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Research

Peeking under the canopy: anomalously short fire-return intervals alter subalpine forest understory plant communities

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Summary

- Climate change is driving changes in disturbance regimes world-wide. In forests adapted to infrequent, high-severity fires, recent anomalously short fire-return intervals (FRIs) have resulted in greatly reduced postfire tree regeneration. However, effects on understory plant communities remain unexplored.
- Understory plant communities were sampled in 31 plot pairs across Greater Yellowstone (Wyoming, USA). Each pair included one plot burned at high severity twice in < 30 yr and one plot burned in the same most recent fire but not burned previously for > 125 yr. Understory communities following short-interval fires were also compared with those following the previous long-interval fire.
- Species capable of growing in drier conditions and in lower vegetation zones became more abundant and regional differences in plant communities declined following short-interval fire. Dissimilarity between plot pairs increased in mesic settings and decreased with time since fire and postfire winter snowfall. Reduced postfire tree density following short-interval fire rather than FRI *per se* affected the occurrence of most plant species.
- Anomalously short FRIs altered understory plant communities in space and time, with some indications of community thermophilization and regional homogenization. These and other shifts in understory plant communities may continue with ongoing changes in climate and fire across temperate forests.

Introduction

Natural disturbances such as fires, pest outbreaks, and hurricanes generate spatial and temporal heterogeneity, shape the structure and function of many ecosystems, and drive evolution in populations of flora and fauna globally (Turner, 2010; Peters *et al.*, 2011; Banks *et al.*, 2013; Keeley & Pausas, 2022). Disturbances vary in their size, severity, frequency, and seasonality, and variation in these disturbance characteristics over long periods of time is embodied in the historical range of variability (Landres *et al.*, 1999; Keane *et al.*, 2009). Biotic communities are typically well adapted to disturbances within these bounded ranges (e.g. Johnstone *et al.*, 2016), and ecosystem structure and function recovers during the interval between disturbances. However, ecosystems may change markedly if disturbances exceed their historical ranges of variability and recovery processes are disrupted (Turner & Seidl, 2023). As anthropogenic climate change alters disturbance dynamics in forests (Coop *et al.*, 2020; Grünig *et al.*, 2023) and aquatic (Daufresen & Boët, 2007; Palmer *et al.*, 2008; Herrera-R *et al.*, 2020) and marine environments (Wernberg *et al.*, 2016; Hughes *et al.*, 2018), there is growing concern for how ecosystems will respond.

Wildland fire is one such disturbance agent being transformed by climate change (Seidl *et al.*, 2017; Bowman *et al.*, 2020). While ecosystems remain resilient under historical fire regimes (i.e. they recover to prefire structure and function; Holling, 1973), deviations from the historical ranges of variability in a fire regime may erode resilience and reorganize the structure and/or composition of biotic communities (Seidl & Turner, 2022). In boreal and temperate coniferous forests, fire is a dominant disturbance agent driving centuries-long forest development trajectories (Tolonen, 1983; Agee, 1993; Veblen *et al.*, 2006; Perry *et al.*, 2011). Observed and projected changes to fire and climate could disrupt this historical disturbance-recovery dynamic as contemporary forests face climate warming (Stevens-Rumann *et al.*, 2018; Rodman *et al.*, 2020; Reich *et al.*, 2022), increasing fire frequency (Turner *et al.*, 2019; Baltzer *et al.*, 2021; Agne *et al.*, 2022), growing fire size and extent of stand-replacing fire (Dennison *et al.*, 2014; Barbero *et al.*, 2015; Parks & Abatzoglou, 2020), and shifting fire distributions (Alizadeh *et al.*, 2021; Xu & You, 2022). For forests adapted to infrequent, high-severity fire, anomalously short fire-return intervals (FRIs) may catalyze postfire reorganization. Tree recruitment may be drastically reduced if forests reburn before reaching maturity (i.e. immaturity risk; Keeley *et al.*, 1999) and surrounding young, short-statured forest provide minimal *ex situ* seed pressure (Gill *et al.*, 2021). Hot, dry microclimate conditions following fire may further limit seedling establishment and growth

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(Hoecker *et al.*, 2020; Wolf *et al.*, 2021). Reduced tree regeneration following anomalous short-interval fire has been increasingly observed (Turner *et al.*, 2019; Whitman *et al.*, 2019; Busby *et al.*, 2020; Hoecker & Turner, 2022; Braziunas *et al.*, 2023) with more expected (Halofsky *et al.*, 2020; Nolan *et al.*, 2021; Rammer *et al.*, 2021; Turner *et al.*, 2022) as climate and fire regimes continue to change (Rogers *et al.*, 2011; Westerling *et al.*, 2011; Henne *et al.*, 2021). However, few studies have focused on the potential effects of short-interval fires on understory vascular plant communities.

The understory plant community is an integral component of forest biodiversity and ecosystem function (Nilsson & Wardle, 2005; Gilliam, 2007). Community recovery following disturbance is driven by myriad factors (Roberts, 2004; Meiners *et al.*, 2015), including the regional species pool (Belote *et al.*, 2009), plant establishment and growth traits (Grime, 1977), and microclimate conditions (Zellweger *et al.*, 2020; Wolf *et al.*, 2021). Following short-interval fire, persistent absence of a tree canopy may directly affect the understory community through altered resource availability (Hart & Chen, 2006) and decreased temperature buffering capacity (Davis *et al.*, 2019; de Frenne *et al.*, 2019). Graminoids and annuals may be favored (Schoennagel *et al.*, 2004; Fairman *et al.*, 2017), as well as species adapted to warmer, drier conditions (i.e. community thermophilization; Gottfried *et al.*, 2012, de Frenne *et al.*, 2013, Stevens *et al.*, 2015, 2019). Such effects may be further amplified in already warm, dry landscape positions (Hoecker *et al.*, 2020) or where tree cover remains sparse (Andrade *et al.*, 2021); reduced tree recruitment following fire in lower montane forests (Donato *et al.*, 2016; Davis *et al.*, 2019; Young *et al.*, 2019) suggests plant communities in arid areas may be particularly vulnerable to change. What's more, natural and prescribed fire may homogenize previously distinct plant communities through homogenization of abiotic conditions (Mattingly *et al.*, 2015; Stevens *et al.*, 2015; Richter *et al.*, 2019; Weeks *et al.*, 2023), but whether such changes occur following anomalously short-interval fire is not known. As changing climate and fire regimes trigger postfire conversion of forest to sparse or nonforest (Coop *et al.*, 2020), elucidating effects on the whole plant community is needed to understand the future of these burned landscapes.

