illilouette and Sugarloaf, respectively (Fig. 1). Based on tree-ring reconstructions, the historical fire regimes in both study areas consisted of frequent (< 10 year) fire, which was dominated by low- and moderate-severity effects (Collins and Stephens 2007). However, analysis of contemporary fires across the entirety of both areas using

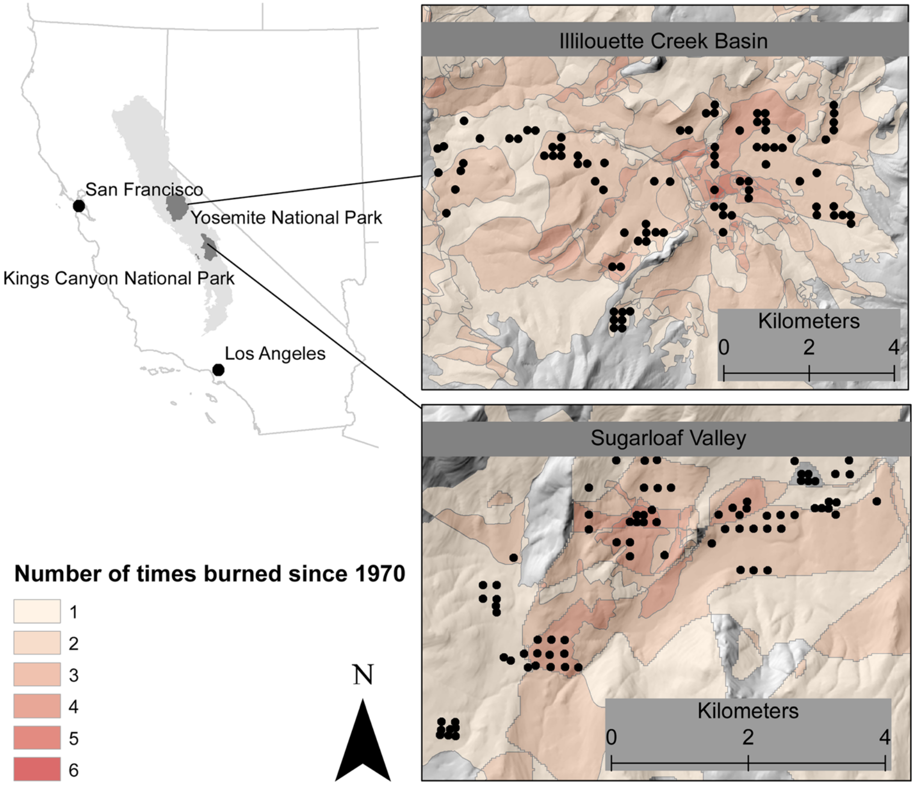

Fig. 1 Study areas were located in California's Sierra Nevada in two wilderness areas with long-established natural fire programs: Yosemite National Park's Illilouette Creek Basin and Kings Canyon National Park's Sugarloaf Valley. Shading indicates the number of times that areas have burned since 1970. Inset maps show sampling plots as black dots in relationship to the topography and number of times burned at each study site. Public data were collected beginning in the early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime

remotely sensed imagery revealed that small patches of high-severity fire were also a component of the fire regimes (Collins and Stephens 2010). Fire exclusion began in the late 1800s and persisted until the early 1970s, when parks adopted a natural fire program, whereby most lightning-ignited fires were allowed to burn relatively unimpeded (van Wagtendonk 2007). In 1970, after nearly 100 years of fire exclusion, Illilouette had much more continuous forest cover than it does presently, after over 45 years of a natural fire program (Boisramé et al. 2016). The change in forest cover resulting from the natural fire program at Sugarloaf is much less pronounced (Stevens et al. 2020).

The study areas span an elevation gradient from 1400 to 3000 m. The areas' Mediterranean-type climate has cool, moist winters, and warm, generally dry summers (Additional file 1: Tables 1.1 and 1.2, Figure 1.1). Monthly climate averages (1981 to 2010) for January minimum temperatures range from 0 to − 8 °C, whereas monthly climate averages (1981 to 2010) for July maximum temperatures range from 24 to 31 °C (Arguez et al. 2010). Annual precipitation varies with elevation and has been predominantly snow dominated with about 500 cm on average (Additional file 1: Table 1.2, Figure 1.1; Arguez et al. 2010). Vegetation types in both study areas range from closed to open conifer forests interspersed with open shrublands, wet meadows, dry meadows, and closed shrublands. While the dominant forest trees are Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), lodgepole pine (*Pinus contorta* Loudon), white fir (*Abies concolor* [Gordon & Glend.] Lindl. ex Hildebr.), and red fir (*Abies magnifica* A. Murray bis), other common trees include sugar pine (*Pinus lambertiana* Douglas), quaking aspen (*Populus tremuloides* Michx.), and western juniper (*Juniperus occidentalis* Hook.). Open forest stands often have sparse understories of bunch grasses, forbs, and shrubs. The understory includes forbs such as Brewer's lupine (*Lupinus breweri* A. Gray var. *breweri*), dogbane (*Apocynum androsaemifolium* L.), broad leaf lupine (*Lupinus latifolius* J. Agardh var. *columbianus*); shrubs such as white thorn (*Ceanothus cordulatus* Kellogg), greenleaf manzanita (*Arctostaphylos patula* Greene), chinquapin (*Chrysolepis sempervirens* [Kellogg] Hjelmq.), and snowberry (*Symphoricarpos mollis* Nutt.); graminoids such as western needle grass (*Achnatherum occidentale* [Thurb. ex S. Watson] Barkworth ssp.

occidentale) and big squirreltail grass (*Elymus multisetus* [J. G. Sm.] Burtt Davy); and ferns such as western bracken fern (*Pteridium aquilinum* [L.] Kuhn var. *pubescens* Underw.).

Field data

We sampled 117 field plots in 2002 (65 in Illilouette, 52 in Sugarloaf), which were selected from a stratified systematic grid with varied spacing of 200 m and 100 m, depending on total area available, number of times burned (none to four), and dominant forest type (Jeffrey pine, lodgepole pine, white fir, and red fir) (Fig. 1; Collins et al. 2016). Most of these plots were resampled in 2012 or 2013. Additionally, in 2012 and 2013, we added 32 plots focused on areas that burned at high severity (16 plots each in study area). These plots were added to capture the potentially different understory responses following high-severity fire, which was under-represented in the original grid. Plots that recently experienced fire varied in proportions similar to that experienced at the landscape level; 21% had no recent fire, 13% experienced very low-severity fire, 39% experienced low-severity fire, 15% experienced moderate-severity fire, and 11% experienced high-severity fire (Stevens et al. 2020). In total, there were 258 samples (plot observations) including 113 plots with two measurements (226 samples) and 32 plots that we measured once. These plots represent a chronosequence of post-fire succession from 1 to 30 years post fire, burned up to four times, had varied fire severities. Thirty plots burned following plot establishment in 2002.

