

Disturbance response across a productivity gradient: postfire vegetation in serpentine and nonserpentine forests

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Abstract. Disturbances such as wildfire play a major role in the diversity, structure and composition of plant communities, however, little is known about the differential impacts of fire across landscapes that vary in characteristics such as soil nutrients and site productivity. Theory predicts that productivity can mediate the impacts of fire for reasons related to broad ecological processes and differential selective forces. For instance, ecosystems with lower site productivity are less limited by space and light and consequently experience less pronounced changes in these resources following a disturbance. Moreover, resource availability related to disturbance and productivity can affect the proportion of plants with competitive versus stress-tolerant life history strategies. In this study, we utilized a model system for testing predictions about productivity and disturbance that included a mixed conifer forest across a gradient of edaphically harsh, ultramafic “serpentine” soils and “nonserpentine” soils in the northern Sierra Nevada (California, USA). We predicted that the magnitude of fire effects on plant diversity from a 2008 wildfire would be positively related to productivity (higher on nonserpentine soils) and that these factors would interact as environmental filters driving post-fire species assemblage. In summer 2013 we established 90 vegetation plots in burned areas and 40 plots outside the fire perimeter as a proxy for pre-fire conditions. We found a unimodal relationship between species diversity and fire severity (peaking at low/moderate severity), and mild evidence post-fire changes were more pronounced on nonserpentine soils. In contrast, we found strong evidence that productivity and fire severity interact as drivers of species composition and functional traits with a higher proportion of resprouting shrubs on nonserpentine soils and, contrary to our prediction, more invaders on serpentine soils. We hypothesize that differences in biomass between serpentine and nonserpentine forests were not substantial enough to elicit a differential diversity response, possibly deriving from a weaker serpentine syndrome in this region that has been previously noted. Our study reveals that differences in productivity can mediate the outcome of disturbances in ways that cannot be detected through standard community diversity metrics, and that consideration of life history trait variation is necessary.

Key words: disturbance; dynamic equilibrium model; fire ecology; fire severity; intermediate disturbance hypothesis; mixed conifer forest; ordination; productivity; serpentine; Sierra Nevada; ultramafic.

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INTRODUCTION

Disturbances such as wildfire play a major role in the structure and composition of plant communities in most terrestrial ecosystems (Grubb 1977, Pickett and White 1985, Johnson and Miyanishi 2010). Just as fires are important in structuring vegetation dynamics, the abundance and arrangement of vegetation (fuels) can have a strong effect on fire behavior, frequency, and intensity (Bond and van Wilgen 1996, Schmidt et al. 2008). Site productivity is one factor that can influence fire regimes since highly productive ecosystems harbor more biomass and faster growth rates, and all other conditions being equal, may facilitate more intense and/or more frequent fires compared to lower productivity ecosystems (Pausas and Bradstock 2007). Furthermore, since resources such as light and space are more limiting in high productivity systems due to increased aboveground competition (Tilman 1982, Reich et al. 2012) the impacts of fire may result in greater changes in those resources compared to more open stands where space and light are already more readily available. Thus, plant communities are responding to much greater changes in resources after a fire on high productivity sites as compared to low productivity sites, and can experience greater changes in diversity (Safford and Mallek 2011).

The relationship between disturbance frequency and/or intensity and species diversity is commonly represented by a unimodal curve, where diversity is maximized at intermediate levels of disturbance (Connell 1978). Ecological theory predicts that diversity is maximized at this stage because it is the optimal point where competitively dominant and opportunistic “seral” species can coexist. The universality of the intermediate disturbance hypothesis (IDH) has been the subject of many theoretical and empirical studies to varying degrees of support (see Mackey and Currie 2001, Fox 2012) and some authors have proposed that this relationship is strongly related to site productivity (Huston 1979, Kondoh 2001, Grime 2006, Huston 2014). Huston’s (1979) dynamic equilibrium model (DEM) predicts that more frequent and/or intense disturbances events are required to counteract competitive exclusion and maximize diversity in high productivity ecosystems, while

low frequency or low intensity disturbances are typically sufficient in low productivity systems. Thus the predictions of the intermediate disturbance hypothesis are only applicable at intermediate levels of productivity (Huston 2014). DEM theory is supported by empirical studies in marine (Agard et al. 1996, Beisner 2001, Contardo et al. 2006) and terrestrial systems (Proulx and Mazumder 1998, Wilson and Tilman 2002, Harrison et al. 2003, Safford and Harrison 2004), but a full understanding of this complex relationship remains untested in many ecosystems. The interaction of site productivity and disturbance on community dynamics may be more pronounced for fire compared to other disturbances since fuel accumulation (productivity) is positively related to fire frequency and intensity in most fire-prone ecosystems (Pickett and White 1985, Huston 2002, Safford and Harrison 2004, Safford and Mallek 2011).

Both fire regime and site productivity also exert evolutionary selective pressures and act as environmental filters that drive the species assemblage and dominant life history strategies of plants that establish in a given community (Keeley et al. 2011). In fire-prone ecosystems, plant populations persist either by individuals enduring fire, avoiding fire, or by having a successful regenerative strategy (Bond and Van Wilgen 1996). Regeneration strategies can be classified into three broad categories including (1) resprouters, species that expand vegetatively from underground storage structures; (2) seeders, species that regenerate from a persistent bank of seeds stored in the soil or the canopy; and (3) invaders, species that colonize from an off-site seed source (typically wind-dispersed). Past work has shown that the frequency and severity of fire can influence the proportion of plants with particular life history and regeneration strategies (Donato et al. 2009, Hollingsworth et al. 2013). For example, there is strong evidence for a life history trade-off between resprouting and seeding shrubs that is tightly linked to disturbance regimes (Bond and Midgley 2003, Clarke et al. 2005, Pausas and Bradstock 2007, Tucker and Cadotte 2013) and some authors propose that this trade-off is also related to site productivity (Bellingham and Sparrow 2000). Since it takes longer for seedlings to develop into reproductive adults and maintain a persis-



Fig. 1. Biomass and fuel differences between nonserpentine (background) and serpentine (foreground) soils in the study area, Plumas National Forest. Photo by M. H. DeSiervo.

tent seed bank, resprouting is generally considered a more prominent regenerative strategy as disturbance frequency (and productivity) increases (Bellingham and Sparrow 2000). The proportion of early seral species (particularly nonnatives) has also been shown to increase with productivity and disturbance intensity (Burke and Grime 1996).

In this study, we compared patterns of post-fire diversity and community assemblage across a gradient of low-productivity “serpentine” soils and higher productivity “nonserpentine” soils in a predominately mixed conifer ecosystem in northern California (USA). The term “serpentine” is used broadly to describe ultramafic rocks and the soils that derive from these parent materials (Alexander 2007). Serpentine soils are characterized by low levels of essential plant nutrients such as nitrogen, phosphorous and calcium, high levels of iron and magnesium, and elevated heavy metals including chromium, nickel, and zinc (Kruckeberg 1984). Due to harsh

site conditions, serpentine ecosystems typically accumulate low levels of biomass, harbor slow-growing vegetation, and have a patchy, discontinuous vegetation structure (Fig. 1; Kruckeberg 1984, Brooks 1987). Serpentine soils also harbor a unique species assemblage, excluding plant species that cannot tolerate the edaphic challenges and providing a refuge to areas of reduced competition for those that can (Harrison and Rajakaruna 2011). The strong selective force exerted by conditions on serpentine soils has led to high rates of plant speciation and endemism, making serpentine the most species rich terrestrial substrate in western North America (Kruckeberg 1984, Brooks 1987, Harrison 2013). Serpentine plants are also known for their stress-tolerant traits including xeromorphic foliage, hyperaccumulation of metals, and high root:shoot biomass ratios (Kruckeberg 1984).