The recent uptick in fire activity across western North America (Abatzoglou & Williams, 2016; Higuera *et al.*, 2021) has contributed to > 50 000 ha of subalpine forest in the US Northern Rocky Mountains reburning at ≤ 23-yr FRIs (Harvey *et al.*, 2016a), an order of magnitude shorter than historical FRIs (100–300 yr; Romme & Despain, 1989, Schoennagel *et al.*, 2003, Whitlock *et al.*, 2008). Here, we used field data from paired plots following recent (1988–2018) short- and long-interval fires as well as published and unpublished data following previous long-interval fires to assess responses of plant community composition to short-interval fire in both space and time in the Greater Yellowstone Ecosystem, Wyoming, USA. Fire rotations in Greater Yellowstone may shorten to < 30 yr by the end of this century (Westerling *et al.*, 2011), and fires in 2016 that burned > 18 000 ha of 16–28-yr-old forest suggest such change is already underway (Turner *et al.*, 2019). We asked: (1) How do understory plant communities vary in space and time following short- vs long-interval fire? (2) Which drivers explain understory community dissimilarity between paired short- and long-interval fires? (3) Which drivers best explain postfire understory plant community composition, and how do responses vary among species? We expected persistent or increasing cover of the understory community following short-interval fire because most taxa can resprout (Anderson & Romme, 1991). However, we expected shifts in community composition as annuals, graminoids, and species adapted to warm, dry conditions increase in abundance (i.e. thermophilization) relative to long-interval fire. We also hypothesized that plant communities from different regions in Greater Yellowstone would be more similar following recent short-interval fires than those in the same general locations following the previous long-interval fire. We expected dissimilarity between communities in paired short- and long-interval plots to be context dependent, with certain conditions increasing and others decreasing paired dissimilarity (Table 1). Finally, across all postfire communities, we expected the likelihood of occurrence of individual species to increase with longer time since fire, shorter FRIs, lower lodgepole pine densities, and more mesic topographic and climatic factors.

Materials and Methods

Study area

Greater Yellowstone is a *c.* 8.9 million ha temperate zone ecosystem at the southern end of the Northern Rockies ecoregion (Harvey *et al.*, 2016b; Hostetler *et al.*, 2021) and centered over Yellowstone and Grand Teton National Parks (YNP and GTNP, respectively). Vegetation varies with elevation: *Artemisia*-dominated shrublands below 1800 m above sea level (asl) transition into lower montane and subalpine forest from 1800 to 2900 m asl. Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) predominates in lower montane forests while lodgepole pine (*Pinus contorta* var. *latifolia*) forms nearly monospecific stands across YNP's midelevation plateaus, with subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*) becoming increasingly prevalent at higher elevations (Despain, 1990). Most soils in the region are volcanic-derived and relatively infertile, with rhyolitic substrates underlying lower montane and lodgepole pine-dominated subalpine forests and andesitic substrates at higher elevations (Despain, 1990; Whitlock, 1993). From 1981 to 2010, average temperature ranged from 22°C in July to −17.1°C in January, with *c.* 531 mm of annual precipitation (Lake Yellowstone, Wyoming, station #485345; Western Regional Climate Center, 2021).

The region's subalpine forests, particularly those dominated by lodgepole pine, are resilient to large, stand-replacing fires that have occurred at intervals of 100–300 yr throughout the Holocene (Romme & Despain, 1989; Schoennagel *et al.*, 2003; Whitlock *et al.*, 2008). For example, stem densities in lodgepole pine forests 11 yr after the 1988 Yellowstone fires, which burned > 250 000 ha of forest as stand-replacing fire, averaged

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Table 1 Potential explanatory variables of Jaccard's dissimilarity between paired understory plant communities following short- and long-interval fire in lodgepole pine-dominated forests in the Greater Yellowstone Ecosystem, Wyoming, USA.

Category	Variable	Units	Description	Hypothesis
Fire	Time since fire (TSF)	yr	Number of years since most recent fire (variable across pairs, consistent within pairs)	Dissimilarity will decrease with increasing TSF as communities converge over time
Site	Topographic moisture index (TMI)	Unitless	Cosine-transformed aspect (degrees) as an index of site aridity; 0 = southwest-facing aspect, 2 = northeast-facing aspect	Dissimilarity will decrease with increasing TMI as more southwesterly sites (and thus lower TMI) exhibit greater differences in composition
Tree density	Relative change in lodgepole pine density (PICOdiff)	Unitless	Proportional increase in log-transformed lodgepole pine density from short- to long-interval plot within pairs	Dissimilarity will increase with PICOdiff as greater differences in canopy cover drive changes in composition
Climate	30-yr normal summer water deficit (WD)	mm	General site summer aridity, measured as evaporative demand exceeding soil moisture availability during summer (June, July, August)	Dissimilarity will increase with WD as differences between paired plots are amplified in sites with greater summer moisture stress
	30-yr normal winter snow water equivalent (SWE)	mm	General site snow conditions, measured as the amount of water available in snow from the previous winter	Dissimilarity will decrease with 30-yr SWE as differences between paired plots are amplified in sites with longer growing seasons and reduced moisture availability
	3-yr postfire winter snow water equivalent (SWE)	mm	Winter snow conditions averaged over the first three postfire years	Dissimilarity will decrease with 3-yr SWE as greater postfire SWE (and thus moisture availability in the spring and early summer) buffer potential compositional changes

Climate variables retrieved from Abatzoglou *et al*. (2018).

c. 29 000 stems ha^{-1} (median 3100 stems ha^{-1}) and exceeded 500 000 stems ha^{-1} where prefire serotiny levels were high (Turner *et al*., 2004). The rest of the plant community exhibited similar resilience owing to prolific resprouting and rapid infilling by native perennials in the years immediately following fire (Anderson & Romme, 1991; Turner *et al*., 1997). However, dominant drivers of community composition changed with time since fire, with early effects of burn severity shifting to strong effects of lodgepole pine density after two decades of forest recovery (Romme *et al*., 2016). By 24-yr postfire, most understory species were less likely to occur in areas with greater lodgepole pine density (Romme *et al*., 2016), but community variability driven by local soil moisture conditions persisted in areas of low canopy cover 30-yr postfire (Andrade *et al*., 2021).

Plot selection

To compare understory responses to short- vs long-interval fire in space, we sampled communities during summer 2021 across 20 plot pairs in which postfire tree regeneration and fuels were assessed by Braziunas *et al*. (2023). Briefly, sites were selected among recent (1994–2018) fires well-distributed across Greater Yellowstone that burned young (< 30-yr-old) and mature (> 125-yr-old) lodgepole pine-dominated forest at high severity (> 92.5% basal area mortality or 675–2000 RdNBR; Miller & Thode, 2007, Harvey *et al*., 2016a; Fig. 1a). Within each site, 1–2 plot pairs were established, with each pair consisting of one plot in an area burned twice at high severity at < 30-yr FRI and one plot in an area burned at high severity in the same most recent fire but not burned previously for > 125 yr (Fig. 1b). Paired plots were selected for topographic similarity and proximity, with all paired plots separated by < 1200 m. To augment our sample size, data from 11 pairs sampled 12 yr after the 1988 Yellowstone fires that met our definition of short-interval fire (Schoennagel *et al*., 2004) were included in our analyses. While variability in abiotic conditions (e.g. elevation and aspect) was captured across pairs, we ensured environmental conditions were consistent within pairs using propensity scores accounting for elevation, aspect, and slope during site selection (Butsic *et al*., 2017). Finally, all plots were dominated prefire by lodgepole pine, and postfire lodgepole pine densities were an order of magnitude lower in plots following short-interval fire (Braziunas *et al*., 2023).

