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The effect of fire interval on post-fire understorey communities in Yellowstone National Park

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Abstract

Questions: How does the time interval between subsequent stand-replacing fire events affect post-fire understorey cover and composition following the recent event? How important is fire interval relative to broad- or local-scale environmental variability in structuring post-fire understorey communities?

Location: Subalpine plateaus of Yellowstone National Park (USA) that burned in 1988.

Methods: In 2000, we sampled understorey cover and *Pinus contorta* density in pairs of 12-yr old stands at 25 locations. In each pair, the previous fire interval was either short (7-100 yr) or long (100-395 yr). We analysed variation in understorey species richness, total cover, and cover of functional groups both between site pairs (using paired *t*-tests) and across sites that experienced the short fire intervals (using regression and ordination). We regressed three principal components to assess the relative importance of disturbance and broad or local environmental variability on post-fire understorey cover and richness.

Results: Between paired plots, annuals were less abundant and fire-intolerant species (mostly slow-growing shrubs) were more abundant following long intervals between prior fires. However, mean total cover and richness did not vary between paired interval classes. Across a gradient of fire intervals ranging from 7-100 yr, total cover, species richness, and the cover of annuals and nitrogen-fixing species all declined while the abundance of shrubs and fire-intolerant species increased. The few exotics showed no response to fire interval. Across all sites, broad-scale variability related to elevation influenced total cover and richness more than fire interval.

Conclusions: Significant variation in fire intervals had only minor effects on post-fire understorey communities following the 1988 fires in Yellowstone National Park.

Keywords: Community ecology; Disturbance ecology; Fire ecology; Functional group; Landscape ecology; Lodgepole pine; *Pinus contorta*; Post-fire succession; Subalpine.

Nomenclature: Dorn (1992).

Abbreviations: YNP = Yellowstone National Park.

Introduction

Life history and functional traits are a useful way to develop a general understanding of the response of plant communities to disturbance characteristics (Connell & Slatyer 1977; Lavorel & Cramer 1999; Pausas et al. 2004). We hypothesize that responses to fire interval depend on (1) life history (short fire intervals should favour annuals; Grime 1977); (2) fire tolerance of perennials (long fire intervals should favour species that recover slowly from fire; Flinn & Wein 1977; Granström & Schimmel 1993); (3) obligate soil seed storage (long fire intervals should favour species that store viable seeds in the soil for long periods; Noble & Slatyer 1980; Rowe 1983); (4) successional status (long fire intervals should decrease the importance of early-successional, shade-intolerant perennials; Peterson & Carson 1996); (5) ability to fix nitrogen (short fire intervals should favour nitrogen-fixers; Newland & DeLuca 2000), and (6) origin (short fire intervals, like other frequent disturbances, should promote establishment of non-natives; Crawford et al. 2001). Examination of such traits in response to disturbance interval may elucidate mechanisms underlying existing disturbance frequency theories (e.g., intermediate disturbance hypothesis; Connell 1978), or suggest alternative models (Pausas et al. 2004) to better predict community response to altered fire frequencies.

Relatively short intervals between disturbances are expected to affect community responses to the most recent fire in ways that relatively long intervals (within the historical range of variability) do not (Connell & Slayter 1977; Paine et al. 1998). Empirical research in many crown-fire ecosystems supports predictions that species abundance or richness may be lower following relatively short fire intervals. For example, in chaparral systems, shrub abundance declined following fire intervals that were significantly shorter than mean historical fire intervals (Zedler et al. 1983, Haidinger & Keeley 1993). In forest systems, the abundance and composition of post-fire shrubs or trees may also respond to the length of the previous fire interval (Noste & Bushy 1987; Luc & Luc 1998; Keeley et al. 1999; Larocque et al. 2000). In high-elevation subalpine forests of Yellowstone, stand-replacing fires recurred historically at average intervals of ~100 to 300 yr (Schoennagel et al. 2003) indicating that fire intervals less than 100 yr are relatively short in this system.

Although previous fire intervals may affect patterns of post-fire regeneration, the environmental template across which disturbances recur can also influence post-fire community composition and abundance (Grime 1977; Myster 2001). Previous studies have shown that successional patterns following disturbance may reflect either environment gradients or disturbance characteristics or a combination of both (McIntyre & Lavorel 1994a, b; Turner et al. 1997). Therefore, it is valuable to control environmental variability while testing for disturbance effects and also to consider the relative importance of environmental and disturbance factors in drawing inferences about the role of disturbance in a particular system.