Circular inventory plots had a 12.62-m radius and covered 0.05 ha. We measured understory cover and species with two point-intercept transects that intersected at plot center and extended to the plot boundary along all cardinal directions. Plants were recorded along the point-intercept transect every 10 cm; in total, the understory transects had 1016 total points with 508 points each for the 0 to 0.5 m and 0.5 to 2 m strata. Shrub cover was quantified based on point-intercept data for shrub species in the 0.5 to 2 m strata, and was absolute cover, which may exceed 100% cover (USDA and NRCS 2020). We recorded all species through timed area searches of up to 1 h, or ceased after 15 min if no new species were found. Species from the timed area search, but not

Table 1 Data sources for explanatory and response variables, the source, and the scale at which they were collected in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Public data were collected from early 1900s. Study data were collected from 2002 to 2013. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime

Variables		Source	Resolution
Understory community response variables			
Percent cover		Point-intercept of understory 0 to 2 m^2 and timed area search	490 m^2
Richness		Timed-area search	490 m^2
Evenness		Point-intercept of understory 0 to 2 m^2 and timed area search	490 m^2
Simpson's diversity		Point-intercept of understory 0 to 2 m^2 and timed area search	490 m^2
Explanatory variables			
Fire	Time since fire	Sequoia-Kings National Park 2012; Yosemite National Park 2012	Varied[a]
	Fire severity	Miller and Thode 2007	30 m^2
	Number of times burned	Miller and Thode 2007	30 m^2
	Pyrodiversity	Miller and Thode, Sequoia-Kings National Park 2012; Yosemite National Park 2012	30 m^2
Environmental	Shrub cover	Point-intercept of shrubs 0.5 to 2 m^2	490 m^2
	Percent slope	Clinometer	490 m^2
	Canopy cover	GRS tube densitometer	490 m^2
	Soil texture	Thien 1979	490 m^2
	Litter depth	Average of six measurements	490 m^2
	Elevation	USGS Digital Elevation Model from Gesch 2007	10 m^2
	Solar radiation	Derived from USGS Digital Elevation Model following McCune and Keon 2002	100 m^2
	Climatic water deficit	Flint et al. 2014	270 m^2

[a] Time since fire is "varied" since the records go back to early 1900s. Excerpt from metadata: "This coverage represents the YOSE fire history from 1930 through 2018. Original data was interpreted from historical fire records held at Yosemite National Park in the late 1980s. GRASS data was converted to Arc/Info coverage format when Yosemite migrated to Arc/Info in 1995. Some vector data was lost in conversion from GRASS. In those instances, polygons were vectorized from raster versions that remained in GRASS. Each year from 1995 to 2000, fires were input into Arc/Info by digitizing 1:24,000 USGS paper maps (7.5″ series) or from Trimble GPS readings. Starting 2001, all larger fire perimeters were acquired through ground GPS or helicopter GPS reconnaissance. Small fire point locations were acquired through ground GPS or helicopter GPS and buffered to approximate fire size"

encountered in the point-intercept transect, had low cover, were recorded as "trace" cover, and given 0.001% for the purpose of analysis. Litter depth was measured, to the nearest centimeter, six times per plot along three fixed transects at 3 and 5 m; results were averaged to obtain one value per plot. Canopy cover was estimated with a densitometer at 25 gridded points within the plot. Soil texture was determined with the "feel method," by holding a small sample of soil in your hand, adding water, and then trying to form a ball and ribbon with the mixture (Thien 1979). We identified loams, sands, sandy clay loams, and sandy loams in the study sites; some plots were only sampled prior to 2012 and no soil texture was recorded.

The response variables were calculated based on the point-intercept data from the two strata and the timed area search. Plants that only occurred in the timed area search were incorporated into the point-intercept data and assigned one point-intercept hit. Understory cover was absolute cover, which may exceed 200% cover. Richness was quantified based on an exhaustive search of all species within the plot. Simpson's diversity ranged from 0 to 1 (Dixon and Palmer 2003; Oksanen et al. 2017) and evenness was calculated, which was adjusted for species richness and ranged from 0 to 1 (Smith and Wilson 1996).

Environmental data

We compiled abiotic environmental data (Table 1) including average climatic water deficit (CWD) from 1981 to 2010 (Flint et al. 2014), solar radiation index (20 m; McCune and Keon 2002), and slope derived from US Geological Survey Digital Elevation Model (DEM). In addition to abiotic environmental variables, plot-based fire history was described with local fire history from 1930 to 2012 (van Wagtendonk 2012; Folger 2019) and Relative differenced Normalized Burn Ratio (RdNBR) fire severity from 1984 to 2012 (Miller and Thode 2007). Fire-severity classes, derived from established relationships between RdNBR and the Composite Burn Index, were very low (RdNBR < 69), low (69 < RdNBR < 315), moderate (316 < RdNBR < 640), and high (RdNBR ≥641) (Miller and Thode 2007). These fire severity classes correspond with the following relative changes in mean canopy cover and tree basal area: 0 and 15% (low and very low), 16 and 89% (moderate), and > 90% change (high) (Miller et al. 2009; Lydersen et al. 2016).

Pyrodiversity index

To explore the effect of pyrodiversity on plant communities, we utilized the approach developed by Ponisio et al. (2016) to calculate a pyrodiversity index. This calculation first involved assessing the uniqueness of fire experience for each 30 × 30 m raster cell in the analysis