To compare understory responses to short- vs long-interval fire in time, we collated plant community composition data from three sources: 12 previously established plots (Turner *et al*., 2019) sampled in 2021, 5 yr after the 2016 Berry Fire in GTNP, which reburned portions of recovering forest from the 2000 Glade Fire, and the 2016 Maple Fire in YNP, which reburned portions of the 1988 North Fork Fire; five plots sampled in 2004, 4 yr after the 2000 Glade Fire (W. H. Romme and M. G. Turner, unpublished data); and eight plots measured in 1993, 5 yr after the 1988 North Fork Fire (Turner *et al*., 1997, Romme *et al*., 2016; Supporting Information Table S1). Plots measured in 2021 were placed within areas reburned at high-severity fire on flat slopes with minimal aspect (Turner *et al*., 2019), four of which were also used in our paired design above. Plots measured in 2004 were established in 2001 in areas of stand-replacing fire as part of a previous study (Turner *et al*., 2007). Forests were *c.* 120 or 150 yr old when burned. Understory plant community composition was sampled annually (2001–2004) using the protocols described below, but only data from 4 yr postfire were used here. Plot selection for plots sampled in 1993 is described in Turner *et al*. (1997). Briefly, nine variably sized patches of stand-replacing fire were selected from throughout the burned area, within which four transects oriented in subcardinal directions were established. For the purposes of this

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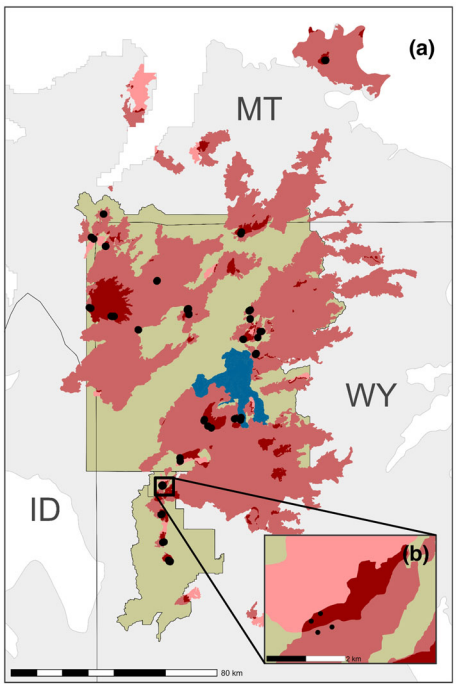

Fig. 1 Study area for assessing the effects of anomalously short fire-return intervals (FRI) on understory plant communities in Greater Yellowstone (gray). (a) Distribution of plots (black points; $n = 62$) across short-interval (< 30-yr) and long-interval (> 125-yr) fires in and around Yellowstone and Grand Teton National Parks (green). Light red areas are always the first fire in a given fire sequence; cinnabar areas may be the first or second fire in a given fire sequence, depending on the fire combinations; dark red areas are areas of short-interval fire, or overlap between successive fires occurring at < 30-yr FRI. (b) Zoomed section of overlapping fires showing pairing. Perimeters for fires predating satellite-derived severity imagery are not included. ID, Idaho; MT, Montana; WY, Wyoming.

analysis, we included community composition data from only the small and large patches at Cougar Creek which are located near or within our plots established following the Maple Fire. Because of differences in study design, we treated each transect in each patch as a plot ($n = 8$) and removed quadrats at the base of each transect near patch center given their proximity to other transects.

Field data collection

With one exception (see below), plant communities were sampled in 0.25-ha plots as described by Romme *et al.* (2016). Percent cover was recorded by species in 25 0.25-m^2 quadrats placed at 5-m intervals along each of three parallel 50-m transects separated by 24 m. A 20 min whole-plot sweep was conducted to detect any species present in the plot not already found in quadrats and determine whole-plot species richness. Voucher specimens were collected for any individual for which species identity could not be determined in the field. Species richness for plots measured in 2004 was determined from quadrats because whole-plot richness was unavailable. While quadrats only cover 6.25 m^2 of each 2500-m^2 plot, previous community sampling in the same general locations found *c.* 95% of species tallied in the plot sweep were also found in quadrats (Romme *et al.*, 2016), so richness may be comparable to that from whole-plot sweeps. Importantly, methods for obtaining richness were always the same within plot pairs for comparisons across space. Elevation, aspect, slope, and distance to unburned live forest edge were recorded from the center of each plot. Live forest edge beyond the range of the laser rangefinder was later estimated with aerial imagery and burn severity perimeters with ArcGIS Desktop 10.6.

For plots sampled in 1993, plant communities were sampled in eight 0.25-m^2 point-intercept frames (Floyd & Anderson, 1982, 1987) at 1-m intervals along an 8-m subtransect, with each subtransect spaced at either 20-m (small patch) or 100-m (large patch) intervals perpendicular to each main transect (Turner *et al.*, 1997).

Question 1: Plant community variability following short- vs long-interval fire

The effects of short- vs long-interval fire on plant communities were assessed using two approaches: (1) across the paired plots ($n = 31$) of long and short FRI; and (2) between plots that were sampled 4 to 5 yr postfire following the previous long-interval fire (2000 Glade or 1988 North Fork fire) and the recent short-interval fire (the 2016 Maple or Berry fire).

Within our paired plots, we identified species unique to either short- or long-interval plots and assessed differences in richness, Simpson's diversity and evenness, total understory cover, and percent cover of individual species. Species were further categorized based on growth form (shrub, graminoid, and forb), lifespan (annual, biennial, and perennial), and native status to determine differences in cover among these groups. We next created a series of abundance-weighted indices to assess community-level responses to short-interval fires. Each species was assigned a drought and shade tolerance value (USDA Plants Database), a minimum and maximum vegetation zone representing its distribution in the Rocky Mountains (0 = plains, 1 = foothills, 2 = lower montane, 3 = subalpine, 4 = alpine; Kershaw *et al.*, 2016), and a thermal and moisture preference value. Each species' thermal and moisture preference was calculated using 30-yr (1989–2018) normal maximum temperature (°C) and annual precipitation (mm) from 4-km resolution TerraClimate data (Abatzoglou *et al.*, 2018) and averaged across that species' range. Ranges were derived from Global Biodiversity Information Facility (GBIF) occurrence data, with duplicate occurrences and occurrences for which uncertainty was > 5 km removed. Evidence for community thermophilization would include lower community-weighted shade tolerance, vegetation zone, and moisture preference, and/or higher drought tolerance and thermal preference. Community-weighted drought and shade tolerance were only calculated using those species for which values were available, consisting of $80.2 \pm 0.02\%$ and $80.8 \pm 0.02\%$ of total community cover, respectively. The above indices provide complementary approaches to assessing community change and were chosen to capture a suite of potential shifts in composition following short-interval fire. Paired *t*-tests were used to test for differences in community-weighted shade and drought tolerance, thermal and moisture indices, and vegetation zones between plot pairs ($n = 31$).

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We next used nonmetric multidimensional scaling (NMDS) to determine whether plant communities following recent (2016) short-interval fires differ from those in the same general locations following the previous (1988 or 2000) long-interval fire. Given we were not interested in testing for potential environmental drivers, NMDS is appropriate for assessing community variability in ordination space. We removed all species present in < 5% of plots to reduce the influence of rare species and then used species presence as the response. Potential shifts in plant community composition from those following the first long-interval fire to those following the second short-interval fire were assessed visually after NMDS in the VEGAN package (Oksanen *et al.*, 2020). We then used Jaccard's dissimilarity index (0 = identical plant communities; 1 = mutually exclusive plant communities) calculated using species presence to determine whether plant communities following the previous long-interval fire from two regions of Greater Yellowstone (YNP near West Yellowstone, MT, and GTNP near Moran, WY) became more similar following recent short-interval fire.