Serpentine versus nonserpentine comparisons are a model system for understanding the interaction between productivity and distur-

bance effects on community dynamics (Safford and Mallek 2011). Surprisingly, only two empirical studies have statistically assessed the effects of fire across serpentine and nonserpentine soils. Safford and Harrison (2004) found that post-fire changes in species richness and diversity were more pronounced in sandstone versus serpentine chaparral vegetation, and it took longer for serpentine sites to return to pre-fire levels of richness, diversity and cover. Similarly, Harrison et al. (2003) found that fire increased diversity in nonserpentine grasslands, but had no effect on serpentine sites. For both studies, non-native weedy species increased disproportionately more on nonserpentine sites after fire.

Unlike chaparral and grassland ecosystems, mixed conifer forests do not typically experience exclusively stand-replacing fires, thus it is impossible to base predictions about fire effects on serpentine vegetation solely on the aforementioned studies. Furthermore, our study site was located in a part of the northern Sierra Nevada, California where evidence suggests that the serpentine syndrome (high native species diversity, low biomass, slow growth, stunted life-forms, etc.) may be less pronounced than in other systems (Clifton 2006, Alexander 2007), possibly due to altered rock chemistry (H. Day, *personal communication*). To our knowledge, our study is the first to statistically investigate the effects of fire on a serpentine forest community, and one of the first to study the ecology of a serpentine system on the milder end of the edaphic spectrum. Similar to other fire ecology studies, we did not have pre-fire data, therefore we utilized sites in nearby unburned forest stands as a proxy for pre-fire vegetation and soils.

Our primary objectives in this study were to observe how fire effects on plant diversity and composition varied across the productivity gradient of our study site. To determine the strength of our productivity gradient we first measured soil nutrient characteristics as well as forest and fuel structure. We hypothesized that soil nutrients (such as the Ca:Mg ratio) would vary significantly across our study area, although our serpentine soils would not be as edaphically harsh compared to other serpentinized areas in California (see above). Despite the “weakened” serpentine syndrome, we hypothesized that

areas with edaphically harsh soils would support fewer trees, corresponding to lower tree basal area (and biomass) and less surface fuels.

After establishing the strength of our productivity gradient, we took a twofold approach towards measuring plant communities; first through predicting community diversity metrics such as species richness, evenness, and diversity, and second, by exploring variation in community composition and life history strategies. In both approaches, we first considered soil fertility (here, measured as Ca:Mg, a strong proxy for productivity; see *Methods*) and fire severity in the context of other explanatory variables such as elevation, solar radiation, overstory cover, and litter and duff depth. If our main effects were revealed as important predictors, we then asked the question: Do soil fertility and fire severity interact as drivers of post fire species diversity/composition? We hypothesized that post-fire increases in species richness, evenness and diversity would follow a unimodal pattern with fire severity (peaking at low/moderate severity), but that the magnitude of increase would be proportional to soil fertility (less pronounced on low productivity, serpentine sites). We also predicted that soil fertility and fire severity would interact as environmental filters driving post-fire community assemblage due to tradeoffs in competitive versus stress-tolerant traits. For example, we predicted that the proportion of competitively dominant resprouting shrubs and seral “fire invaders” would increase with higher soil fertility and fire severity, and that low productivity soils would harbor more species with stress-tolerant characteristics (e.g., perennial life form and seeding reproductive strategies).

METHODS

Study site and plot selection

Our study site consisted of a 2400 ha area of the North Fork Feather River canyon in Plumas County, California that was burned by the Rich Fire in 2008, and adjacent unburned forest stands outside the fire perimeter (40.05° N, 121.13° W). The entire study was located within the Plumas National Forest. The Rich Fire was characterized by high spatial complexity with varying levels of low to high severity burning in a primarily mixed conifer forest landscape. Approximately half of

the burned area was on ultramafic serpentinized peridotite (serpentine) substrate from the Feather River Ophiolite (Ehrenberg 1975). Other substrate types within our study site include Paleozoic metamorphic rocks (schist, greenstone, slate), and small amounts of more recent volcanic rocks (andesite, andesitic tuff). Elevations ranged from 760 m to 1930 m. This region is characterized by a Mediterranean climate with warm, dry summers and cool, wet winters. Common tree species include white fir (*Abies concolor*), California red fir (*Abies magnifica* var. *magnifica*), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*) and sugar pine (*Pinus lambertiana*). A smaller portion of our study site, restricted to ultramafic soils, included open low-growing shrub communities dominated by leather oak (*Quercus durata*) with scattered conifer cover in the overstory.

Across this region of the northern Sierra Nevada, soil type is an important driver of understory plant composition in mixed conifer forests. Dominant shrubs in mature nonserpentine forests include greenleaf manzanita (*Arctostaphylos patula*), huckleberry oak (*Quercus vaccinifolia*), bush chinquapin (*Chrysolepis sempervirens*), serviceberry (*Amelanchier alnifolia*), and pine-mat manzanita (*Arctostaphylos nevadensis*). *Arctostaphylos patula*, *Arctostaphylos nevadensis* and *Amelanchier alnifolia* are also common in serpentine forests, as well as caribou coffeeberry (*Frangula purshiana* subsp. *ultramafica*) and arching ceanothus (*Ceanothus arcuatus*). Common herb species in nonserpentine forests include broad leaf starflower (*Trientalis borealis* ssp. *latifolia*), white-veined wintergreen (*Pyrola picta*), little prince's pine (*Chimaphila menziensisii*) and false Solomon's seal (*Maianthemum racemosum*) and common herbs in the serpentine forest understory include spreading phlox (*Phlox diffusa*), deltoid balsamroot (*Balsamorhiza deltoidea*), and yarrow (*Achillea millefolium*).

To examine fire effects on understory vegetation, we established 130 16-m radius (~800 m²) circular vegetation plots in summer 2013; 90 plots within the perimeter of the Rich Fire, and 40 plots within 300 m of the fire perimeter as a proxy for pre-fire conditions. Potential plot centers were established on the vertices of a 200 m north-south Geographic Information Systems (GIS) grid

overlaid across the fire area and were stratified according to soil type (serpentine and non-serpentine), estimated fire severity (derived from Forest Service LANDSAT-TM-based fire severity mapping) and by a solar radiation index, (ArcMap GIS 10.1; ESRI, Redlands, California, USA). We avoided surveying plots with high levels of anthropogenic disturbance (such as post-fire salvage logging) but included plots with low-levels of disturbance (such as post-fire planting, logging more than 50 years ago, or minor fuel removal treatments). We assessed fire severity on a six rank categorical scale: (0) unburned; (1) light patchy burn pattern, very little overstory mortality, groups of surviving shrubs/saplings; (2) lightly burned, isolated overstory mortality (more live trees than dead), most saplings/shrubs dead; (3) moderately burned, mixed overstory mortality (approximately equal number of live and dead trees), understory mostly burned to ground; (4) high severity, significant proportion of overstory killed (more dead than live trees), understory almost completely burned; and (5) high severity burn, total/near mortality of overstory (almost all dead trees), understory burned to ground. Due to the heterogenous nature of our study area, it was impossible use a continuous variable (such as overstory mortality) to assess fire severity. Using our 6-rank system, we could assign plots with varying levels of pre-fire tree cover into the appropriate fire severity categories. For example, some of our plots contained very little pre-fire overstory cover, but burned at high fire intensity.