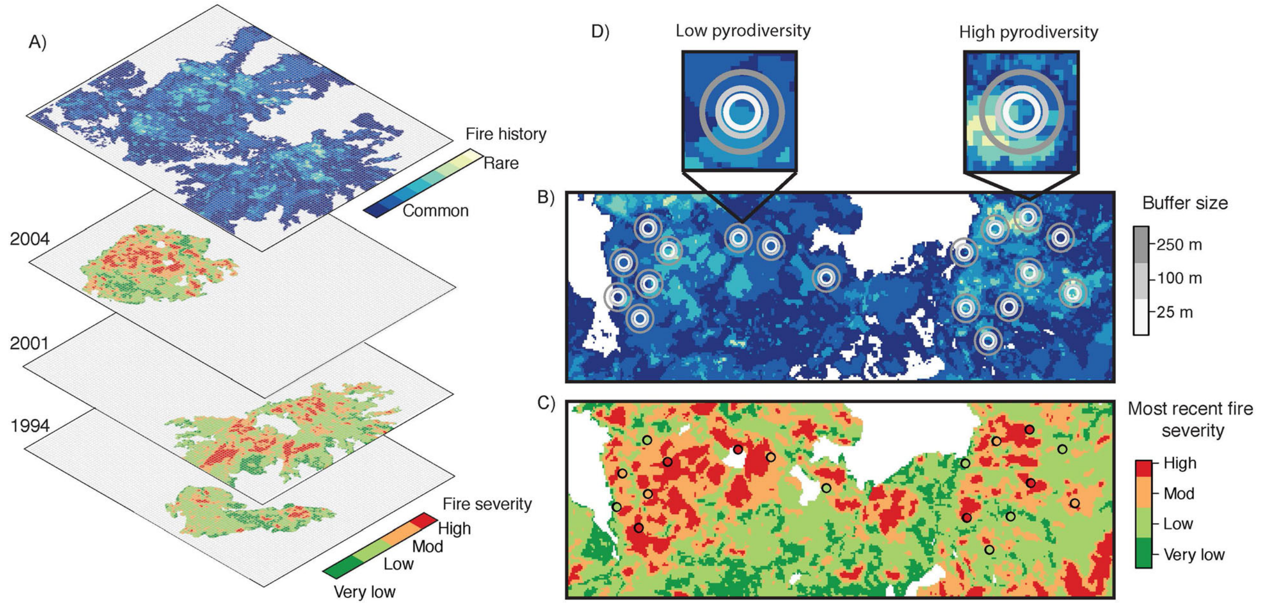

Fig. 2 Method used to estimate pyrodiversity in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. **A** Each 30 × 30 m raster cell was assigned a fire history classification based on the fires and severities it experienced (three representative fires depicted). **B** The diversity of fire, either weighted for the similarity of fire history or unweighted, was calculated within buffers around the monitoring sites. Concentric circles represent plots in a small region with a subset of buffers around them. **C** The most recent fire's severity was also included as a possible interaction with pyrodiversity. Open dots represent plots in a small region. **D** An example of sites with relatively low and high pyrodiversity

area at both study sites (Fig. 2). The analysis area was delineated by a 250-m radial buffer around each field plot. For each cell, we used the sequence of fires and the severity of each of those fires to define their fire histories. This resulted in more than 300 unique fire histories (i.e., combinations of fire frequency, time since last fire, and severity throughout both study sites). We then calculated the diversity of individual-cell fire experiences within the buffers surrounding the plot (25, 50, 75, 100, and 250 m buffer). Whereas Ponisio et al. (2016) used only Simpson's diversity of fire experiences in the different-sized buffer areas, we included three additional diversity measures, namely, functional divergence, functional richness, and functional dispersion, resulting in four different formulations of the pyrodiversity index (Mason et al. 2005; Villéger et al. 2008). Simpson's diversity describes the richness and abundance of fire experiences; it ranges from 0 to 1, where 0 represents no diversity and 1 represents infinite diversity. Functional divergence describes how different the fire experiences were in a buffer surrounding a plot; it ranges from 0 to 1, where a low number indicates that most fire experiences were similar to the average fire experience, whereas a larger value indicates that the fire experiences were more extreme than the average fire experience. Functional richness is the amount of niche space filled by species in the community; it was constrained to range from 0 to 1, where larger numbers indicate more fire experiences. Functional dispersion is the weighted pyrodiversity metric for which Simpson's diversity of fire history experience is weighted by similarity; it ranges from 0 to 1, where 0 indicates that all fire experiences are shared and 1 indicates that all fire experiences were unique.

We then calculated the weighted pyrodiversity score based on fire characteristics, mainly the year the fire occurred and its severity, into traits for each pixel and then used a functional dispersion metric to calculate the diversity of fire "traits" (Ponisio et al. 2016: supplemental material). Each raster cell's fire history was thus weighted based on the similarity of fire traits. Within a fire, severity is a ranked trait. For example, within a single fire, a low-severity pixel 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, giving more recent fires greater weight than those that occurred later. The weighted diversity of fire history for buffers were calculated around each plot (Laliberté and Legendre 2010).

Table 2 Overview of the three equations and their variables used to understand plant communities in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Response variables were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. The response variables had unique combinations of explanatory variables due to the questions that were being asked. Plot-neighborhood fire experience includes pyrodiversity indices for buffers surrounding the plots. Plot-based fire experience includes most recent fire severity and time since last fire. The interaction of plot-based fire experiences includes the most recent fire severity and time since last fire. The interaction of plot-neighborhood and plot-based fire experiences includes pyrodiversity and the most recent fire severity, and pyrodiversity and time since fire. Environmental variables include elevation, slope, climatic water deficit (CWD), heat load, canopy cover, litter depth, and soil texture. All equations included the random effect of park, plot, and survey year. The equation assessing richness had one additional environmental variable: shrub cover

Variables	Equation		
	1	2	3
Response variables			
Cover	X		
Evenness	X		
Richness		X	X
Simpson's		X	X
Explanatory variables			
Plot-neighborhood fire experience		X	X
All pyrodiversity indices for all plot buffers		X	
One pyrodiversity index for one plot buffer			X
Plot-based fire experience	X	X	X
Interaction of plot-based fire experiences	X		
Interaction of plot-neighborhood and plot-based fire experiences			X
Environmental	X	X	X
Random effects	X	X	X

Analyses

We constructed generalized linear mixed effects models to test how environmental and fire processes influence plant communities in R 3.1.2 (Bates et al. 2014, 2015; Kuznetsova et al. 2016). We assumed a Gaussian distribution unless model fit was poor, and then we used square root transformation or Poisson depending on the dispersion of the data and model residuals (Additional file 2: Table 2.1). Model dispersion and residuals fit statistical assumptions of normality and homogeneity of variance. We used a series of three equations to understand what influenced the plant communities' richness, Simpson's diversity, evenness, and percent cover (Table 2).

Cover and evenness were assessed with one equation (Additional file 2: Equation 2.1; Table 2). The most recent fire experience was a strong ecological filter, so we tested plot-based fire attributes, including time since fire, most recent fire severity, and number of times burned as explanatory variables. To test the interaction of plot-based fire attributes, we examined the interaction of time since fire and the most recent burn severity at the plot scale. Other environmental variables (elevation, slope, climatic water deficit, heat load, canopy cover, litter depth, soil texture) were also included to account for environmental influence. Lastly, we included site identity (park and plot) and survey year as random variables to account for the multiple surveys taken through time at the same plots.