Question 2: Drivers of dissimilarity across paired short- and long-interval fire

We used multiple regression to identify drivers of community dissimilarity between paired plots following short- and long-interval fire. In lieu of model selection, candidate predictors were selected from a suite of topographic, biotic, and climate variables based on *a priori* hypotheses of effects on plant community dissimilarity (Table 1). Our response variable was the Jaccard's dissimilarity for each plot pair ($n = 31$). We considered abundance-based dissimilarity (i.e. Bray–Curtis) as well, but less variation in dissimilarity across pairs was explained (Fig. S1). Climate variables were retrieved from TERRACLIMATE (Abatzoglou *et al.*, 2018) and were included to capture effects of both ambient climate conditions and climate during early postfire recovery on community dissimilarity. While 3-yr postfire summer water deficit was originally considered, it was removed given its collinearity with other predictors and variance inflation factor > 4. Lodgepole pine density was log-transformed before analysis to satisfy assumptions of normality. Predictors were *z*-transformed (mean = 0, SD = 1) before analysis to allow comparison of model coefficients. Model residuals did not exhibit heteroscedasticity or serial autocorrelation (Durbin-Watson test statistic = 2.07, $P = 0.82$), and a quantile-quantile plot revealed residuals to be normally distributed.

Questions 3: Drivers of postfire species' distributions and community composition

We used a multilevel modeling (MLM; Gelman & Hill, 2007) framework to test for differences in plant community composition across plots following both short- and long-interval fire ($n = 62$). MLMs provide powerful inference on individual species distributions and whole community composition by extracting the effects of environmental variables on each species and groups of species simultaneously (Jackson *et al.*, 2012). With species presence as the response, fixed effects for each predictor in a MLM can be interpreted as that factor's effect on all species' presence (i.e. understory community richness), whereas the random effect for each species-by-predictor combination represents that species' response to a given predictor after accounting for its fixed effect. The sum of each predictor's fixed effect with each species' random effect thus yields the overall effect of that predictor on that species. This framework has previously been used to determine drivers of variability in plant community composition following the 1988 fires (Romme *et al.*, 2016) and has proven informative across taxa and study systems (Jackson *et al.*, 2014; Bartrons *et al.*, 2015; Barker *et al.*, 2018; Paulson *et al.*, 2021).

The MLM was run for those taxa present in ≥ 5% of plots and identified at least to genus ($n = 80$), with taxon presence as the response. We included the ambient climate variables used in the above multiple regression (Question 2); lodgepole pine density (stems ha^{-1}), distance to road or trail (m), topographic moisture index (i.e. northeasterliness, or cosine-transformed aspect as a measure of site aridity; Beers *et al.*, 1966), and slope (degrees) to capture site characteristics; and time since fire and fire interval (short or long) to capture fire history characteristics. Predictors were *z*-transformed (mean = 0, SD = 1) before modeling. The MLM was fit using the glmer function in the LME4 package (Bates *et al.*, 2015) with a binomial family and logit link. Significance of each random effect was tested for using likelihood-ratio tests, and variance explained by the model (marginal R^2 for fixed effects and conditional R^2 for both fixed and random effects) was determined with the theoretical method for binomial distributions using the r.squaredGLMM function in the MUMIN package (Barton, 2020). Predictors were not highly correlated (variance inflation factor < 4). All statistical analyses and data visualization were conducted in R v.3.6.3 (R Core Team, 2020).

Results

Plant community variability following short vs long-interval fire

We identified 168 species across all plot pairs ($n = 31$; Table S2). Richness was relatively high (*c.* 35 species per 0.25-ha plot), but, along with cover, diversity, and evenness, did not differ between plot pairs (Table 2). Among species, 29 were recorded only following short-interval fire (Table S3), and 22 only following long-interval fire (Table S4). Of these, the graminoids, annuals, and biennials that were unique to either fire-interval class were found only following short-interval fire (Fig. S2). Six of seven nonnative species unique to either fire-interval class were found only following short-interval fire (Fig. S2), but none were new to the regional flora (Table S3). Among the most abundant species (total relative abundance > 0.7), five were more abundant following short-interval fire, including four forbs, two annuals, and one symbiotic nitrogen fixer (Table 3). The relative abundance of annuals increased while the relative abundance of perennials decreased following short-interval fire (Fig. S3), but no differences in the percent cover of graminoids, forbs, or relative abundance of shrubs were found (Fig. S4).

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Table 2 Average (±SE) richness, understory cover, diversity, and evenness of paired plant communities following short- vs long-interval fire in Greater Yellowstone ($n = 31$ plot pairs).

Index	Short-interval	Long-interval	t	P-value
Richness	36.6 ± 1.7	35.3 ± 2.3	−0.65	0.52
Understory cover (%)	32.7 ± 3.4	28.2 ± 2.9	−1.85	0.07
Simpson's Diversity	0.8 ± 0.01	0.8 ± 0.02	−0.77	0.45
Simpson's Evenness	0.2 ± 0.01	0.2 ± 0.01	0.39	0.70

Table 3 Percent cover of the most abundant understory species in paired communities following short- vs long-interval fire in Greater Yellowstone.

	Cover (%)			
Species	Short-interval	Long-interval	t	P
Forb				
Achillea millefolium	**0.31**	**0.16**	−2.0	**0.050**
Agoseris aurantiaca	0.05	0.02	−2.0	0.060
Antennaria microphylla	0.20	0.09	−1.9	0.067
Arnica cordifolia	0.31	0.67	2.0	0.057
Campanula rotundifolia	0.17	0.03	−1.9	0.064
Cirsium arvense	0.18	0.16	−0.3	0.767
Collomia linearis	**0.12**	**0.05**	−2.1	**0.046**
Chamaenerion angustifolium	2.01	2.25	0.6	0.544
Eurybia merita	0.77	1.36	1.3	0.215
Gayophytum diffusum	**0.16**	**0.03**	−2.9	**0.007**
Hieracium albiflorum	0.13	0.31	1.9	0.065
Lupinus argenteus	**2.37**	**1.22**	−2.1	**0.043**
Taraxacum officinale	0.61	0.44	−1.6	0.128
Graminoid				
Agrostis scabra	0.35	0.08	−1.3	0.211
Carex geyeri	**5.76**	**3.54**	−2.1	**0.048**
Carex rossii	2.19	2.18	0.0	0.998
Calamagrostis rubescens	3.55	3.36	−0.2	0.862
Shrub				
Ceanothus velutinus	1.29	0.01	−1.0	0.325
Mahonia repens	0.08	0.40	1.9	0.070
Spiraea betulifolia	2.63	2.78	0.2	0.854
Vaccinium scoparium	1.59	2.26	0.8	0.421

All five species that differed in cover with fire interval were more abundant following short-interval fire. Relative abundance of listed species in short-interval = 71.1%; long-interval = 77.5%. Bolded P-values are significant at $\alpha = 0.05$ following paired t-tests.