We examined the effect of the previous fire interval on post-fire vegetation patterns following the 1988 fires in Yellowstone National Park (YNP) by asking: (1) how do understorey communities (measured by total cover, species richness, diversity and functional group abundance) respond to variation in fire interval? and (2) what is the importance of fire interval relative to broad-scale (variables related to elevation) or local-scale (slope and aspect) environmental variability in structuring post-fire understorey communities?

Methods

Study area

We studied the subalpine plateaus of Yellowstone National Park in NW Wyoming that are dominated by *Pinus contorta* (Lodgepole pine) forests (Despain 1990). Elevation reflects two broad-scale environmental gradients in the park; soil fertility (Despain 1990) and serotiny (the proportion of seeds within closed cones of *P. contorta* which open with fire; Tinker et al. 1994). Although soils are generally infertile throughout the subalpine plateaus, soils are more fertile on andesite or detrital substrates, which are largely restricted to higher elevations. Levels of serotiny, which are highly correlated with post-fire densities of *P. contorta*, are highest at lower elevations (Tinker et al. 1994). Therefore, post-fire *P. contorta* densities are relatively dense at lower elevation but relatively sparse at higher elevations (Schoennagel et al. 2003). Local-scale environmental variability reflects variation in slope and aspect.

During the summer of 1988, severe fires burned ca. 45% of the park affecting ≥ 200 000 ha of forest on the subalpine plateaus (Christensen et al. 1989; Turner et al. 1994). Such large fires have occurred in Yellowstone in the past, most recently in the early 1700s (Romme 1982, Romme & Despain 1989), while smaller fires occur more frequently. Large fires are typically driven by high winds under extreme drought conditions (Christensen et al. 1989; Renkin & Despain 1992). Subsequent analyses of the 1988 fires indicate that climate and weather rather than fuels primarily affected the extent of the fires (Romme & Turner 2004). Although mean fire intervals within stands historically varied between 100-300 yr on the subalpine plateaus (Schoennagel et al. 2003), under extreme weather conditions such as 1988 stands of all ages burned (i.e. previous fire intervals varied widely). Therefore, the 1988 fires burned ca. 32 000 ha of forest on the subalpine plateaus that had previously burned within the last 100 years, with some stands experiencing ≤ 10 yr between stand-replacing fires. This event created a unique opportunity to study how understorey vegetation responds to a broad range of previous fire intervals without confounding variation in time since the last fire.

Field sampling

During the summer of 2000, we sampled understorey cover and *P. contorta* density in paired 12-yr old stands at 25 locations (Fig. 1). At each location, we sampled paired short (≤ 100 yr) and long (≥ 100 yr) fire intervals to allow comparison of fire interval effects while controlling for environmental variation. Although there is overlap in the interval categories, at each location the short fire interval is always shorter than the long fire interval (Fig. 3). Overlays of a Geographical Information System (GIS) layer of historical fires during the 1900s with a layer of 1988 fire extent and severity located 25 short fire intervals across the landscape. All fires considered were stand-replacing. To define the spatial extent of each short interval patch, we traced the overlapping perimeters of the 1988 and historic fires from historical aerial photos (1 : 40 000 - 1 : 60 000) onto topographic maps. A plot was randomly located within each of these short fire interval patches.

Adjacent to each short interval plot (≤ 100 yr) we randomly located a long fire interval plot in a topographically similar patch that also burned in 1988, but which had not burned previously within the last 100 years (Fig. 2). All plots were at least 75 m from the unburned forest edge and from isolated trees within the burn perimeter to reduce effects of distance to unburned seed source and to ensure that sampling occurred within known fire perimeters. To confirm the length of each