To investigate whether pyrodiversity begets biodiversity, we used a series of two equations to examine if the plot-based and plot-neighborhood fire experiences influenced biodiversity (Table 2; Additional file 2: Equations 2.2 and 2.3). Characteristics of the most recent fire, such as fire severity and time since fire, were also explanatory variables because these factors strongly influence plant communities that develop after fire (Turner et al. 1999; Wang and Kemball 2005; Swanson et al. 2010). Shrub cover was also an explanatory variable for richness because some studies show a connection between shrubs and understory diversity (Bohlman et al. 2016; Richter et al. 2019). Simpson's diversity and richness were assessed with a preliminary equation (Equation 2) to determine which pyrodiversity metrics and buffer scales were most likely to influence biodiversity. In preliminary tests, we modeled the main effect of all pyrodiversity metrics for all buffers together (Equation 2; Tables 3 and 4). The 30 models' Akaike Information Criterion (AIC; Mazerolle 2016) values were compared and the model with the lowest AIC had its pyrodiversity metric and scale used to parameterize the final analysis with the environmental variables.

Lastly, for all response variables, we compared full and reduced models with all combinations of variables and included one to six variables (Table 2; Additional file 2: Equations 2.1 and 2.3). AIC values were compared, and the model with the lowest AIC is presented (Mazerolle 2016). Marginal R^2 was calculated as the proportion of variance explained by fixed factors alone, and conditional R^2 was calculated as the proportion of variance explained by both fixed and random factors (Nakagawa and Schielzeth 2013; Lefcheck 2015). Random effects were dropped from R^2 calculations if their variance and standard deviation were zero.

Table 3 Pyrodiversity metric models describing plant richness in order of increasing model *Akaike Information Criterion* (AIC) values (Table 2; Additional file 2: Equation 2.2) in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. The analysis using Equation 3 (Additional file 2: Equation 2.3) included functional divergence at 50 m. Public data were collected beginning in early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime

Buffer (m)	Pyrodiversity metric	AIC
50	Functional divergence	1582.32
100	Simpson's diversity	1586.58
75	Simpson's diversity	1587.34
50	Functional dispersion	1588.12
50	Simpson's diversity	1588.30
75	Functional divergence	1589.85
100	Functional richness	1593.33
75	Functional dispersion	1598.83
75	Functional richness	1599.58
25	All pyrodiversity indices	1602.51
100	Functional divergence	1602.98
250	Functional richness	1605.58
25	Functional richness	1606.05
25	Simpson's diversity	1606.74
100	Functional dispersion	1608.21
250	Simpson's diversity	1609.48
25	Functional dispersion	1609.67
250	Functional dispersion	1609.86
250	Functional divergence	1610.77
25	Functional divergence	1611.10
75	All pyrodiversity indices	1611.93
100	All pyrodiversity indices	1612.16
50	All pyrodiversity indices	1612.89
250	All pyrodiversity indices	1615.00

Results

Illilouette had 298 plant species in 146 plot measurements while Sugarloaf had 172 plant species in 116 plot

Table 4 Pyrodiversity metric models describing plant Simpson's diversity in order of increasing model *Akaike Information Criterion (*AIC) values (Table 2; Additional file 2: Equation 2.2) in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. The analysis using Equation 3 (Additional file 2: Equation 2.3) included functional divergence at 100 m. Public data were collected beginning in early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime

Buffer (m)	Pyrodiversity metric	AIC
100	Functional richness	142.7677
100	Functional dispersion	145.2036
75	Functional richness	147.8647
50	Functional richness	149.3709
25	Functional richness	150.7116
100	Simpson's diversity	154.6558
250	Simpson's diversity	154.8857
75	Simpson's diversity	158.3128
250	Functional richness	158.5818
25	Functional divergence	158.6048
75	All pyrodiversity indices	160.3570
100	All pyrodiversity indices	160.5580
100	Functional divergence	162.1130
75	Functional divergence	162.3816
250	Functional divergence	162.9640
25	All pyrodiversity indices	163.3871
50	All pyrodiversity indices	163.4339
75	Functional dispersion	163.6863
50	Simpson's diversity	165.2377
250	All pyrodiversity indices	166.7517
250	Functional dispersion	168.8335
25	Simpson's diversity	170.1983
50	Functional divergence	170.6432
25	Functional dispersion	170.7138
50	Functional dispersion	171.2003

measurements. The two sites only had 20 species in common, so the majority of species detected were unique to each site. In total, there were 379 taxa identified, including 11 tree species, 47 shrub species, 38 graminoid species, 275 forb species, and two epiphytes. Non-native plants did not occur in 2002, and only 11 plots had non-native plants during resampling (Additional file 3: Table 3.1). Despite low understory cover, the understory was a surprisingly rich community (Figs. 3A, B). Simpson's diversity (Fig. 3C) as well as evenness (Fig. 3D) were moderately high throughout the study areas. Evenness was often high, suggesting that plots were more likely to have even abundance rather a few dominant plants (Fig. 3D).

Understory cover ranged from 2 to 34% with a mean of 9% (Fig. 3A), which was significantly influenced by fire and the environment: fire severity ($P < 0.002$ to $>$ 0.3), times burned ($P < 0.01$), and canopy cover ($P < 0.001$) (marginal $R^2 = 0.10$, conditional $R^2 = 0.64$, residual degrees of freedom = 248; Fig. 4). Canopy cover had the largest impact on understory cover: it increased from 6 to 13% as canopy cover decreased. Other variables significantly affected understory cover, but had lesser magnitudes of influence. Increase in the number of times burned from none to three decreased mean understory cover by 1.5%. Recent fire severity affected understory cover; moderate-severity fire had the highest understory cover at 7%, while low-severity fire had 6 to 7% understory cover and high-severity fire had 4% understory cover. One third of understory cover variation could be explained through variables analyzed.

Richness ranged from four to 49, with a mean of 18 (Fig. 3B). Preliminary models determined that the best combination of pyrodiversity scale and index type was functional divergence at 50 m (Additional file 2: Equation 2.2; Table 3); however, pyrodiversity did not significantly affect richness by itself ($P = 0.43$; marginal $R^2 = 0.00$, conditional $R^2 = 0.64$, residual degrees of freedom = 232). In our best model (Additional file 2: Equation 2.3), richness was significantly influenced by fire and the environment: the interaction of fire severity and pyrodiversity ($P < 0.0001$), CWD ($P < 0.02$), and soils ($P < 0.03$) (marginal $R^2 = 0.20$, conditional $R^2 = 0.70$, residual degrees of freedom = 218, Fig. 5). For areas with moderate-severity fire, as functional divergence within 50 m increased from 0 to 0.8, richness increased from 26 to 57 species. Sandy loams had the greatest species richness with 34 species, and the other four soil textures had between 26 to 28 species each. CWD had an inverse relationship with richness; as CWD increased from 360 to 620, richness decreased from 23 to 17 species.