Sampling methods

At each of our 130 plots, we collected approximately 25 g of soil at 5–10 cm depth from four random locations and combined them to create one sample per plot. Samples were air dried and analyzed at a soil nutrient analysis lab in Arcata, CA for levels of Ca, Mg, N, P, K, Fe and pH. At the same four locations where we collected soil, we took measurements of litter and duff depth, which were combined for an average litter and duff depth per plot. We also recorded environmental variables including slope percent, and aspect, which we combined to create an index of solar radiation using equations from McCune and Keon (2002).

To compare serpentine and nonserpentine

forest structure, we measured diameter at breast height (dbh) for all trees above 7.6 cm within an 11.3 m radius circular plot nested within the larger vegetation plot. These data were used to estimate basal area and stand biomass using allometric equations from Jenkins et al. (2003). We also utilized surface fuels and coarse woody debris data taken from 24 unburned plots in 2011 and 2012 to compare fuel loads between serpentine and nonserpentine forests (M. H. DeSiervo, *unpublished data*). Most of these plots subsequently burned in the Chips fire in 2012, and were not resampled in 2013. Surface fuels data were collected from four Brown's transects (Brown 1974), laid out in the cardinal directions. Starting at the edge of the plot, 1 hour (diameter = 0.0–0.64 cm), 10 hour (0.64–2.5 cm), 100 hour (2.5–7.6 cm), and 1000 hour (diameter > 7.6 cm) fuels were tallied along the first 3 m, 100 hour, and 1000 hour fuels only for the second 3 m, and 1000 hours fuels for the remainder of the transect. Diameter and length were recorded for all 1000 hour fuels that crossed the transects.

For all 130 plots surveyed in 2013, we recorded understory plant species within the 16 m diameter circle and assigned an ocular estimate of percent cover to each taxon. All vegetation data were collected from May to July 2013 by the same two observers. Plots visited in May and June were visited a second time in mid-summer to record plant species that were unidentifiable in the early part of the season. Almost all plants were identified to species in the field, while some were collected, pressed, and identified at a later time. After data collection, species were classified according to origin (native and nonnative), life-cycle (perennial/biennial and annual) and life-form (tree, shrub, forb, graminoid, fern). Additionally, we researched the fire regeneration strategies of the most common woody and herbaceous plants across our study site, and classified each taxon based on information in the literature (USDA Forest Service 2014). Regeneration strategies were classified as one of the following: (1) invader, species that colonize from transported seeds (2) seeder, species that regenerate from on-site seeds stored in the seed bank (3) resprouter, species that regenerate asexually from adventitious buds or root crowns or (4) avoider, species with little to no fire-related adaptations. Since obligate seeding (versus re-

sprouting) is a derived trait, facultative seeding species (such as *Ceanothus integerrimus*) were included with resprouting species for data analysis.

Data analysis

We used multiple analyses of variance (MANOVA) to test for differences in soil nutrients between serpentine and nonserpentine, burned and unburned plots. To examine and describe the gradient of soil nutrients across our study site, we also used non-metric multidimensional scaling (NMDS) ordination utilizing a Bray-Curtis dissimilarity index with the metaMDS function in the VEGAN package in R (Oksanen et al. 2009). We used the correlation coefficients of soil nutrients with both axis 1 and axis 2 scores to assess which nutrients were the most responsible for the variation described in the ordination. Because of the exceptionally high correlation of the Ca:Mg ratio with axis 1 (ranging from the lowest productivity serpentine sites to the highest productivity nonserpentine sites), we used this ratio in subsequent regression analyses as a continuous variable as a proxy for serpentine "status", hereon termed soil fertility. We tested for the relationship between soil fertility, plot basal area and biomass using linear regression. We also compared fuel loads between serpentine and nonserpentine plots using MANOVA. We could not use soil fertility as a continuous variable for this portion of the data analysis because the fuels data taken in 2011 and 2012 came from different plots than the soil, trees, and understory vegetation data in 2013. All statistical analyses were conducted in R (R Development Core Team 2010).

To assess the role of soil fertility, fire severity, and other environmental factors on community diversity metrics, we developed multiple regression models predicting species richness, species evenness, and Shannon diversity. For each dependent variable, we created a full model including our main effects: soil fertility and fire severity (0–5) and a suite of environmental variables including elevation, solar radiation, percent overstory cover, and litter and duff depth. Prior to analysis we assessed each predictor univariately to determine if it was best fit by a linear or curvilinear relationship, and we chose the relationship that maximized model

goodness of fit. Fire severity, for example, showed a curvilinear relationship with species richness, species evenness, and Shannon diversity. Additionally, all data were tested for normality and heteroscedasticity of residuals and data transformations were applied when necessary. All percent cover data were arcsine square root transformed or square root transformed to meet the assumptions of regression analysis. To eliminate insignificant predictors, we first performed backwards stepwise regression using the stepAIC function in the MASS library (Venables and Ripley 2002). If we detected our two main effects (soil fertility and fire severity) in the reduced model, we then compared four candidate models with soil fertility and fire severity univariately, an additive model with both predictors, and model with a soil fertility \times fire severity interaction effect. We use this model selection technique as a hypothesis test to predict if fire had differential impacts on community dynamics according to soil fertility. Models were compared using Akaike's information criterion corrected for small sample size (AICc).

To visualize differences in the understory community composition of our plots based on environmental gradients (soil fertility, fire severity, and other parameters), we used detrended correspondence analysis (DCA). DCA is an ordination technique that can be used to assess similarities and differences between plant communities, and determine the importance of different environmental gradients in governing species assemblage patterns. Only burned plots were included in this portion of the analysis and downweighting of rare species (present in fewer than 5% of all plots) was used to reduce the influence of infrequent taxa in our analysis. We used the correlation coefficients of environmental gradients to the axis scores to assess which gradients were the most responsible for the variation described in the ordination. The DCA ordination was performed using the decorana function in the VEGAN package in R (Oksanen et al. 2009). To formally test the hypothesis of community differentiation based on fire severity, soil fertility and their interaction, we conducted a two-way permutational multivariate analysis of variance (perMANOVA) using a Bray-Curtis distance matrix and 1000 permutations. PerMANOVA utilizes permutation methods to evaluate

differences in composition based on continuous or categorical variables (soil fertility and fire severity in our case) using an ecological distance matrix (pairwise comparisons between plots) as the dependent variable. To test for significance, an *F*-statistic is calculated and then compared to a null distribution generated by randomly reshuffling the data with each permutation.

Finally, we used canonical correspondence analysis (CCA) to examine the influence of environmental gradients on dominant life history and regeneration strategies amongst our sites. The primary difference between this ordination technique compared to DCA is that CCA is a direct gradient analysis where explanatory variables (in our case soil fertility, fire severity and elevation) were incorporated into the ordination. We chose this technique because it can be used to explicitly test hypotheses as opposed to others which are primarily used for exploratory analyses. To perform the CCA, we took our plots \times species matrix (used in the first DCA ordination) and multiplied it by a species \times traits matrix, composed of four traits (1) origin, (2) lifecycle, (3) lifeform, and (4) reproductive strategy (see *Sampling methods*) (Diaz 1992). For multistate traits (lifeform and reproductive strategy) we recoded these as binary traits using dummy variables. The matrix multiplication resulted in a plots \times traits matrix which was subjected to the CCA ordination. To formally test the hypothesis of non-random assemblage based on the constraining variables in the CCA ordination, we used the permutation based significance test ANOVA.CCA in the VEGAN package in R with 1000 permutations (Oksanen et al. 2009).