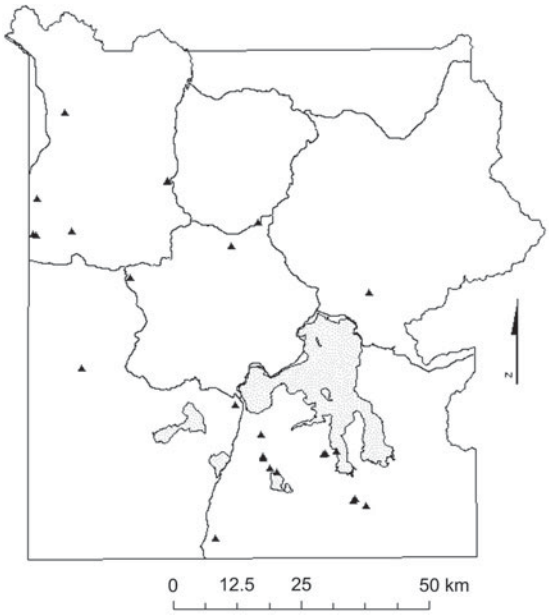

Fig. 1. A map of 25 sampling locations throughout the park where understorey community composition and lodgepole density were sampled in paired short and long interval plots. Stippled areas represent lakes. Lines mark all roads and the boundary of Yellowstone National Park.

fire interval, we cored several of the largest dead trees in each 0.5-ha plot. If intact cores could not be gathered from large burned trees, we cored the largest trees in the adjacent patch that did not burn in 1988, but was within the historic burn perimeter (see Fig. 2).

Short fire intervals ranged from 7-100 yr and long fire intervals ranged from 100-395 yr. Although the distinction between short and long fire intervals is somewhat arbitrary, mean fire intervals experienced over the subalpine plateaus were 135-310 historically (Schoennagel et al. 2003), so fire intervals < 100 yr are relatively short. Although there is overlap in the bounds of the two interval classes, the mean short fire interval is 27 yr while the mean long fire interval is 211 yr. The mean (and median) difference between paired fire intervals at a location is 173 (171) yr, with paired differences ranging from 28-347 yr (Fig. 3).

In each plot we estimated understorey cover, species richness and tree density. Percent cover by species was measured within forty 0.25-m^2 quadrats placed every 5 m along four 50-m transects, laid 25 m apart. We also recorded percent cover occupied by rocks. For each plot, cover data were averaged over all 50 quadrats by species. For species richness, the number of species rooted within the quadrats was counted and summed across quadrats. Post-fire tree densities were also recorded by species in 2 m × 50 m belt transects centred along the same transects where understorey cover was estimated. 26% of the sites recorded tree species other than *Pinus contorta*, but these species only comprised an average of ≤ 1% of the total sapling density at each of those sites. Therefore, we only report *P. contorta* densities, estimated by summing stem counts across the four 100-m^2 belt transects in each plot and scaling to stems per ha. Elevation, aspect and slope were recorded at each site in the field.

In a GIS, additional environmental information was derived for each plot. We categorized soil fertility at each site as either infertile on rhyolite substrate (0) or relatively fertile on andesite/lacustrine substrates (1) by overlaying a map of classified soil substrates (Yellowstone GIS Lab) with the sampling points. Similar overlay analysis determined burn severity (surface burn, severe surface or crown fire) for each plot from a classified Thematic Mapper scene (30 m × 30 m) taken the summer after the 1988 fires (Turner et al. 1994). Distance to the closest unburned forest edge from the centre of each plot was also calculated from the burn severity map. The majority of the paired plots (n = 16) were ≤ 400 m apart, with none ≥ 1500 m apart.

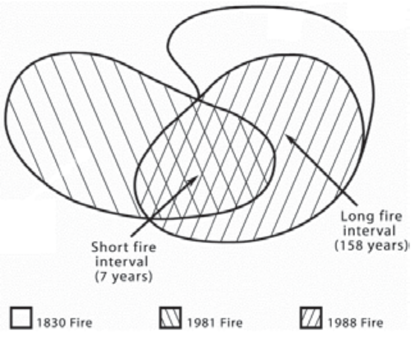

Fig. 2. A schematic depiction of the sampling design at each location with example dates. All sampling occurred in 2000. In this example the short fire interval is 7 yr, whereas the long fire interval is 158 yr. All stands sampled experienced 12 yr since the most recent fire.

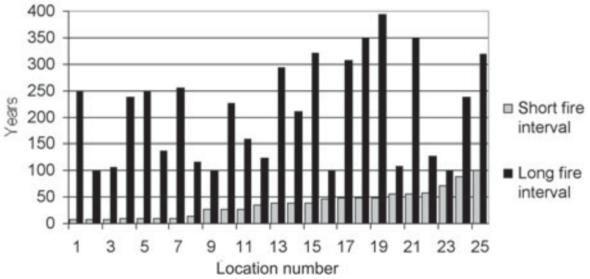

Fig. 3. Summary of the relative length of short and long fire intervals sampled at 25 paired plots, with site pairs sorted by length of the short fire interval.