Simpson's diversity ranged from 0 to 1 with a mean of 0.44 (Fig. 3C). Preliminary models determined that the best combination of pyrodiversity scale and index type was functional richness at 100 m (Additional file 2: Equation 2.2; Table 4); however, pyrodiversity did not significantly affect Simpson's diversity by itself ($P = 0.67$; marginal $R^2 = 0.00$, conditional $R^2 = 0.25$). Furthermore, our hypothesis that pyrodiversity influenced Simpson's diversity was not supported when other variables were included (Additional file 2: Equation 2.2; $P = 0.14$). In our best model (Additional file 2: Equation 2.3), Simpson's diversity was only influenced by canopy cover ($P < 0.0001$; marginal $R^2 = 0.14$, conditional $R^2 = 0.33$, residual degrees of freedom = 223; Fig. 6A). Simpson's diversity and canopy cover had an inverse relationship. As

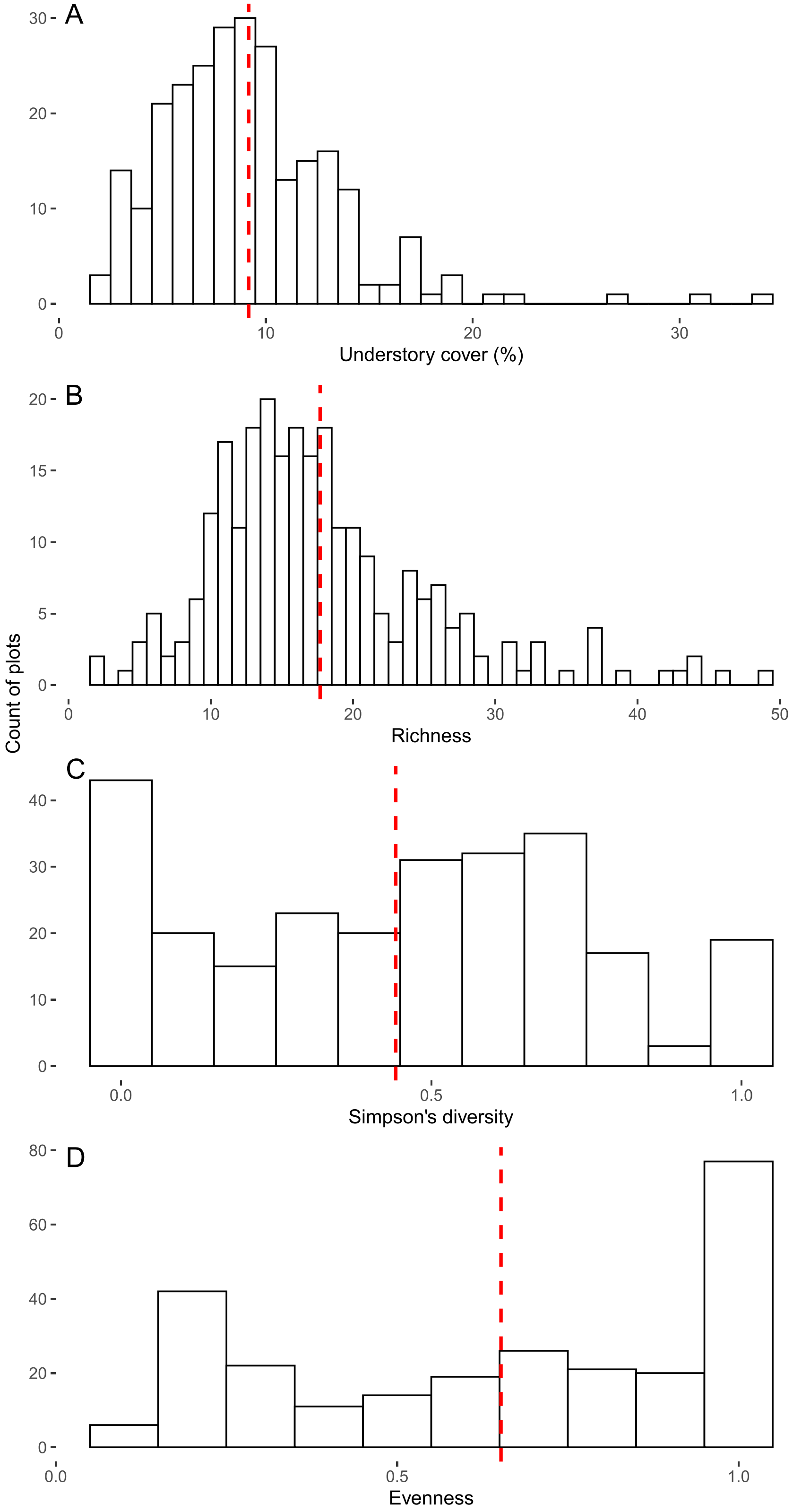

Fig. 3 (See legend on next page.)

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Fig. 3 Histograms of plant community summary variables: **A** percent understory cover, **B** richness, **C** Simpson's diversity, and **D** evenness, from both study sites combined. Each graph has the data mean, for each variable indicated by a dashed red line. Data were collected from 2002 to 2013 in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA, to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime

canopy cover decreased from 100 to 0%, Simpson's diversity increased from 0.36 to 0.75. Plots with low canopy cover had greater species richness, and understory species had similar abundance. In contrast, plots with greater canopy cover had fewer species and were dominated by a few species.

Evenness ranged from 0.11 to 1 with a mean of 0.65 (Fig. 3D) and was inversely proportional to canopy cover ($P < 0.001$; marginal $R^2 = 0.05$, conditional $R^2 = 0.35$, residual degrees of freedom = 230; Fig. 6B). As canopy cover decreased from 100 to 0%, evenness increased from 0.63 to 0.71. Plots with low canopy cover had greater evenness, which means that species had similar cover. In contrast, plots with greater canopy cover had lower evenness and were dominated by a few species.

Discussion

This study deepens the understanding of the natural range of variability for understory plant communities and the processes that contribute to the variability in forests adapted to frequent fire (Safford and Stevens 2017). From the onset the natural fire programs through 2012, 27 and 10 fires > 40 ha occurred in Illilouette and Sugarloaf, respectively. This rich fire history in both areas maintained overall low and spatially variable surface fuels, reduced tree cover, and ultimately resulted in highly heterogeneous forest structure and composition (Boisramé et al. 2016; Collins et al. 2016).