The community-level minimum vegetation zone was lower following short-interval fire and the range of vegetation zones (i.e. the difference between each species minimum and maximum vegetation zone) was greater (Fig. 2a), indicating a greater abundance of more widely distributed species capable of growing at lower elevations. Community moisture index and shade tolerance were lower following short-interval fire, but community thermal index and drought tolerance did not differ with fire interval (Fig. 2b–d).

Plant communities following recent (2016) short-interval fire overlapped little in ordination space with communities in the same general area following the previous long-interval fire (Fig. 3). Further, the regional separation of communities following the previous long-interval fire was reduced when those communities reburned at short FRI, particularly along NMDS axis 1. Indeed, mean dissimilarity (±SE) between plots from two regions of Greater Yellowstone decreased slightly from 0.77 (±0.01) following the previous long-interval fire to 0.73 (±0.01) following the recent short-interval fire despite comparable time since fire. However, dissimilarity among communities following the same short-interval fire increased from 0.49 (±0.02) following the previous long-interval fire to 0.63 (±0.02) following the recent short-interval fire, indicating this response is scale dependent.

Drivers of dissimilarity across paired short- and long-interval fire

Paired understory plant communities following short- vs long-interval fire exhibited considerable dissimilarity (Jaccard's = 0.77 ± 0.02) and selected predictor variables explained more than one-third of the variation in dissimilarity across communities ($R^2_{adj} = 0.39$). Paired communities were more similar with greater time since fire and 3-yr postfire winter snow water equivalent and less similar with greater 30-yr normal winter snow water equivalent (Fig. 4). The climate variables had roughly twice as strong an effect on community dissimilarity than time since fire.

Drivers of postfire species' distributions and community composition

The variables included in our MLM explained more than half of the variation in species distributions among plots ($n = 62$; conditional $R^2 = 0.53$), but very little of this was via the fixed effects (i.e. on community richness; marginal $R^2 = 0.03$). At the community level, any species was more likely to occur (i.e. richness was greater) in plots with lower lodgepole pine density, on southwesterly aspects (i.e. TMI approaching 0), with longer time since fire, and greater 30-yr winter snow water equivalent (i.e. greater average winter snowfall; Table 4). Distance to road or trail, fire interval, slope, and 30-yr summer water deficit were not important as fixed effects.

At the species level, all predictors except fire interval were important (fixed plus random effect ≥ |0.20|) in explaining the presence of at least one taxon ($n = 80$), with directions of effect varying among species (Table S5). Thirty-year summer water deficit and lodgepole pine density were the most important predictors for the most taxa (32.5% of taxa each), followed by 30-yr winter snow water equivalent (18.8%) and time since fire (16.3%), with distance to road or trail and slope the most important for only one taxon each. Two-thirds (36) of taxa responding to 30-yr summer water deficit were more likely in areas of greater summer aridity, but 7 of 10 graminoids showed the opposite trend (Table S5). Most (44 of 51) taxa responding to lodgepole pine density were less likely in areas of higher density; the seven taxa that were more likely to occur with increasing lodgepole pine density included three shrubs (*Arctostaphylos uva-ursi*, *Salix scouleriana*, and *Vaccinium scoparium*) and *Hieracium albiflorum*,

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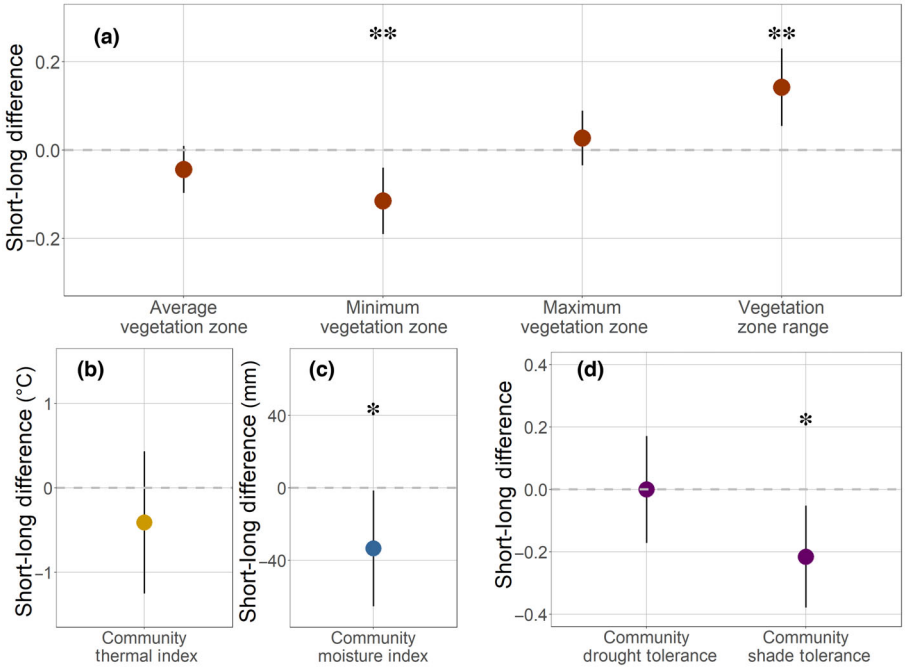

Fig. 2 Differences in abundance-weighted community indices between paired plots following short- and long-interval fire in Greater Yellowstone ($n = 31$). *, $P < 0.05$; **, $P < 0.01$ (following paired t-tests). Vertical black bars represent 95% confidence intervals. (a) Average, minimum, maximum, and range of vegetation zones (defined as the difference between each species' minimum and maximum range). The relative abundance of species with lower minimum vegetation zones and a greater range of vegetation zones increases following short-interval fire. (b) Community thermal index and (c) community moisture index. The relative abundance of species capable of growing in lower moisture conditions increases following short-interval fire. (d) Community drought and shade tolerance of species (data from USDA Plants Database; species weighted against total cover only of species for which drought and shade tolerance values were available). Communities following short-interval fire are made up of relatively more shade-intolerant species.

one of the more abundant forbs following long-interval fire. Of the 60 taxa responding to 30-yr winter snow water equivalent, all but two shrubs, *Rosa woodsii* and *Symphoricarpos albus*, were more likely to occur in areas of greater average winter snowfall. Ten of 57 taxa were more likely to occur with shorter time since fire, including three graminoids (*Carex rossii*, *Elymus trachycaulus*, and *Stipa* sp.), two shrubs (*Ribes viscosissimum* and *Spiraea betulifolia*), and two annuals (*Gnaphalium palustre* and *Pseudognaphalium macounii*). Non-native species (*Cirsium arvense*, *Phleum pratense*, *Taraxacum officinale*, and *Tragopogon dubius*) generally occurred in areas of greater average winter snowfall, lower lodgepole pine density, and after longer time since fire. Though only important for fewer than 10 taxa each, distance to road or trail always increased likelihood of occurrence, whereas northeasterliness always decreased likelihood of occurrence. Finally, 75% (21) of taxa responding to slope were more likely on steeper slopes.