Data analysis

Fire interval effects

The paired plot design permitted analysis of understorey response to fire interval class while minimizing confounding effects of variables like the time-since-last fire, elevation, aspect, slope, distance to unburned edge, soil fertility, and rock cover (Table 1). We compared mean total cover, species richness, Shannon's and Simpson's diversity indices, and coefficients of variation of total cover per plot and by species using paired t-tests. We also assessed differences in the abundance of various functional groups classified according to: (1) life history (annual vs. perennial); (2) life form (graminoid, herb, shrub); (3) fire tolerance (intolerant species defined from the literature by observed inability to resprout following severe fire, meristems recorded as 'shallow' or reported average depth of the meristem < 10 cm below the soil surface); (4) soil seed storage where scarification by fire is necessary for germination; (5) successional status (defined by reported shade tolerance or classification as early- or mid-to-late successional); (6) ability to fix nitrogen; and (7) non-native origin (see App. 1). For each plot we summed mean cover values of species classified within each functional group, then applied paired *t*-tests to determine the influence of fire interval class on that group. Rare species present in ≤ 5% of the plots were excluded. We also correlated overall compositional dissimilarity between paired plots with differences in fire interval. Dissimilarity was calculated as city-block distance (CBD):

$$\sum \left| A_{L,j} - A_{S,j} \right| \qquad (1)$$

where, $A_{L,j}$ = cover of species *j* in long fire interval plot *L* and $A_{S,j}$ = cover of species *j* in short fire interval plot *S* (McCune & Grace 2002). The difference in fire interval between paired plots was calculated as a ratio of (short fire interval)/(long fire interval). A Pearson correlation coefficient was calculated for these two measures of difference between the paired plots.

Table 1. Summary of mean values of independent variables from paired short (≤ 100 yr; *n* = 25) and long (≥ 100 yr; *n* = 25) fire interval plots with the range of each variable across all plots (*n* = 50) and results from paired *t*-tests.

	Short fire interval	Long fire interval	Variable range	*p*-value
Fire interval (years)	38	211	7-395	≤0.0001
Elevation (m)	2377	2378	2011-2618	0.491
Aspect (deg)	132	118	30-296	0.395
Slope (%)	4.5	4.4	0-32	0.476
Distance to unburned edge (m)	130	171	75-850	0.210
Soil fertility$^{1)}$	0.28	0.28	0-1	0.500
Burn severity$^{2)}$	2.1	2.6	1-3	0.026
Rock cover (%)	2.2	1.1	1-8	0.162
Lodgepole pine density(stems/ha)	2991	7577	25-56,025	0.036

$^{1)}$ Categorical: 0 = infertile, 1 = relatively fertile; $^{2)}$Categorical: 1 = surface burn, 2 = severe surface burn, 3 = severe canopy burn.

Table 2. Mean values of understorey cover and diversity indices for paired short (≤ 100 yr; *n* = 25) and long (≥ 100 years; *n* = 25) fire interval plots. The *p*-values are based on paired *t*-tests.

	Short fire interval	Long fire interval	*p*-value
Total cover (%)	22.3	22.5	0.486
Mean species richness (no. species)	84	92	0.607
Mean Shannon Diversity Index (*H*)	2.4	2.4	0.668
Mean Simpson Diversity Index (*D*)	0.85	0.84	0.534
CV total cover/plot (%)	38	45	0.720
CV total cover/species (%)	180	192	0.245
No. rare species (present in ≤ 5% of plots)	26	29	

Next we examined understorey responses to a gradient of all fire intervals and a subset of short fire intervals that would not have been captured by the paired plot analysis above. We separately regressed all fire intervals (7-395) and short fire intervals (7-100 yr) against total cover, species richness and functional group abundance. To analyse the community response to short fire intervals in more depth, we performed non-metric multidimensional scaling ordinations (NMS) on species composition and abundance at each short fire interval

Table 3. Results from simple linear regressions of total cover, species richness and functional group abundance against the continuous independent variable short fire interval (7-100 yrs; *n* = 25). Dependent variables, regression coefficients, correlation coefficients (*r*-values), and *p*-values shown. Variables with significant *p*-values in bold. All independent variables represent percent cover plot^{-1} except species richness which is the number of species plot^{-1}.