Goal 1: Describe plant communities that develop in frequent-fire upper-elevation mixed conifer forests

The plant communities that developed in frequent-fire upper-elevation mixed conifer forests had relatively low cover, overall, and a wide range of richness, diversity, and evenness. The two sites only had a small portion of species in common and non-native species were rare. Species diversity was dominated by forbs and graminoids, and shrub diversity also contributed greatly.

Our results are similar to paleo-ecology studies based on phytoliths and sediment cores. These studies demonstrated that forests that once experienced frequent fire had abundant shrubs and herbs (Anderson and Carpenter 1991; Brunelle and Anderson 2003), with few continuous grasses (Kerns et al. 2003; Evett et al. 2006; Kerns et al. 2006; Evett et al. 2007).

Goal 2: Determine if pyrodiversity influences understory plant species richness and diversity and determine the scale at which pyrodiversity might be important

Pyrodiversity appears to influence plant communities in these upper-elevation mixed conifer forests, but in a more indirect manner. Richness was influenced by the

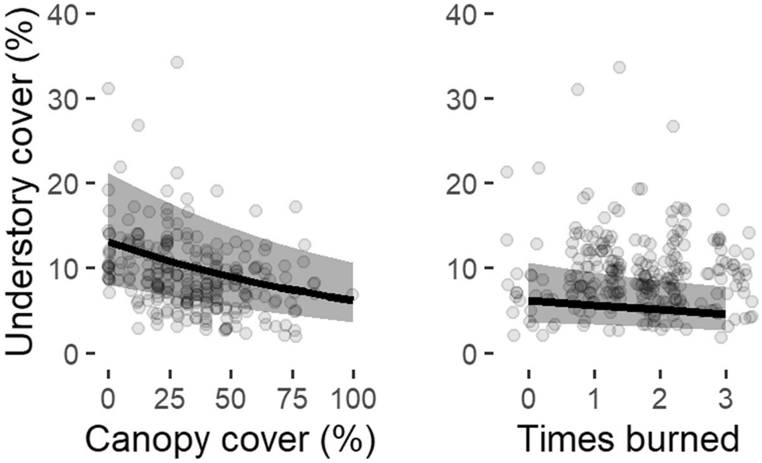

Fig. 4 Understory plant cover response to tree canopy cover and the number of times burned throughout the study in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Public data were collected beginning in early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. Understory cover response to burn severity is not depicted because of a small effect size. Curves represent the regression coefficients, shaded areas are the 95% confidence intervals, and dots are the data

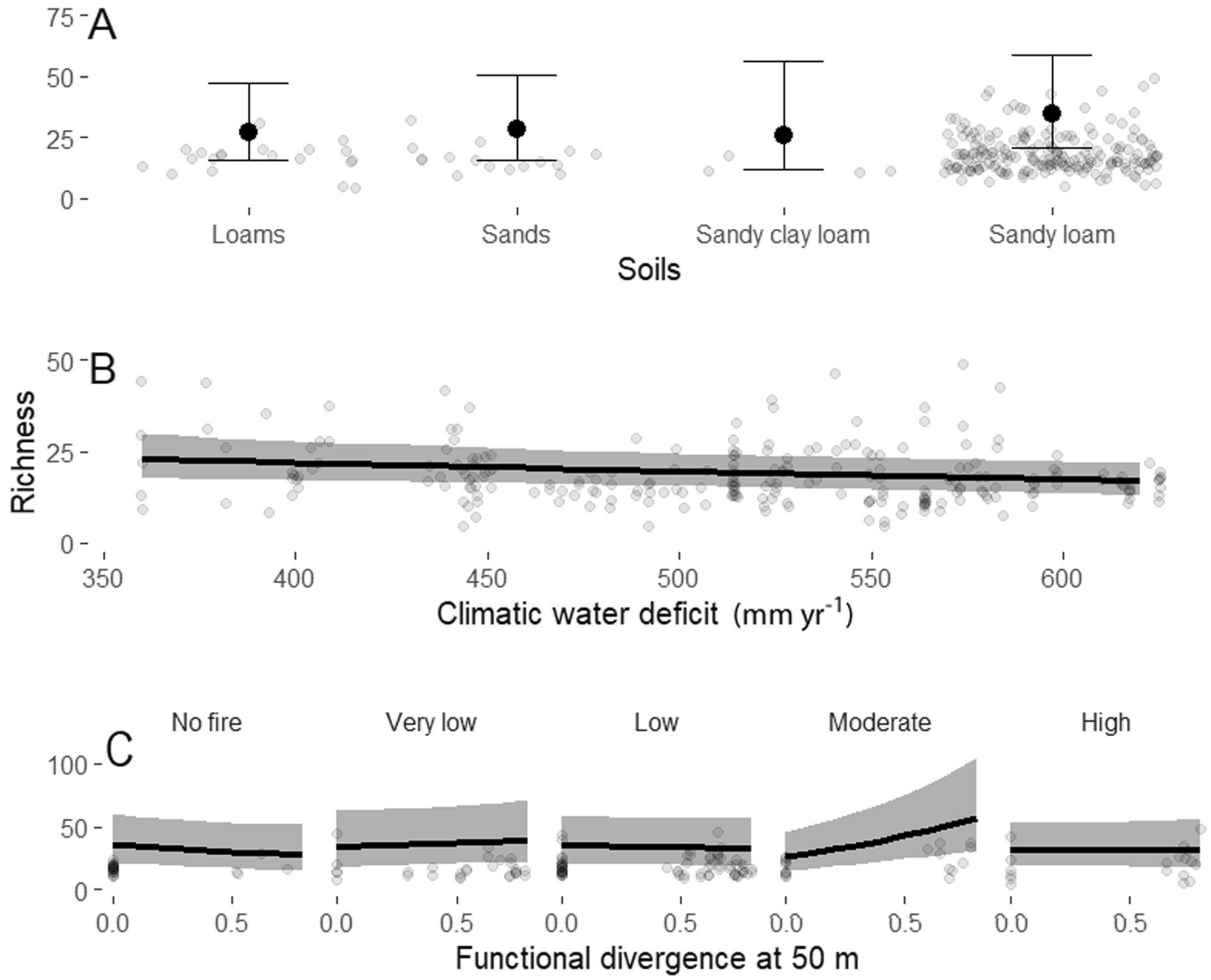

Fig. 5 Species richness response to **A** soils, **B** climatic water deficit (CWD), and **C** the interaction between burn severity and functional divergence throughout the study in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Public data were collected beginning in early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. The interaction between burn severity and functional divergence is significant, although only moderate-severity fires had a unique pattern. For **A**, whisker plots represent the regression coefficients: whiskers indicate the 95% confidence intervals, black dots are the mean, and gray dots are the data. For **B** and **C**, curves represent the regression coefficients, shaded areas are the 95% confidence intervals, and gray dots are the data

most recent burn severity and the interaction of pyrodiversity within 50 m of the plot. The functional divergence formulation of the pyrodiversity metric within 50 m of the plot describes different fire experiences such as an area with repeated high-severity fire adjacent to an area that has only had one low-severity fire. These areas could be at the intersection of different environmentally driven plant communities such as lush, moist meadows embedded within drier forests. Another example could be a fire's behavior derived from weather, including changes in temperature, wind, and relative humidity, which create a matrix of high- and low-severity fire patches and fire-derived plant communities near one another (Collins and Stephens 2010). Or, these areas could also have a combination of environmental and fire-driven plant communities that influenced their diversity.