RESULTS

Soil

The mean Ca:Mg ratio for nonserpentine plots was four times greater than the serpentine mean in unburned plots, and six times greater in burned plots (Table 1). We detected greater concentrations of soil K for burned nonserpentine compared to serpentine sites, and greater concentrations of NO₃⁻ for serpentine versus nonserpentine unburned plots; however all other macronutrients and pH were not significantly different (Table 1). Soil Fe was only significantly greater on nonserpentine versus serpentine un-

Table 1. Soil variables for unburned ($n = 40$) and burned ($n = 90$) serpentine and nonserpentine vegetation plots. Values given are means \pm 1.0 SD. Bonferroni-adjusted P -values are presented from MANOVA for effects of soil type on listed variables. Unburned plots: Wilks' lambda = 0.194, $df = 1, 86$, $P < 0.0001$; burned plots: Wilks' lambda = 0.198, $df = 1, 36$, $P < 0.0001$.

Soil parameters	Unburned			Burned		
	Nonserpentine	Serpentine	P	Nonserpentine	Serpentine	P
pH	6.13 \pm 0.19	6.42 \pm 0.35	NS	6.42 \pm 0.41	6.62 \pm 0.33	NS
Soil Ca (ppm)	9.75 \pm 4.07	5.72 \pm 2.14	NS	18.2 \pm 15.9	6.75 \pm 4.33	<0.0001
Soil Mg (ppm)	2.48 \pm 1.21	10.65 \pm 6.83	<0.0001	2.78 \pm 2.12	7.94 \pm 3.67	<0.0001
Ca:Mg ratio	4.44 \pm 1.21	0.81 \pm 0.69	<0.0001	6.68 \pm 3.12	0.97 \pm 0.55	<0.0001
Soil K (ppm)	6.62 \pm 4.71	4.95 \pm 4.85	NS	6.70 \pm 4.30	3.63 \pm 1.76	<0.0001
Soil NO ₃ ⁻ (ppm)	5.26 \pm 6.51	8.89 \pm 6.58	0.0080	8.75 \pm 11.97	5.36 \pm 3.60	NS
Soil PO ₄ ⁻ (ppm)	8.22 \pm 4.09	9.24 \pm 4.33	NS	17.56 \pm 23.67	9.00 \pm 5.44	NS
Soil Fe (ppm)	43.90 \pm 12.28	64.37 \pm 21.07	0.0002	36.41 \pm 13.46	39.61 \pm 12.87	NS

burned plots (Table 1). NMDS ordination of soil nutrient data resulted in a two-dimensional solution with a final stress of 14.42% (Appendix: Fig. A1). The ordination reveals a clear distinction between soil samples from serpentine and nonserpentine plots, driven almost entirely by the first axis. All soil parameters were moderately to strongly correlated with NMDS axis 1, with the Ca:Mg ratio (the most common indicator of serpentine soils) strongly correlated to NMDS axis 1 ($r^2 = 0.76$; Appendix: Table A1). We used the Ca:Mg ratio as a continuous gradient of soil fertility in subsequent regression analyses.

Forest and fuel structure

Serpentine plots contained fewer trees, lower basal area, and lower tree biomass (Appendix: Table A3). Linear regression analysis revealed that the Ca:Mg ratio was positively related to plot basal area ($R^2 = 0.22$, $df = 39$, $P = 0.003$;

Appendix: Fig. A2) and plot tree biomass ($R^2 = 0.23$, $df = 39$, $P = 0.003$; Appendix: Fig. A3). Surface fuel loadings (1, 10 and 100 hr fuels) were more than twice as high in unburned non-serpentine versus unburned serpentine plots (Wilks' lambda = 1.248, $df = 1, 22$, $P = 0.025$), but 1000 hour fuels were not significantly different (Appendix: Table A2).

Community diversity metrics

All multiple regression models using environmental variables to predict species richness, species evenness, and Shannon diversity were significant, but the percentage of variance explained was relatively low (16–19%; Table 2). Fire severity was a marginally significant predictor for species richness ($r^2 = 0.03$, $P = 0.06$) and a significant predictor for evenness ($r^2 = 0.15$, $P < 0.01$) and Shannon diversity ($r^2 = 0.12$, $P = 0.02$) and showed a unimodal relationship with both

Table 2. Best multiple regression models for predicting species richness, Shannon diversity and Pielou's evenness for 130 understory vegetation plots as determined through stepwise backwards model selection using Akaike's information criterion (AIC).

Dependent variable	Predictor	Parameter estimate	P	r^2	Model				
					Intercept	Adjusted R^2	df	F	P
Species richness	Fire severity†	-0.18	0.06	0.03	58.5	0.16	4, 120	7.00	<0.01
	Litter and duff	-4.7	<0.01	0.09					
	Solar radiation	-8.9	0.04	0.03					
	Elevation	-0.01	0.05	0.03					
Species evenness	Soil fertility	-0.07	<0.01	0.06	0.85	0.18	2, 122	15.95	<0.01
	Fire severity†	-0.01	<0.01	0.15					
Shannon diversity	Soil fertility	-0.34	0.07	0.09	3.28	0.19	4, 120	8.22	<0.01
	Fire severity†	-0.02	0.08	0.12					
	Solar radiation	-0.52	0.09	0.02					
	Overstory	0.65	0.09	0.02					

† Fire severity is a quadratic term with six levels (see *Methods*).

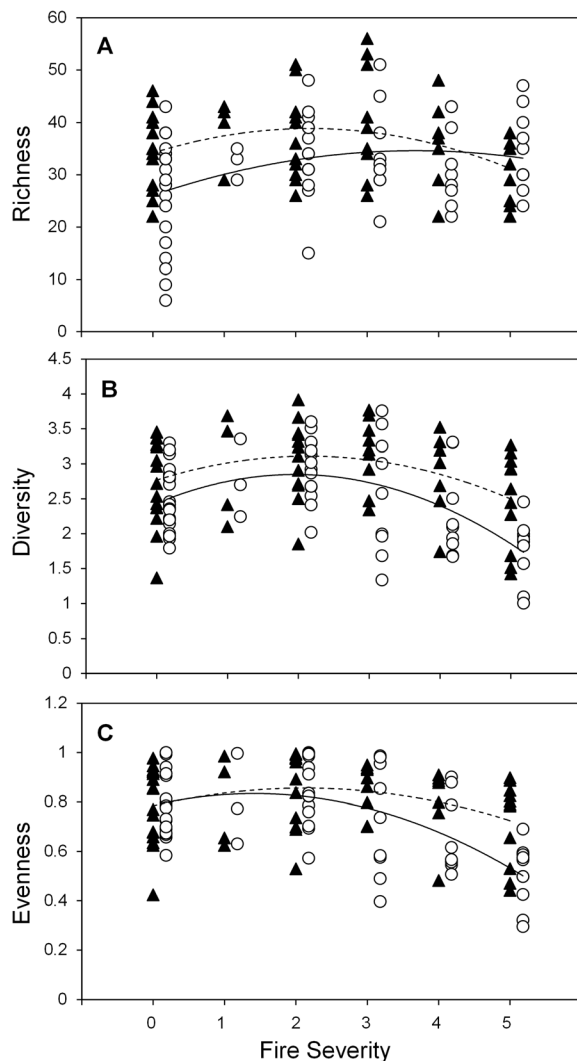


Fig. 2. Quadratic regressions depicting the unimodal relationship between fire severity and (A) species richness, (B) Shannon diversity index, and (C) Pielou's evenness in 130 understory vegetation plots. All analyses were done with soil fertility as a continuous variable, but are represented here as categorical variables with black triangles denoting serpentine plots (dashed regression line) and white circles denoting nonserpentine plots (solid regression line). See methods for descriptions of fire severity classes.

dependent variables, peaking at low/moderate severity (Fig. 2). Soil fertility was a significant predictor of species evenness ($r^2 = 0.06$, $P < 0.01$) and a marginally significant predictor for Shannon diversity ($r^2 = 0.9$, $P = 0.07$) but was not

present in the best multiple regression model for species richness.