Dependent variable	Regression coefficient	Correlation coefficient	*p*-value
Log (total cover)	– 0.006	– 0.418	0.037
Species richness	– 0.242	– 0.589	0.003
Herbs	– 0.034	0.122	0.569
Grasses	– 0.045	0.305	0.147
Shrubs	0.016	0.386	0.056
Annuals	– 0.011	– 0.393	0.052
Perennials	– 0.046	0.134	0.431
Log (fire-tolerant spp.)	– 0.005	0.178	0.404
Fire-intolerant spp.	0.037	0.433	0.035
Shade-intolerant spp.	0.021	0.133	0.536
Log (soil seed storage spp.)	0.015	0.227	0.299
Shade-tolerant spp.	– 0.177	0.387	0.062
Log (nitrogen-fixing spp.)	– 0.013	– 0.508	0.013
Exotic species	– 0.019	0.271	0.190

plot and calculated the percent variance in the community data captured by the first two ordination axes. All independent variables (see Table 1) were subsequently correlated with these two primary axes to determine which ones captured the most variance in the understorey community data. Lastly, we correlated total cover, species richness and individual species abundances with the axis representing a gradient in short fire intervals to characterize broadly the community response to this gradient in short fire intervals. All ordinations were performed on pruned data sets that excluded rare species (species occurring in ≤ 5% of the plots) and plots more than two standard deviations beyond the mean average distance between all other plots (to avoid undue influence of outliers). The number of rare species pruned prior to each analysis is listed in Table 2. In all analyses we log-transformed variables to homogenize variances and improve normality (see Table 3).

Relative importance of factors affecting post-fire understorey communities

We regressed the results of the principal components analysis (PCA) of independent environmental variables against total cover and richness in order to summarize the importance of fire interval relative to broad- and local-scale variability in structuring post-fire understorey communities across the YNP landscape. We first derived orthogonal components from all independent variables measured using PCA (Table 1). Component loadings were based on a Varimax rotation, and only components with eigenvalues ≥ 1.0 were selected. Then we regressed the orthogonal components against understorey cover and richness to assess their significance in explaining variance in the post-fire community. This analysis permitted a summary evaluation of the degree to which disturbance characteristics relative to environmental variables affected post-fire understorey abundance and diversity across the Yellowstone landscape.

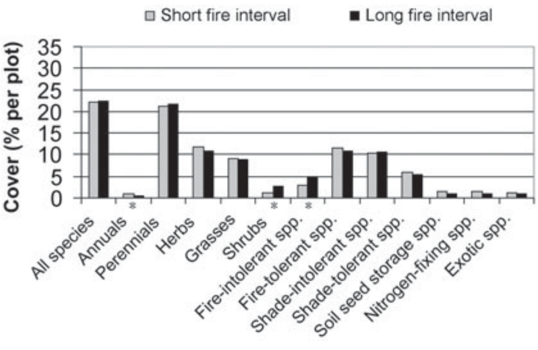

Fig. 4. Comparison of functional group responses (mean % cover per plot) to fire interval classes across all sites ($n = 50$). Significant differences judged by paired t-tests for fire interval class, where * indicates variables significant at $\alpha = 0.05$.

Results

Fire interval effects

The environmental variables (elevation, aspect, slope, distance to unburned edge, soil fertility, and rock cover) all varied among sites but not between the paired short and long fire interval plots within sites, as planned (Table 1).

Burn severity and *Pinus contorta* density were higher following longer fire intervals, however. Previous work found that burn severity and serotiny increase with pre-fire stand age (Turner et al. 1999; Schoennagel et al. 2003) and could not be controlled between paired plots. Paired short and long fire interval plots did not differ in mean percent cover, species richness, or other broad measures of diversity (Table 2). Perennials with the potential to resprout following fire dominated the understorey communities and did not respond to the two broad fire interval classes (Fig. 4). Some plant groups, however, did respond to fire interval class (Fig. 4). Mean cover of annuals was significantly higher in the short fire interval class, while fire-intolerant perennials were significantly less abundant following short fire intervals. Woody perennials (shrubs), the most dominant life form within the fire-intolerant group, had significantly lower cover following short fire intervals. Regression analysis, where fire interval was treated as a continuous variable, reflected these same trends, however annuals were not significant in the regression analysis. Community similarity increased with the ratio of short to long fire intervals between paired plots ($r = 0.351$), weakly indicating that more similar fire intervals were associated with more similar understorey communities.