There are differences in the scale at which pyrodiversity best predicts biodiversity for different taxa in these mixed conifer forests. The neighborhood size of fire experience that best predicts plant community diversity (50 m) is smaller than the one identified for pollinators, plant-pollinator interactions (150 m; Ponisio et al. 2016), and bats (500 m; Steel et al. 2019). Bird diversity was also positively influenced by pyrodiversity at 100 m, which was the only scale tested (Tingley et al. 2016). It is likely

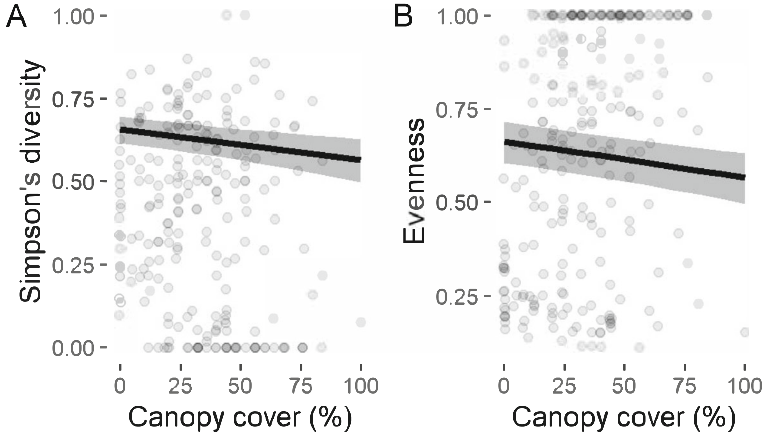

Fig. 6 Understory plant species **A** Simpson's diversity and **B** evenness responses to tree canopy cover throughout the study in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Public data were collected beginning in early 1900s. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. Curves represent the regression coefficients, shaded areas are the 95% confidence intervals, and dots are the data

that pyrodiversity has a relationship with biodiversity for these taxa at many scales and that focusing on the scale that "best predicts biodiversity" is unnecessary in a management context.

There are two major pyrodiversity metrics: those that examine the heterogeneity of recent fire severity in the neighborhood and those that examine the fire severity of fires where remotely sensed information exists. The formulation of the pyrodiversity metric that influenced plant community richness and functional divergence is different from that identified by Ponisio et al. (2016), which was the Simpson's formulation of the metric. The difference may have arisen because the current study includes comprehensive, long-term data across two sites, whereas Ponisio et al. (2016) used a small subset of plots (18 of 149 plots sampled for two sequential years) and focused on plants with flowers that pollinators visited, in Illilouette only. Others have defined pyrodiversity as the heterogeneity of burn severity around a survey point and examined its relationship to the diversity of birds and bats (Tingley et al. 2016; Steel et al. 2019; Steel et al. 2021). Additional research is needed to determine the important scales and type of pyrodiversity for other taxa, and in ecosystems managed by treatments other than fire.

Goal 3: Understand the most important environmental and fire variables that influence plant communities through space and time

Understory plant communities were influenced by a combination of environmental and fire characteristics. Most plant community descriptors (understory plant cover, Simpson's diversity, and evenness) were influenced by canopy cover. Plot-based fire history, including fire severity and number of times burned, had a low influence on understory plant cover. Plant richness was influenced by the environment (soils and CWD), plot-based fire experience (burn severity), and plot-neighborhood fire experience (functional divergence within 50 m of the plot).

Many modern studies investigate how individual species and local plant communities respond to fire (Turner et al. 2003; Chase 2007) and often focus on one or possibly two aspects of a fire regime (Saxon 1984; Knapp and Keeley 2006; Parr and Andersen 2006; Clarke 2008). For example, large fires with extensive stand-replacing effects tend to homogenize microenvironments and select for rapidly colonizing species across the landscape (Pausas and Verdú 2008). In contrast, variable fire effects consisting of generally low- to moderate-severity fire with small stand-replacing patches can create heterogeneous landscape patterns and diverse microenvironments (Hessburg et al. 2016). Such fires may influence gamma diversity by increasing niches for species to inhabit (Perry et al. 2011) or by influencing species turnover between unique habits while species richness remains the same throughout the region. Our study supplements these studies with a better understanding of understory plant cover, richness, diversity, and evenness within forests, and how environment, fire history, and pyrodiversity influence them.

Canopy cover can be directly proportional to the severity of disturbance (Collins et al. 2007a; Collins et al. 2007b), and it can also be influenced by edaphic characteristics of a given site (Kane et al. 2014). In this study, canopy cover was the only significant factor explaining Simpson's diversity and evenness, and it also had the largest effect on understory cover. Canopy cover had an inverse relationship with Simpson's diversity, evenness, and understory cover, reducing canopy cover through frequent fire enhances the understory plant community. Similarly, low forest canopy cover maintained through timber and mechanical treatments may also increase understory cover and diversity of plant communities (Battles et al. 2001). North et al. (2005) teased apart the environmental factors influenced by an open canopy, including both light and moisture competition, and their work suggests that the most important factor may be moisture. The relationship between decreased canopy cover and increased moisture is not clear after fire due to the interactions of tree transpiration, shade, and snow interception, and how canopy loss can influence evaporation and sublimation (Boisramé et al. 2018). Despite the uncertainty about the relationship between canopy and moisture, we demonstrated a strong increase in understory cover and diversity when canopy cover decreases. In our study sites, the most pronounced increase in soil moisture occurred when high-severity forest fire led to the creation of habitats dominated by wetland vegetation (Boisramé et al. 2018). If fire is restored across Sierra Nevada and some mixed conifer forests are replaced with wetland vegetation, downstream flows could increase, with positive influence on the understory plant cover and diversity.