Since our main effects (soil fertility and fire severity) were present in the best multiple regression models for Shannon diversity and species evenness, we ranked their predictive ability univariately, and in combination using AICc, using a cutoff of $\Delta\text{AICc} > 2$ to differentiate between models. For Shannon diversity, the model incorporating a soil fertility \times fire severity interaction effect and the model with additive main effects were equally predictive ($\Delta\text{AIC} = 0.43$; Appendix: Table A5), however; for species evenness, the model with the soil fertility \times fire severity interaction was significantly better than the additive model despite containing an extra parameter ($\Delta\text{AIC} = 4.31$; Appendix: Table A5). For both dependent variables, the models containing both parameters were significantly better than the univariate models ($\Delta\text{AIC} = 9.27$, $\Delta\text{AIC} = 8.71$; Appendix: Table A5).

Community composition and functional traits

We recorded a total of 232 plant taxa across our study area, including 12 species of trees, 34 shrubs, 161 forbs, 5 ferns and 20 graminoids (see Supplement). Fewer than 2% of all observed taxa could not be identified to the species level due to missing flower/fruit parts or phenological timing. In these cases, taxa were left at the genus or family level and were treated either as unique species or grouped with other taxa in data analyses. The overlap in flora between serpentine and nonserpentine sites was 63% (141 taxa) and 18% (42 taxa) were found only on serpentine soils. At least one nonnative plant was found at 85% of our sites, however average percent cover was very low ($<2\%$). Surprisingly, nonnatives were found more often in serpentine compared to nonserpentine plots (63% versus 43%). Non-native richness increased with fire severity for both serpentine and nonserpentine plots (Appendix: Table A4).

The first two axes of the DCA ordination of vegetation cover data accounted for 80% of the variance with eigenvalues of 0.50 and 0.29 respectively (Fig. 3). Elevation had the strongest influence on plant composition ($r^2 = 0.70$, $P < 0.001$; Appendix: Table A6), closely followed by soil fertility ($r^2 = 0.67$, $P < 0.001$; Appendix: Table A6). The influence of fire severity on plant

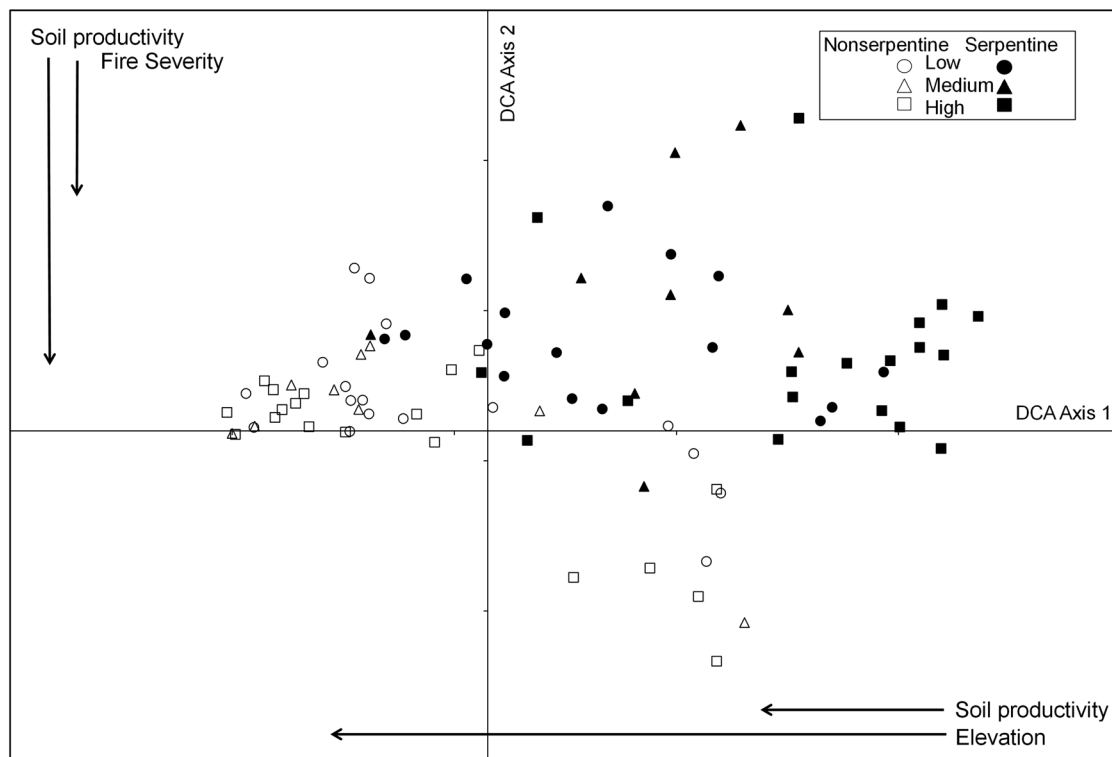


Fig. 3. Detrended correspondence analysis (DCA) ordination of understory vegetation from 90 burned plots. Coding of fire severity classes is reduced into three categories with circles representing fire severity class 1 and 2, triangles as fire severity class 3 and squares as fire severity class 4 and 5 (see *Methods* for description). White symbols denote nonserpentine plots and black symbols denote serpentine plots. Solid black arrows represent the correlation coefficients of significant environmental gradients with DCA axis 1 and 2. Arrow length and direction correspond to the magnitude and direction of the correlation (Appendix: Table A6).

composition was also significant, but not as strong as the aforementioned gradients ($r^2 = 0.15$, $P < 0.001$; Appendix: Table A6). The DCA ordination revealed that plant communities were first separated by soil type, and secondarily by fire severity (Fig. 3). A two way perMANOVA revealed that understory plant communities were significantly different across the soil fertility gradient ($F_{3,87} = 15.07$, $P = 0.001$) and the fire severity gradient ($F_{3,87} = 3.93$, $P = 0.001$). Furthermore the interaction of these two parameters was significant ($F_{3,87} = 3.52$, $P = 0.003$). Nonserpentine plots were compositionally more similar among the fire severity classes with an average Bray-Curtis distance of 0.69 compared to serpentine plots with an average Bray-Curtis distance of 0.80.