Across the short interval plots (7 - 100 yr), total cover, species richness, and the abundances of annuals and nitrogen-fixing species all increased in apparent response to shorter fire intervals (Table 3). Fire-intolerant species and shrubs decreased with shorter fire intervals over this range. Exotic cover, which was low overall (Fig. 4), did not vary consistently across the short fire interval sites (Table 3).

The ordination of short fire interval plots (≤ 100 years) produced two axes that accounted for 45% and 32% (total 77%) of the variance in community composition (Table 4). Axis 1 was positively correlated with total plant cover and species richness ($r = 0.606$ and 0.719 respectively) and negatively correlated with fire interval ($r = –0.676$) and *P. contorta* density ($r = –0.415$, Table 4). Thus, very short interval fires (ca. 40 yr or less) co-occurred with low tree densities and higher understorey cover and richness. There were 12 species more abundant following very short fire inter-

Table 4. Independent variables correlated with primary non-metric multidimensional scaling axes, which capture variance among species abundance and composition across the short fire interval plots (≤ 100 yr; n = 25). Variance in the understorey community captured by Axis 1 = 44.8% and Axis 2 = 31.9% for a total of 76.7% of the total variance explained. Boldface figures represent the highest correlations with Axis 1.

Correlation of independent variables with axes		
	Axis 1	Axis 2
Fire interval	**-0.676**	0.116
Elevation	0.072	-0.214
Aspect	0.220	-0.105
Slope	0.369	-0.024
Burn severity	-0.234	-0.108
Distance to unburned edge	0.288	-0.010
Lodgepole pine density	-0.415	-0.353
Rock cover	-0.005	-0.442
Soil fertility	0.253	0.148
Correlation of summary understorey variables with axes		
	Axis 1	Axis 2
Total cover	**0.606**	-0.055
Species richness	**0.719**	-0.124

Table 5. Results from principal component regression analysis. **A.** Loadings of independent variables on the three primary components and percent variance captured by each component. Total variance captured is 59.2%. Boldface figures represent the highest correlations. **B.** Results from separate linear regressions of total cover and species richness across all sites (fire interval = 7-395 yr) and short fire interval sites only (7-100 yr). Significant principal components, regression coefficients, p-values and r^2-values are shown for each regression model.

A.	Principal component loadings		
	PC1	PC2	PC3
Pinus contorta density	**– 0.829**	0.149	0.203
Elevation	**0.756**	– 0.112	0.403
Soil fertility	**0.575**	– 0.088	– 0.058
Aspect	0.347	**0.724**	– 0.211
Rock cover	– 0.130	**0.713**	0.188
Slope	0.301	**0.697**	– 0.056
Fire interval	0.092	– 0.070	**0.811**
Burn severity	– 0.472	0.239	**0.535**
Distance to unburned edge	– 0.457	– 0.431	– 0.110
Variance captured	27.61	18.78	12.84

B.

Regression models	Principal components	Regression coefficient	p-value	r^2
All sites (n = 50)				
1. Total cover	PC1	0.084	≤ 0.0001	0.400
2. Species richness	PC1	3.059	≤ 0.001	0.305
Short fire interval sites (n = 25)				
1. Total cover	PC3	– 0.119	0.005	0.295
2. Species richness	PC3	– 4.045	0.044	
	PC1	2.463	0.038	0.472

vals, indicated by high positive correlations with Axis 1 in the ordination of short interval plots. These species included annuals (*Cerastium arvense*, r = 0.503; *Collomia linearis*, r = 0.594; *Gayophytum diffusum*, r = 0.429; *Gentianella amarella*, r = 0.442; and *Rumex acetosella*, r = 0.491) and two non-native perennials (*Taraxacum officinale*, r = 0.526, and *Trifolium pratense*, r = 0.497). Perennials associated with short fire intervals included *Lupinus argenteus* (r = 0.511), a perennial nitrogen fixer, *Anaphalis margaritacea* (r = 0.454), *Carex geyeri* (r = 0.475), *Calamagrostis rubescens* (r = 0.577) and *Geranium viscosissimum* (r = 0.484). Two slow-growing woody plants *Vaccinium scoparium* and *Penstemon fruticosus*, were negatively correlated with Axis 1 (–0.355 and –0.345 respectively) and were sparser following very short intervals across the 7-100 yr fire interval gradient.