Discussion

Our study contributes new understanding of how anomalous short-interval, stand-replacing fires affect subalpine forest understory plant communities. Understory communities following short-interval fire were increasingly composed of annuals, shade-intolerant species, and species capable of persisting at lower elevations and with reduced moisture availability. However, understory percent cover and diversity did not differ with fire interval, suggesting some resilience of understory communities to more frequent fires. We found changing FRI affected the understory via reduced postfire tree densities (which are a direct result of short-interval fire; Braziunas *et al.*, 2023), indicating changes in postfire forest structure that result from anomalously short-interval fire cascade to the understory (Fig. 5). Short-interval fire also eroded regional differences in understory communities, as distinct communities following the previous long-interval fire became more similar following the recent short-interval fire despite comparable time since fire. However, dissimilarity among communities following the same short-interval fire increased, suggesting understory change following short-interval fire remains scale and context dependent. Differences between paired plots burned at short vs long FRI were greater in areas of greater average (30 yr) snowfall but attenuated with time since fire and greater postfire snowfall, implicating the timing and availability of moisture in the magnitude of community differences following short-interval fire. Finally, average winter snowfall and summer aridity had both positive and negative effects on the presence of individual species, suggesting complex changes in understory community composition as climate continues to change across western North America.

Short-interval fire alters plant community composition in space and time

Reduced community moisture index and lower community shade tolerance following short-interval fire suggest differences in community composition expected with warmer, drier soils (Hoecker

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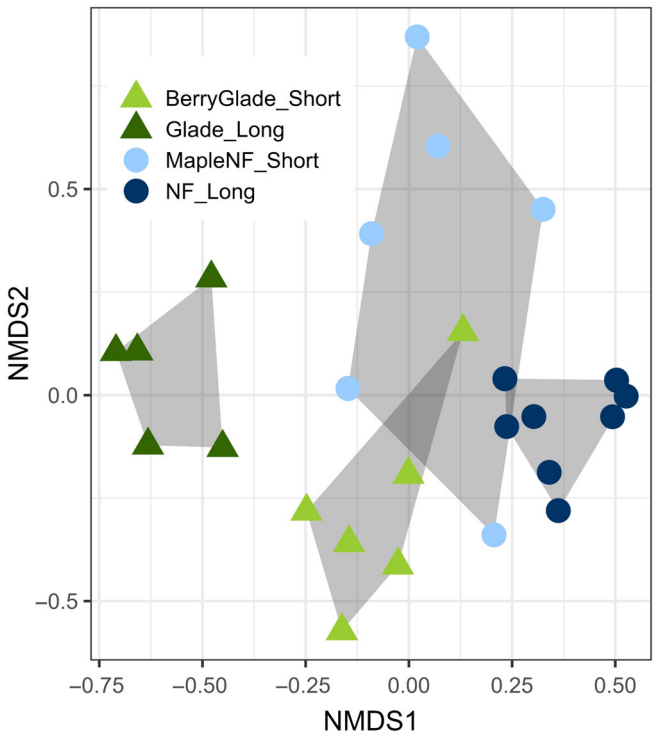

Fig. 3 Nonmetric multidimensional scaling (NMDS) ordination of plant communities in either Grand Teton (green triangles) or Yellowstone National Park (blue circles) and burned in either the original long-interval fire (darker shade) or the recent short-interval reburn of the original long-interval fire (lighter shade). BerryGlade_Short, plant communities 5 yr after the Berry Fire reburn of the Glade Fire at short-interval; Glade_Long, plant communities 4 yr after the long-interval Glade Fire; MapleNF_Short, plant communities 5 yr after the Maple Fire reburn of the North Fork (NF) Fire at short-interval; NF_Long, plant communities 5 yr after the long-interval NF Fire. Communities closer to one another in ordination space are more similar.

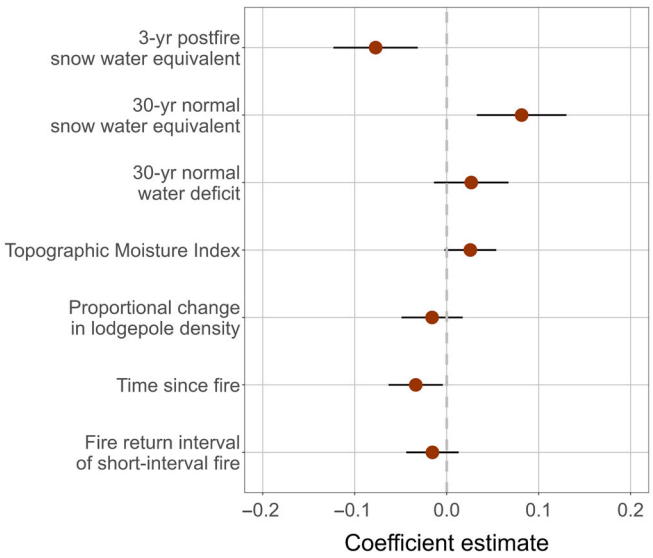

Fig. 4 Standardized coefficient estimates following multiple regression of Jaccard's dissimilarity between paired plots following short- and long-interval fire in Greater Yellowstone ($n = 31$). Community dissimilarity increased with greater 30-yr snow water equivalent and decreased with greater 3-yr postfire snow water equivalent and longer time since fire. Horizontal black bars represent 95% confidence intervals. $R^2_{adj} = 0.39$.

Table 4 Coefficients of fixed and random effects in the multilevel model for plant species present in at least 5% of 62 plots across short- and long-interval reburns in the Greater Yellowstone Ecosystem.

	Effect	
Coefficient	Fixed	Random
Intercept	−1.83***	2.39***
30-yr normal snow water equivalent	0.32***	0.14**
30-yr normal water deficit	0.10	0.36***
Lodgepole pine density	−0.28***	0.22***
Distance to road or trail	0.10	0.03
Topographic moisture index	−0.10*	0.03
Slope	0.07	0.11***
Time since fire	0.22**	0.22***
Fire interval	−0.002	0.001

Positive fixed effects are interpreted as community richness increasing with that variable; negative as community richness decreasing with that variable. Significant random effects indicate species-specific responses to that variable. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

et al., 2020) and increased sunlight via a 10-fold reduction in postfire lodgepole pine densities (Turner *et al.*, 2019; Braziunas *et al.*, 2023). These shifts are consistent with expectations of community thermophilization, a process increasingly observed following natural (de Frenne *et al.*, 2013; Stevens *et al.*, 2015, 2019; Zellweger *et al.*, 2020; Christiansen *et al.*, 2022) and manipulated (de Frenne *et al.*, 2015; Liu *et al.*, 2018; Govaert *et al.*, 2021) changes in temperature and moisture conditions that can persist even after canopy closure (Dietz *et al.*, 2020). Short-interval fire also triggered increasing abundance of species capable of growing in lower (and potentially warmer and drier) vegetation zones. Upslope migration of various taxa with climate change has occurred in many mountainous regions globally (Kelly & Goulden, 2008; Feeley *et al.*, 2011; Vitasse *et al.*, 2021) and may be necessary for population persistence (Anderson & Wadgymar, 2019). Plant populations in communities following historical FRIs may not keep pace with climate warming, accruing greater climatic debt relative to those following anomalously short FRIs (Richard *et al.*, 2021).