The first two axes of the CCA ordination of functional trait data accounted for 97% of the

variance (59% and 38%, respectively) (Fig. 4). Within the constrained ordination space, elevation had a negative correlation with CCA axis 1, fire severity was negatively correlated with CCA axis 2, and soil fertility was correlated with both axes almost equally. The permutation test revealed that elevation ($F_{1,84} = 13.25$, $P < 0.001$), soil fertility ($F_{1,84} = 11.25$, $P < 0.001$) and fire severity ($F_{1,84} = 8.13$, $P < 0.001$) were all significant parameters influencing functional trait composition (Appendix: Table A7). High fire severity, high soil fertility plots were associated with shrubs and a resprouting fire adaptation strategy. Low fire severity, low soil fertility plots had a greater proportion of geophyte, herbs, graminoids and a perennial life history. Surprisingly, nonnative plants with invading fire adaptation strategies were the most dominant in high fire severity, low soil fertility plots. The fire

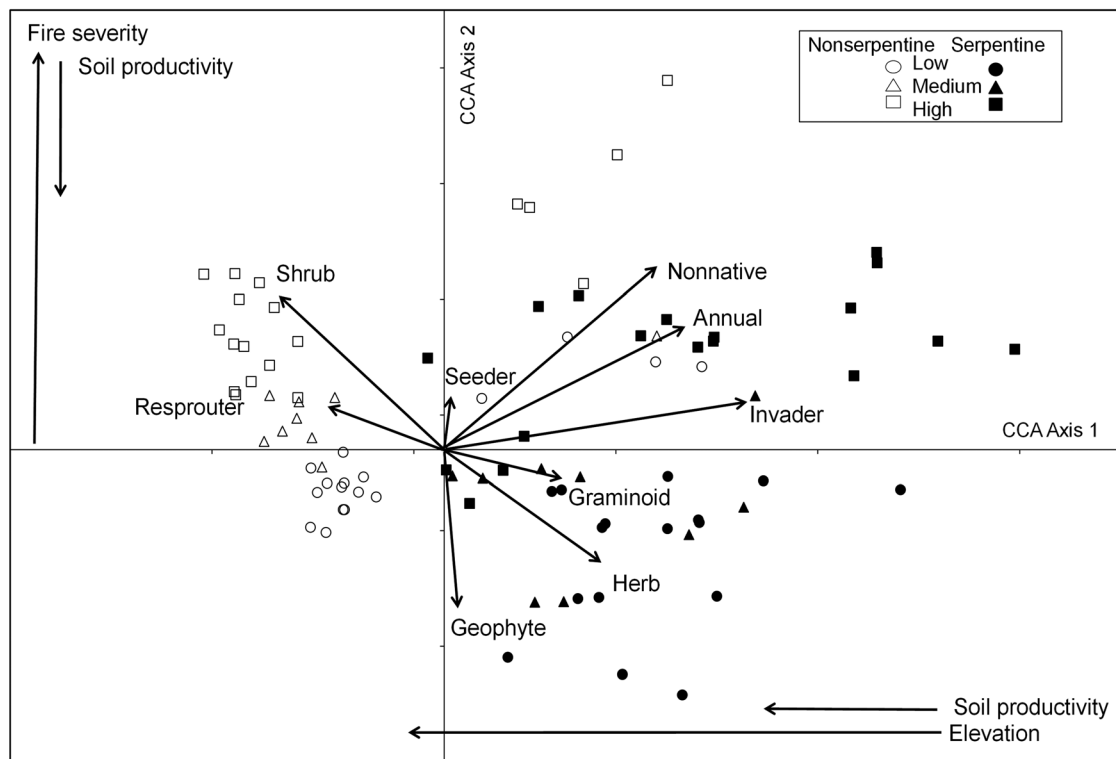


Fig. 4. Canonical correspondence analysis (CCA) ordination of functional trait data from 90 burned plots. Coding of fire severity classes is reduced into three categories with circles representing fire severity class 1 and 2, triangles as fire severity class 3 and squares as fire severity class 4 and 5 (see *Methods* for description). White symbols denote nonserpentine plots and black symbols denote serpentine plots. Solid black arrows represent the correlation coefficients of significant environmental gradients with CCA axis 1 and 2. Vectors indicate the functional traits that were significant within the ordination space. Arrow length and direction correspond to the magnitude and direction of the correlation (Appendix: Table A6).

adaptation strategy “seeding” was not strongly associated with any group (Fig. 4).

DISCUSSION

Strength of the productivity gradient: the serpentine “context”

Although the serpentine syndrome typically includes high species diversity, low biomass, slow growth, stunted lifeforms, and patchy vegetation structure, these characteristics exist on a spectrum of intensity due to the wide variation in serpentine soils and the habitats they span. Several ecologists have made generalizations about vegetation in the northern Sierra Nevada that point to a less pronounced serpentine syndrome compared to other serpentine subregions in California, however, this has not

been extensively studied. For example, Alexander (2007) notes that the vegetation is only “marginally different” on and off serpentine substrate in the Sierra Nevada, and Clifton (2006) states that in comparison to other vegetation types in the Plumas National Forest, plant communities on serpentine soils differ only in their species composition. Our results (see below) support these generalizations about the serpentine syndrome in the Sierra Nevada and suggest that although there may not be strong differences in species richness between serpentine and nonserpentine forests, there is considerable variation in community composition and functional traits.

Across our study area, there was a strong variation in nutrients (Appendix: Fig. A1) driven primarily by the Ca:Mg ratio (Appendix: Table A1); however, the high relative ratio (nearly 1:1)

is substantially higher than other serpentine subregions in California. For example serpentinized regions in the North Coast ranges typically have Ca:Mg ratios closer to 0.5 and regions of the Klamath-Siskiyou have been shown to have Ca:Mg as low as 0.1 (Grace et al. 2007). The high Ca:Mg ratio of our study site may be due to hydrothermal alteration of the bedrock (H. Day, *personal communication*). Whatever the source, our serpentine sites are not as edaphically harsh as many other sites in California and this probably affected the strength of the productivity gradient and the serpentine syndrome in our study area. Despite relatively less edaphic conditions, we observed a positive linear relationship between soil fertility and tree basal area (Appendix: Fig. A1) and tree biomass (Appendix: Fig. A2). Furthermore, surface fuel loads were two times greater on nonserpentine versus serpentine unburned sites (Appendix: Table A2). These results indicate that the serpentine soils in this region still have a measureable impact on plant productivity and our study area serves as an appropriate system to test the ways that productivity and disturbance interact with regard to community dynamics.

Community diversity metrics and ecological theory

Compared to other environmental parameters, fire severity was one of the strongest predictors in our study, and we found the highest plant diversity (evenness and richness) in plots that burned at low or moderate severity. Not surprisingly, diversity was lowest in unburned controls and in severely burned plots (Fig. 2). The unimodal pattern of diversity we observed in this system supports the recent findings of Stevens et al. (*unpublished manuscript*) in a study investigating fire severity \times plant diversity patterns in wildfires across the Sierra Nevada. Before Euroamerican settlement of California, yellow pine and mixed conifer forests in the Sierra Nevada supported regimes of very frequent, mostly low severity fire (Van Wagtenonk and Fites-Kaufman 2006, Van de Water and Safford 2011), and the relative rarity of high severity, stand-replacing fire over time and space has led to a general lack of fire followers in the flora. If this system was characterized by large areas of high severity fire (e.g., chaparral, Rocky

Mountain lodgepole pine), we would have expected to find the highest diversity in high severity plots where understory communities are highly dependent on a suite of fire following species that occupy the so-called “postfire regeneration niche” (Grubb 1977). Our results contribute to a growing body of literature that mixed conifer forests in the Sierra Nevada likely supported a low to moderate severity disturbance regime and that post-fire diversity is maximized at levels that mimic the natural fire regime for this system.