Relative importance of fire interval

Principal component analysis defined three primary orthogonal components from the set of nine independent variables (Table 1). These components represented (1) a broad-scale gradient in elevation correlated with variation in pine density and soil fertility (2) local topography (defined by slope and aspect and rockiness), and (3) disturbance (defined by fire interval and burn severity, Table 5a). In regression analyses of across all plots, total cover and richness were best explained by component 1 which captured 40% and 30% of the variance in these variables, respectively (components 2 and 3 were not significant - Table 5b). Both cover and richness were higher where pine densities were low and soil fertility was relatively high. In contrast, across the subset of 25 plots with fire intervals ≤ 100 yr, component 3 was significant in regressions of total cover and species richness. Total cover declined with increases in component 3, corresponding to longer burn intervals and higher fire severity (r^2 = 0.30, Table 5b). Species richness responded similarly, declining with component 3 but also increasing in response to component 1 (total r^2 = 0.47). Overall, across all sites, total cover was best explained by variation in pine density and soil fertility rather than fire interval, although fire interval and severity was significant in regressions of short fire intervals only.

Discussion

Understorey responses to fire interval

The understorey communities in Yellowstone were generally dominated by resprouting perennials resilient to wide variations in fire interval, although some species and functional groups responded to fire interval (Fig. 4, Table 3). Annuals were more abundant following short fire intervals; they were more abundant in sites classed as short fire intervals (≤ 100 yr) and varied inversely with fire interval over the 7- to 100-yr range. This is consistent with predictions that ruderal species dominate more frequently disturbed sites (Grime 1977). The presence of ruderals in young stands that escaped fire in 1988 would facilitate dispersal of annuals into nearby patches that burned in 1988. Ruderals should be less abundant in older, less-frequently disturbed stands adjacent to longer fire interval patches. We expect the age of adjacent unburned patches to affect post-fire composition more in small (≤ 1 ha) fire patches (Turner et al. 1997).

Fire-intolerant perennials increased with increasing fire interval both when compared between broad-fire interval classes and across a gradient of short fire intervals ranging between 7-100 yr long. These species were generally more abundant after longer intervals during which they apparently had time to recover from the last fire before the next fire occurred. Woody perennials often show reduced vigour or survivorship under high fire frequencies because they cannot produce or maintain sufficient storage organs between frequent disturbance events (Keeley & Zedler 1978; Bellingham & Sparrow 2000). Indeed, the relative percent cover of shrubs is low in younger *P. contorta* stands and increases with stand age (Brulisauer et al. 1996). Slow-growing woody perennials such as *Arctostaphylos uva-ursi, Linnaea borealis, Penstemon fruticosus* and *Vaccinium scoparium* recover slowly after fire (McLean 1968; Flinn & Wein 1977; Granström & Schimmel 1993, Turner et al. 1997) and were less abundant following short fire intervals in this study.

The 1988 fires charred the soil to an average depth of 14 mm (Turner et al. 1999). Non-woody species with shallow meristems can also suffer fire damage (McLean 1968; Flinn & Wein 1977). If these plants are damaged, they recover slowly or not at all. In contrast, non-woody species with deep meristems (e.g. *Arnica cordifolia, Aster meritus, Carex geyeri, Geranium viscosissimum, Phacelia* spp., *Taraxacum officinale*) resprout easily. Fire-tolerant species did not respond to fire interval in this study and dominated the understorey community. As the time between fires shortens, fire-intolerant species may be unable to recover sufficiently before the next fire occurs, decreasing their abundance following short fire intervals.

We found nitrogen-fixing species to be more abundant following very short fire intervals, as observed in Midwestern US prairies (Leach & Givnish 1996). Nitrogen availability declines after fire in many western coniferous forests (Monleon et al. 1997; Newland & DeLuca 2000), and total nitrogen may be depleted following repeated burns (Maclean & Wein 1980). This would give nitrogen fixers a competitive advantage following short fire intervals. The primary nitrogen fixer in this system is *Lupinus argenteus*, which also has a deep taproot allowing it to easily resprout after fire.