Short-interval fire also altered plant communities in time. At the regional scale, understory plant community dissimilarity was *c.* 5% lower following two recent short-interval fires than among those following the previous long-interval fires. However, at local scales (i.e. within a single short-interval fire), dissimilarity was *c.* 30% greater, highlighting the potential influence of fine-scale drivers on postfire composition. Many drivers of decreased community dissimilarity (i.e. homogenization) have previously been identified, including historical land use (Velland *et al.*, 2007), non-native species introductions (Qian & Ricklefs, 2006), silvicultural treatments (Macdonald & Fenniak, 2007; Jaeger *et al.*, 2022), and fire severity (Weeks *et al.*, 2023). Repeat short-interval fires (i.e. 'triple burns') observed elsewhere (Fairman *et al.*, 2017; Agne *et al.*, 2022) are not yet prevalent in Greater Yellowstone, so whether continued deviations from historical fire

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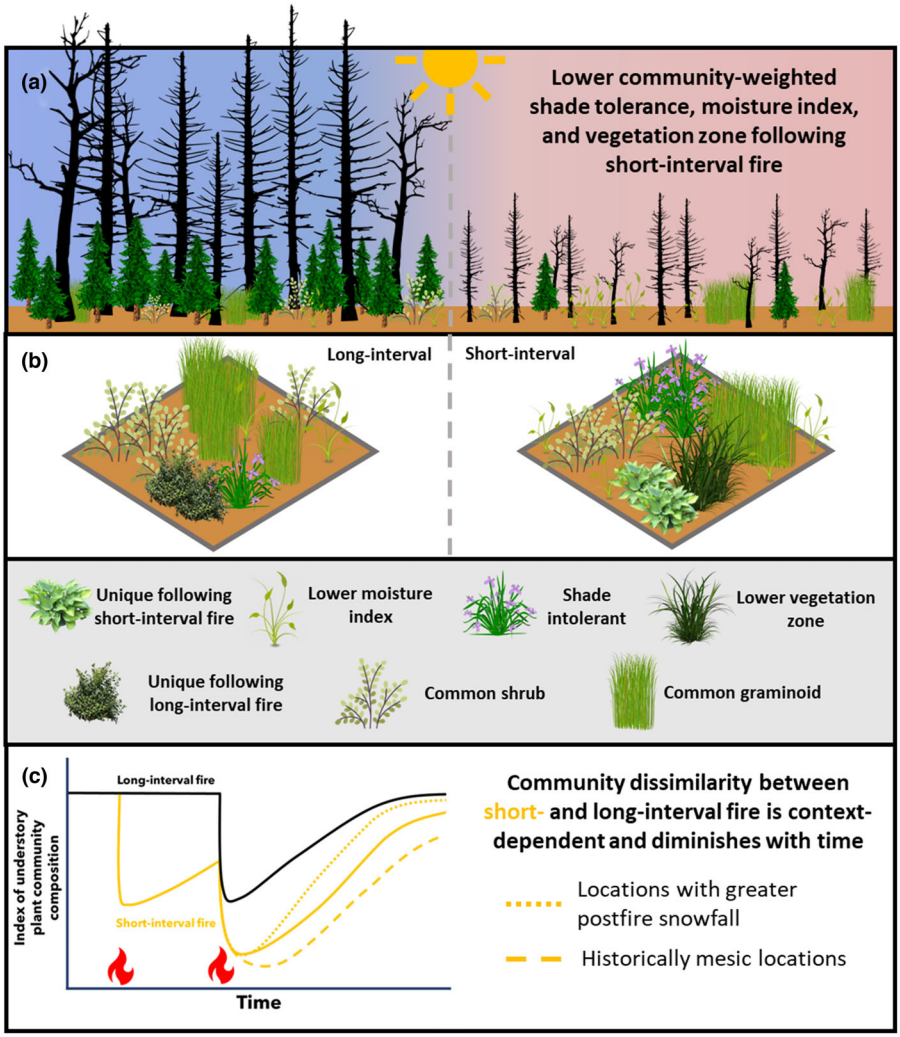

Fig. 5 Conceptualization of key effects of anomalously short fire-return intervals (FRIs) on understory plant communities in the Greater Yellowstone Ecosystem. (a) Several key environmental conditions vary between areas burned at either short or long FRI that drive changes in community composition, including lower postfire tree regeneration (Turner *et al*., 2019; Braziunas *et al*., 2023) and warmer, drier soils (Hoecker *et al*., 2020). (b) Example quadrats illustrate primary changes to community composition, including the presence of species unique following each short- and long-interval fire and a greater abundance of shade-intolerant species, species adapted to lower moisture availability, and species capable of persisting in lower vegetation zones following short-interval fire. However, community cover and diversity did not differ, and several common species were present in each interval class. (c) Compositional shifts in communities between paired short- and long-interval fires are context dependent, with greater dissimilarity in historically mesic locations and lower dissimilarity with greater postfire snowfall and longer time since fire.

regimes fully homogenize plant communities despite the importance of site-specific environmental conditions (see below) remains to be seen. With 28–59% of currently forested area in Greater Yellowstone vulnerable to regeneration failure by 2100 (Rammer *et al*., 2021), any change is likely to be widespread.

Despite shifts in composition, other aspects of plant communities following short-interval fire did not differ greatly from those following historical FRIs, indicating potential resilience of the understory. Though percent cover of annuals was low, their relative abundance increased approximately threefold following short FRIs, consistent with ruderal species benefitting from more frequent disturbance (Grime, 1977). However, unlike past studies (Schoennagel *et al*., 2004; Fairman *et al*., 2017; Reilly *et al*., 2020), differences in percent cover and relative abundance of shrubs, graminoids, and non-native species were slight or non-existent, and biotic cover did not decrease following short FRIs as in western North American boreal forests (Whitman *et al*., 2019). Many perennials in Greater Yellowstone resprout postfire (Anderson & Romme, 1991), a common fire-adapted trait across woody and herbaceous taxa (Clarke *et al*., 2013), and plant communities are largely resistant to invasion by non-natives (Wright & Tinker, 2012; Romme *et al*., 2016). These mechanisms conferring resilience remained intact following short-interval fires both in our system and in Pacific Northwestern forests adapted to a mixed-severity fire regime (Donato *et al*., 2009).

Effect of short-interval fire on plant communities depends on environmental conditions

Understory community dissimilarity between plot pairs varied across the landscape, indicating susceptibility of communities to change following short-interval fire is context dependent. Counter to expectations, dissimilarity increased in areas of greater average snowfall where spring and early summer moisture availability is likely greater. Such mesic conditions contributed to shorter fire seasons and longer FRIs historically (Schoennagel *et al*., 2003), making short FRIs a relative anomaly compared with drier areas. Forest loss in relatively mesic areas following short-interval fire may expose plants to arid conditions to which they are unaccustomed, whereas communities in areas of lower average snowfall may already resemble those following short-interval fire. Community differences following short-interval fire were buffered by greater postfire winter snowfall, however, likely via increased

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moisture availability in spring and early summer. Mean annual snowfall in Greater Yellowstone has already declined 8.9 cm decade^{-1} since 1950 (Hostetler *et al.*, 2021), a trend expected to continue (Barnett *et al.*, 2005; Lute *et al.*, 2015; Gergel *et al.*, 2017). Paired plots also became more similar with longer time since fire, but shortened future fire rotations (Westerling *et al.*, 2011) would leave less time for community convergence before subsequent reburns. Together, these findings suggest a somewhat counter-intuitive result – plant communities in relatively mesic locations are most vulnerable to change, especially because those mesic conditions that buffered community change may become less prevalent by centuries' end.