Soil fertility was only a significant predictor in two of our three multiple regression models (Shannon diversity and species evenness). Due to the weakened serpentine syndrome in this region, serpentine soils do not appear to harbor more species, a unique result compared to several other serpentine vegetation studies (Harrison et al. 2003, Safford and Harrison 2004, Jules et al. 2011). Despite this finding, our results indicate that serpentine soils in this region support a more even species distribution (Fig. 2; Appendix: Table A5). We hypothesize that the relationship between soil fertility and evenness is strongly tied to inter-specific competition. Since serpentine plants are primarily limited by edaphic stressors and overall biomass accumulation is low, competition for resources is low and the ecosystem can support a more even distribution of plants. Due to differences in productivity, we hypothesized that fire effects on plant diversity would be higher in nonserpentine forests in accordance with the predictions of the dynamic equilibrium model (DEM). We see mild support for this theory for species evenness, where the shape of the unimodal curve between species evenness and fire severity was more pronounced for higher productivity (nonserpentine) plots (Fig. 2). We did not observe the same trend for Shannon diversity and species richness, and in this way, our results differ from the two other published serpentine fire studies (Harrison et al. 2003, Safford and Harrison 2004).

Because of the high landscape heterogeneity throughout our study area we were unable to control for a multitude of environmental parameters that influence plant community dynamics (such a litter and duff accumulation, solar radiation, and elevation) and thus we incorporated those variables as covariates in our analy-

sis. Even with these covariates, our best multiple regression models were relatively weak in explanatory power (16–19%). Furthermore since our study includes a single fire event, we were unable to account for potential feedbacks between fire severity and plant communities over multiple fire events (Odion et al. 2010). Our results may suggest only mild differences in diversity response across a soil fertility gradient because differences in fuel and biomass were not large enough to illicit a strongly differential response. Although our study area varied in productivity, it is likely that our entire gradient fell within an intermediate range, where the theoretical predictions of the IDH and the DEM are identical. Similar to our study, Svensson et al. (2007) found that varying levels of productivity did not affect the unimodal disturbance-diversity relationship in a marine subtidal community. Svensson et al. (2007) also used nutrient conditions as a proxy for site productivity, and makes the point that more practical definitions of productivity might be necessary to support the predictions of the DEM.

Community composition and functional traits

Our results show strong support for the hypothesis that soil fertility and fire severity interact as environmental filters shaping post-fire community assemblage. The DCA ordination revealed significant differences in community composition primarily due to soil fertility and secondarily according to fire severity, suggesting that soil type is a more important factor influencing community composition versus fire severity in this system. The difference in species assemblage on serpentine versus nonserpentine soils is not surprising, and is consistent with other literature regarding serpentine species assemblage (Harrison et al. 2003, Safford and Harrison 2004).

Our results indicate that differences in community composition are likely driven by trade-offs in stress-tolerant versus competitive traits. Consistent with other literature (Kruckeberg 1984, Safford et al. 2005, Alexander 2007) we found a heightened presence of perennial forbs and geophytes in association with low fertility serpentine soils. Both perennial life history (multiple annual cycles) as well as geophyte physiology (presence of underground storage

organs such as corms and bulbs) are advantageous strategies for conserving resources, and are therefore beneficial adaptations in edaphically harsh conditions (Grime 2006). These traits were not associated with all fire severities, but were driven by low and moderate severity plots. In high severity serpentine plots, we found a greater proportion of annual fire “invaders” (Fig. 4), which was primarily driven by the nonnative grass *Bromus tectorum* and the nonnative herb *Lactuca serriola*. This finding is contrary to most literature which characterizes serpentine communities as being more resistant to invasion compared to more productive soils (Harrison et al. 2003, Going et al. 2009, Jules et al. 2011). We hypothesize that the invaders within this system are particularly successful in low productivity, highly disturbed communities because of the availability of bare ground (reduced competition from other species) and the less harsh soil chemistry compared to other serpentine areas. Since our entire study area was located near forest service roads this is unlikely to be a factor in the difference between serpentine and non-serpentine sites. The relatively high proportion of high severity fire that does not reflect historical conditions (Miller et al. 2009, Miller and Safford 2012, Mallek et al. 2013) may be another reason for this novel result.

We did not find strong support for a tradeoff between resprouting and seeding reproductive strategies based on soil fertility. We hypothesized that resprouting would be more dominant as both soil fertility and fire severity increased since rapid vegetative expansion is thought to be a more advantageous strategy when resources and competition are high (Pausas and Bradstock 2007). At the other end of the spectrum, seeding is thought to be a more advantageous strategy on lower productivity soils because of longer fire return intervals, allowing more time for seeds to persist in the seed bank. As predicted, resprouting shrubs (primarily *Garra fremontii*, *Arctostaphylos patula* and *Ceanothus cordulatus*) were more dominant on higher productivity, non-serpentine soils but there was no obvious trend with seeding shrubs. Herbaceous seeders including *Gilia capitata*, *Collinsia parviflora*, *Gayophytum diffusum* and *Cryptantha* sp. were relatively common on both soil types providing further evidence that there was not a strong preference

for seeding reproductive strategy on serpentine soils.

We found the greatest proportion of shrubs and resprouting life history in association with high severity, nonserpentine plots. Areas with high primary productivity that burn at high intensities experience the greatest net change in resources (space and light) as a result of the fire. Since these sites are less limited by edaphic stressors, there is less allocation of resources towards stress-tolerant traits and a greater allocation of resources towards competitive traits, such as rapid vegetative expansion. In this mixed conifer forest ecosystem, resprouting shrub species such as *Arctostaphylos patula* and *Ceanothus* sp are among the quickest to gain resources and rapidly dominate the post-fire community. The dominance of one or two shrub species corroborates our findings of the lowest species richness and evenness in high severity, high soil fertility plots.

CONCLUSION

We found that variation in productivity across this mixed conifer forest community contributed to differences in post-fire vegetation patterns. Although we only found mild evidence for a differential fire response when assessing community metrics, we did find strong evidence that soil fertility and fire severity interact as drivers of community assemblage by filtering for advantageous life history strategies. In this way, our results show that productivity can mediate the outcome of disturbances in ways that cannot be measured by standard community metrics, and that detecting these differences relies on careful consideration of variation in life history strategies.

Since our study focused on a single fire event and did not attempt to quantify fire history, we cannot make any assertions about differences in historical or present fire regimes between forests on serpentine versus nonserpentine soils. We found evidence of lower fuel loads, and lower tree basal area (biomass) on serpentine sites; however the unimodal diversity curve was not substantially altered by these differences, suggesting that they may have been too subtle to illicit a differential response for this particular fire. It is possible that the difference in fuel

loading between serpentine and nonserpentine forests in this region was more substantial in the pre-fire suppression era, and our results would have been different. Further investigation of fire history across a productivity gradient would be necessary to answer this question. Furthermore, our results may not match the theoretical predictions regarding productivity and disturbance because the fire we studied was so far outside the parameters of “normal” for this ecosystem, and thus did not provide an example of a “typical” response.