While others found that shrub cover influenced understory richness (Bohlman et al. 2016; Richter et al. 2019), our study does not support that conclusion. Bohlman et al. (2016) examined the long-term impacts of removing shrubs in a chronosequence on US Forest Service lands that had been fire suppressed and had large patches of high-severity wildfire. In contrast, our study examined the long-term impacts of managed wildfire in a site with a nearly restored fire regime sampled with repeated measures and, while high-severity fire was present, it was mostly in small patches (Collins and Stephens 2010). Some of our important response variables were similar to Bohlman et al. (2016), including a moisture variable and fire severity. However, our analyses also identified pyrodiversity and soil texture as important explanatory variables. These differences could be due to the contrasting recent fire histories between the two studies, but it is also necessary to point out that we only had a few shrub plots with more than 20% shrub cover (n = 6). Future research examining the role of shrubs in areas with restored fire regimes in the Sierra Nevada mixed conifer forest may elucidate trends that we could not detect.

Previous studies suggested a unimodal pattern of understory plant diversity that peaked in low- to moderate-severity fire in Sierra Nevada mixed conifer forests following the intermediate disturbance hypothesis (DeSiervo et al. 2015; Stevens et al. 2015; Richter et al. 2019). While we also found that recent moderate-severity fires contributed to high richness, we found fire severity alone was not the best fire-related predictor of richness. Rather, it was the interaction of moderate-severity fire and pyrodiversity at 50 m. Fire severity alone may not have been a strong predictor of richness because it could lead to more than one distinct vegetation community. For example, recent high severity fire (n = 23) led to both shrub fields and dense grasslands at our sites (Boisramé et al. 2017). The dense grasslands were often lush meadows that had the highest species richness recorded in our study, while plots with 20% or greater shrub cover (n = 6) had slighter higher than average species richness. Furthermore, fire severity may be a weak predictor for diversity because historical fire regimes had a mixture of fire severities. We had a few unburned plots, but these were likely unburned due to site conditions such as low productivity or rockiness rather than fire suppression. We also had plots with recent high-severity fire, but these were likely within the range of historical size rather than large, high-severity patches that have lower diversity (DeSiervo et al. 2015; Stevens et al. 2015; Richter et al. 2019; Miller and Safford 2020). Perhaps we did not detect a signal for the intermediate disturbance hypothesis because our study sites were intermediate and we did not sample the extreme disturbance levels. Lastly, "disturbance" in this system is a combination of severity, patch size and shape, and fire frequency, and thus, it is not surprising that severity, a single component of disturbance, is not a strong determinant of community characteristics.

Ultimately, this study provides novel insights into the drivers and patterns of understory communities in areas with restored fire regimes. We tie the modern vegetation conditions to a key ecological process, fire, which has been nearly restored at our study sites. These results may apply to other dry coniferous forests in the western US.

Conclusion

Sierra Nevada mixed conifer forests have changed dramatically since Euro-American influence. Prior to colonization, the forests experienced frequent fire that created large, open stands of trees, interspersed with meadows, shrub fields, and early or successional forest habitats (Safford and Stevens 2017). More than a century without fire left dense, homogenous forests with little sunlight on the forest floor. This change could alter the understory plant community.

Frequent fire has restored forest structure in some areas of upper-elevation Sierra Nevada mixed conifer forests. In these areas, understory plants have low cover yet high diversity. Pyrodiversity and canopy openness foster different types of understory diversity. While there is concern about shrub fields limiting diversity elsewhere (Bohlman et al. 2016), our results suggest that this is not an issue when the forest structure and fire regime are nearly restored. Based on our findings, we recommend reducing tree canopy cover within large landscapes to increase understory plant cover and diversity and, when possible, fostering pyrodiversity to support rich understory plant communities.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-021-00111-6.

Additional file 1. Climate data in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. Climate data spans from 1981 to 2013. Table 1.1 National Oceanic and Atmospheric Administration (NOAA) nearest weather stations used based on elevation and distance from study site. Please note that there were weather stations that were physically closer to the sites, but much lower in elevation, and therefore not appropriate for comparison. Table 1.2 Annual precipitation and snow calculated from monthly climate normals for each weather station. Yosemite Park Headquarters and Yosemite Village 12W both had significant snow throughout the year, but it was not recorded. Monthly climate normals were computed for the 30-year period from 1981 to 2010 (Arguez et al. 2010). Figure 1.1 Monthly climate normals computed for the 30-year period from 1981 to 2010 for minimum temperature, average temperature, maximum temperature, snow, and precipitation (Arguez et al. 2010).

Additional file 2. Statistical methods used in our study in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. Public data collection began in the early 1900s. Equation 2.1 We tested the effect of plot-based fire experience and environmental factors on plant cover and evenness using the following equation, where γ is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities. Equation 2.2 We tested the main effect of pyrodiversity metrics at buffers around the plot (including 25, 50, 75, 100, and 250 m), times since fire, and most recent burn severity on plant cover and evenness using the following equation, where γ is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities. Equation 2.3 We ultimately tested the effect of plot-based fire experience, plot-neighborhood pyrodiversity, and environmental factors on plant Simpson's diversity and richness. We tested the main effect of the best pyrodiversity metric and buffer size (Tables 3, 4), its interaction with time since fire and most recent burn severity, and environmental variables, using the following equation, where γ is the response variable, fixed effects are bolded, and random effects are plain text. The interaction between time since fire and most recent fire severity enabled us to compare the trajectories of the plant communities as they matured after different fire severities. Table 2.1 Model family and transformation for each understory plant community response variable.

Additional file 3. Biological information for our study in the Illilouette Creek basin in Yosemite National Park and Sugarloaf Valley in Kings Canyon National Park, California, USA. Field data were collected from 2002 to 2013 to observe naturally occurring patterns of forest and understory structure and composition in relationship to fire regime. Table 3.1 Non-native plants found from 2011 through 2013 including the study site in which they were found, their growth habit, and duration based on USDA Plants, species name, California Integrated Pest Management (Cal-IPM) harmfulness rating (Bell et al. 2015; USDA and NRCS 2020), and the number of plots where they occurred. NA = not applicable.

Abbreviations

CWD: Climatic water deficit; RdNBR: Relative differenced Normalized Burn Ratio

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Authors' contributions

KW collected field data, identified plants, completed analysis, and wrote the manuscript. LP assisted with the analysis and assisted in writing the manuscript. BC collected field data and assisted in writing the manuscript. TM designed monitoring protocol and collected field data. DF collected field data, identified plants throughout the study, and advised on the study. SS helped write the manuscript and has overseen this project for more than 15 years. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and analyzed are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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