Climate, site, and fire characteristics influence understory species' distributions

Understory richness and individual species' presence were influenced by climate, site, and fire characteristics following short- and long-interval fires. The presence of all species increased with time since fire and in areas of greater average winter snowfall but decreased with lodgepole pine density and on northeasterly aspects. Community richness 24 yr after the 1988 Yellowstone fires similarly increased with time since fire and decreased with lodgepole pine densities (Romme *et al.*, 2016), but decreased with postfire mean annual precipitation. The lack of a direct effect of fire interval on species presence revealed that species' distributions were driven by other factors associated with FRI, especially postfire tree density, which was an order of magnitude lower following short- vs long-interval fire (Braziunas *et al.*, 2023) and influences competition for light, water, and nutrients. Observed (Turner *et al.*, 2019; Braziunas *et al.*, 2023) and predicted (Hansen *et al.*, 2020; Rammer *et al.*, 2021; Turner *et al.*, 2022) forest loss in the region with shorter FRIs may increase understory community richness at the expense of species that benefit from greater lodgepole pine density, provided climate conditions remain suitable.

Species-specific responses illustrate potential shifts in the structure and function of understory communities with changing climate and fire (Table S5). *Vaccinium scoparium*, a widely distributed shrub, was more likely to occur in areas of greater average snowfall, at greater lodgepole pine density, and with longer time since fire, all conditions likely to become less common through the end of this century. Conversely, *Carex geyeri*, the most abundant understory species across plots (Table 3), was more likely to occur in areas of greater average summer water deficit and at lower lodgepole pine density, indicating it may benefit from continued changes to climate and fire regimes. Regarding function, *Lupinus argenteus*, the primary nitrogen-fixing plant species in the region, became more abundant following short-interval fire and was more likely to occur in areas of greater average summer aridity. *Ceanothus velutinus*, a facultative nitrogen fixer in lower montane areas, was more likely to occur at lower lodgepole pine density. As nitrogen-fixing plants are more abundant in high-light environments given energetic costs of dinitrogen fixation (Vitousek *et al.*, 2002; Houlton *et al.*, 2008; Taylor & Menge, 2018), conditions following short-interval fire appear suitable. However, *Lupinus* and *Ceanothus* cover is patchy and low at the landscape level, so consequences for nitrogen fixation remain uncertain. Many graminoids may also benefit from more frequent fire, as each of the six graminoid species responding to lodgepole pine density was more likely to occur with lower stem densities. Graminoids and other understory herbs may become primary sources of fuel where trees are sparse or absent given their high surface area to volume ratio and low bulk density (Brown, 1970; Hoffmann *et al.*, 2012). Though overall graminoid cover was only slightly higher following short-interval fire ($P = 0.064$), three graminoids (*Carex geyeri*, *Carex rossii*, and *Calamagrostis rubescens*) comprised nearly one-third of understory cover, suggesting even slight changes in abundance could influence the amount and continuity of fine fuels (Mitchell *et al.*, 2006) and thus future surface fires.

Considerations and conclusions

Several limitations to our study bear consideration. While our paired study design improves our ability to draw inferences, we cannot draw causal links between environmental drivers and community responses without manipulative experiments. Further, site selection was constrained by the availability and accessibility of short- and long-interval fires proximal to one another and with comparable abiotic conditions. However, while the occurrence and distribution of anomalously short-interval fire is driven by several self-regulating factors, these effects often diminish within two decades following the first fire (Harvey *et al.*, 2016a), and extreme fire weather conditions often override fuels limitation in subalpine forests (Turner & Romme, 1994). Thus, we expect the potential for prefire conditions to confound our results to be small.

Our study revealed that postfire understory plant communities adapted to infrequent, stand-replacing fires shifted following anomalously short FRIs, with understory community reassembly driven by restructuring of the forest overstory (Seidl & Turner, 2022). Our results highlight the importance of assessing the whole plant community. Changes in the relative abundance of understory taxa may be early indicators of ecosystems adapting to a changing environment while aggregate metrics such as diversity and cover may miss shifts in species assemblages. Continued changes to climate and disturbance regimes are increasingly likely through the end of this century, and land managers are expected to make decisions on whether to resist, accept, or direct change (Millar *et al.*, 2007; Schuurman *et al.*, 2022). Contemporary understory plant communities following short-interval fire may illustrate the future of subalpine forest plant communities should managers choose to accept fire- and climate-driven forest change. With ongoing disturbance-driven changes to ecosystems worldwide, elucidating postdisturbance community dynamics will prove crucial as a baseline against which alternative recovery pathways and management scenarios may be compared.

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This research was conducted on the past and present homelands of many indigenous nations and tribes, including the Crow,

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Shoshone-Bannock, and Blackfeet who were forcibly removed during the creation of the national parks (Spence, 1999) but remain connected to the region today. We thank Paul Boehnlein, Nick Tipper, Julia Warren, Diane Abendroth, and Becky Smith for field assistance; Bill Romme for assistance with plant identification; Tania Schoennagel for previously published data; and Tony Ives and Ben Zuckerberg for statistical advice. This manuscript was improved by constructive comments from Tony Ives, Julia Warren, Bill Romme, and two anonymous reviewers. Funding for this study was provided by the Joint Fire Science Program's Graduate Research Innovation Award (20-1-01-6), National Science Foundation (DEB-2027261), and the University of Wisconsin-Madison Vilas Trust. NGK and KHB acknowledge support from the Department of Integrative Biology, University of Wisconsin-Madison. KHB also acknowledges support from the International Chapter of the PEO Ventura Neale Trust Endowed Scholar Award and from the European Research Council under the European Union's Horizon 2020 research and innovation program (Grant Agreement 101001905).

Competing interests

None declared.

Author contributions

KHB and MGT designed the study; NGK, KHB, and MGT collected data; NGK analyzed data; NGK and MGT wrote the paper with contributions from KHB.

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Data availability

Data have been deposited to the Environmental Data Initiative (EDI) repository: https://doi.org/10.6073/pasta/d06aeedf63f5e0cf71669679ffd5df01.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Standardized regression coefficients of multiple regression of various explanatory variables on Bray–Curtis dissimilarity between paired short- and long-interval plots ($n = 31$).

Fig. S2 Unique species by growth form, lifespan, and status after short- and long-interval fire.

Fig. S3 Differences in cover by lifespan in paired short- and long-interval plots ($n = 31$).

Fig. S4 Differences in cover by growth form in paired short- and long-interval plots ($n = 31$).

Table S1 Summary of datasets used in analyses for Q1.

Table S2 List of species identified across all short- and long-interval plots ($n = 62$).

Table S3 List of species unique to plots following short-interval fire ($n = 31$).

Table S4 List of species unique to plots following long-interval fire ($n = 31$).

Table S5 Species-level responses to environmental variables across all short- and long-interval plots ($n = 62$).

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