Although the cover of exotics was low (Fig. 4), two exotics were more abundant following very short fire intervals: *Taraxacum officinale* and *Trifolium pratense*. The higher total understorey cover observed following short fire intervals is not due to an increase in exotics, however. Generally, non-natives are sparse in Yellowstone and did not increase in extent or abundance following the 1988 fires (Turner et al. 2003). Although exotic species invasions are a significant concern in other post-fire systems (Crawford et al. 2001; Griffis et al. 2001), exotic cover did not increase appreciably even in frequently burned sites in this study. This suggests that seeding or other management to reduce the spread or persistence of exotic species following fires are not justified in these remote, subalpine systems where exotics are rare.

We hypothesized that successional status would also affect understorey responses to fire interval. Given that the perennial species present before fire determines the pool of species able to resprout after fire, we expected early-successional perennials to be more abundant following short fire intervals and late-successional perennials to be more abundant after long fire intervals (Peterson & Carson 1996). Although annuals were more abundant following short fire intervals, perennials that varied in successional status exhibited no consistent response to fire interval. This suggests that successional status is not a reliable trait in systems dominated by perennials with the ability to resprout following disturbance (Menges & Waller 1983). Most of the species studied that occupy the understorey of mature stands can vigorously resprout following fire and remain dominant in young post-fire stands, which may be a common strategy in stand-replacing fire systems (Bellingham & Sparrow 2000; Pausas et al. 2004, Vesk & Westoby 2004).

Perennial cover, which dominated the understorey, was relatively unaffected by fire interval (Table 3, Fig. 4), as observed in other fire adapted systems (Beckage & Stout 2000; Vlok & Yeaton 2000). Resprouting perennials dominated Yellowstone understories directly following the 1988 fires (Turner et al. 1997) and remained dominant 12 years later (Fig. 4). Perennials also dominate the understorey in other stand-replacing fire communities (Keeley & Zedler 1978; Schoennagel & Waller 1999; Bellingham & Sparrow 2000; Pausas et al. 2004). Resprouting by perennials thus appears to be a successful strategy for plants occupying communities dominated by stand-replacing fires (Turner et al. 1997; Bellingham & Sparrow 2000; Pausas et al. 2004; Vesk & Westoby 2004). Even fires that recur at short intervals (relative to historic norms) had little effect on the resprouting perennials that dominate this community.

Although perennial cover was relatively unaffected by fire interval, total cover and richness was highest following very short fire intervals. These responses although highly inversely correlated with fire interval ($r = -0.676$), were also highly inversely correlated with *P. contorta* densities ($r = -0.415$) in the ordination analysis. Closed and open cone production tends to be lower in younger *P. contorta* stands (Koch 1996). Hence, stands that burn at very short intervals will have lower post-fire *P. contorta* densities relative to stands that burn at longer intervals (Schoennagel et al. 2003). Therefore, the increase in understorey cover following very short fire intervals may be in part due to the effects of fire interval on *P. contorta* densities, although this could not be tested directly. Nonetheless, higher cover and richness following very short intervals contrasts with results from previous studies where regeneration was negatively affected by very short fire intervals (Connell & Slatyer 1977; Zedler et al. 1983; Noste & Bushy 1987; Haidinger & Keeley 1993; Paine et al. 1998).

Relative importance of fire intervals

The PCA analysis shows that broad-scale environmental variability related to elevation, represented primarily by pine density and soil fertility, strongly affected post-fire understorey plant cover and species richness across the Yellowstone landscape. Previous work in Yellowstone also showed that geographic location plays a primary role in determining community composition, although these post-fire communities also respond to fire size and severity (Turner et al. 1997). Post-fire *P. contorta* density varies with elevation, reflecting broad-scale patterns of serotiny across the park (Tinker et al. 1994), and is negatively correlated with understorey cover in Yellowstone (Turner et al. 1997, 1999). Fertile, andesite-derived soils are largely restricted to higher elevations and are positively correlated with understorey cover and richness (Taye 1995; Turner et al. 1997). These broad-scale gradients had significant influence on post-fire abundance and richness irrespective of large variation in fire interval. However, total cover and species richness responded to fire interval and burn severity once previous fire intervals become less than 100 years, although these effects appear to be minor. How long do such effects persist? Recent work suggests that environmental gradients begin to exert more influence as succession proceeds beyond 12 years after fire (Turner et al. 2003). The effect of fire interval may have been more pronounced the first few years following fire, which our current study did not track. However, if the effects of fire interval are truly this ephemeral, this system may be resilient to even fairly major shifts in disturbance regimes.

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