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SUPPLEMENTAL MATERIAL

APPENDIX

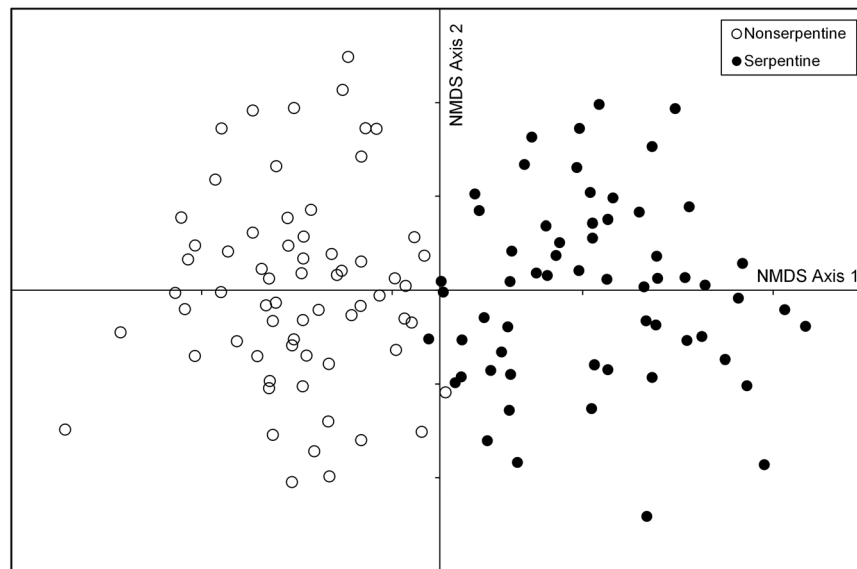


Fig. A1. Nonmetric multidimensional scaling (NMDS) ordination of soil nutrient data from 130 plots, collected in summer 2013. Vector information presented in Table A1. Arrow length and direction correspond to the magnitude and direction of the correlation of vectors with the NMDS axes.

Table A1. Correlation coefficients for seven soil nutrient parameters and the first two NMDS axes. (see Fig. A1). *P*-values are based on 999 permutations.

Vectors	NMDS1	NMDS2	R^2	<i>P</i>
Ca:Mg	−0.99	−0.09	0.76	<0.001
Mg	0.74	0.67	0.74	<0.001
K	−0.35	0.94	0.42	<0.001
Ca	−0.56	0.83	0.38	<0.001
Fe	0.53	−0.84	0.24	<0.001
P	−0.85	−0.53	0.08	<0.050
N	−0.44	−0.89	0.04	NS

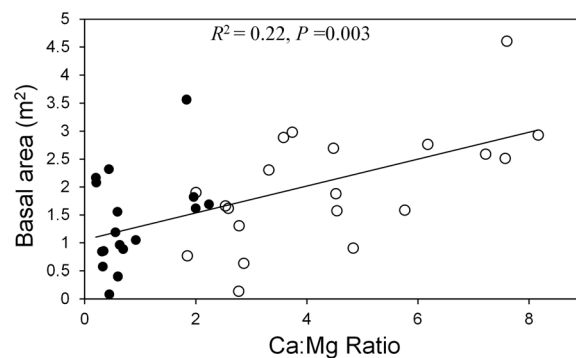


Fig. A2. Linear regression between Ca:Mg ratio and plot basal area for 40 unburned plots.

Table A2. Data for 1, 10, 100 and 1000 hr fuels for nonserpentine and serpentine plots. Values given are means \pm 1.0 SD. Bonferroni-adjusted P -values are presented from MANOVA for effects of soil type on listed variables. Wilks' lambda = 0.57, df = 1, 22, P = 0.026.

Fuel variables	Unburned		P
	Nonserpentine	Serpentine	
1 hr fuels (kg/ha)	2646.05 \pm 377.89	1023.71 \pm 230.84	0.0001
10 hr fuels (kg/ha)	15314.63 \pm 2312.50	5899.18 \pm 882.35	0.0010
100 hr fuels (kg/ha)	21122.55 \pm 4030.64	10647.27 \pm 2446.16	0.0369
1000 hr fuels (kg/ha)	42776.00 \pm 10240.55	42501.8 \pm 9756.16	NS

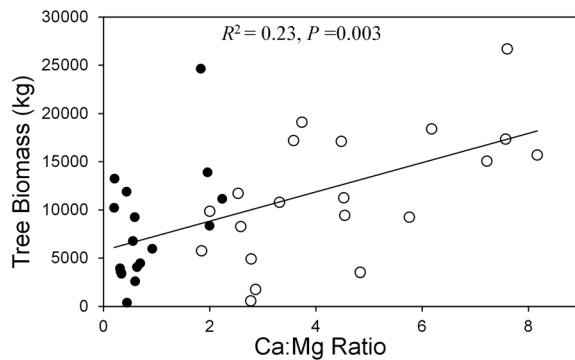


Fig. A3. Linear regression between Ca:Mg ratio and plot tree biomass (kg) for 40 unburned plots.

Table A3. Forest structure data for 130 burned (n = 90) and unburned (n = 40) plots and fuels data from unburned plots (n = 24). See *Methods* for description of fire severity categories. Values given are means with SD in parentheses.

Characteristic	Nonserpentine				Serpentine			
	Unburned (0)	Low (1, 2)	Medium (3)	High (4, 5)	Unburned (0)	Low (1, 2)	Medium (3)	High (4, 5)
No. trees/plot	32.05 (7.66)	18.93 (1.04)	19.13 (1.24)	17 (0.93)	13.1 (1.98)	14.86 (3.04)	13.46 (2.67)	8.26 (2.00)
Tree dbh (cm)	22.85 (0.90)	29.75 (1.77)	24.61 (1.45)	25.20 (1.58)	28.53 (1.77)	29.63 (1.98)	23.64 (1.67)	23.88 (2.14)
Tree height (m)	10.05 (0.31)	12.18 (0.49)	9.89 (0.41)	10.58 (0.53)	11.32 (0.53)	11.37 (0.59)	8.93 (0.68)	9.17 (0.67)
Plot basal area	2.01 (0.23)	1.87 (0.30)	1.29 (0.23)	1.27 (0.30)	1.34 (0.21)	1.76 (0.18)	1.04 (0.24)	0.67 (0.31)
Plot biomass (kg)	11682 (1488)	11544 (2072)	7417 (1481)	7880 (2196)	7867 (1407)	11943 (1769)	6095 (1643)	3996 (2202)

Table A4. Native and non-native species richness for serpentine and nonserpentine plots by fire severity (0–5). See *Methods* for description of fire severity categories. Values given are means \pm 1.0 SE.

Fire severity	Nonserpentine		Serpentine	
	Native richness	Non-native richness	Native richness	Non-native richness
0	30.70 \pm 2.59	2.00 \pm 0.00	35.60 \pm 2.51	1.40 \pm 0.40
1	36.00 \pm 1.53	N/A	41.75 \pm 3.17	1.33 \pm 0.33
2	37.00 \pm 2.34	2.33 \pm 0.56	37.30 \pm 2.38	1.60 \pm 0.31
3	36.20 \pm 3.42	1.57 \pm 0.36	38.70 \pm 3.47	2.00 \pm 0.43
4	33.11 \pm 2.68	1.60 \pm 0.40	36.29 \pm 3.11	1.83 \pm 0.48
5	32.20 \pm 2.08	2.78 \pm 0.59	29.00 \pm 1.56	2.00 \pm 0.33

Table A5. Akaike's information criterion corrected for small sample size (AICc) table ranking four candidate models predicting Shannon diversity and species evenness. AICc is based on $2 \times \log$ likelihood and the number of parameters (K) in the model. Models are ranked by raw Akaike's information criterion score (AICc), difference in AIC values between models (Δ AICc), and Akaike weights (w_i).

Dependent variable	Model	K	AICc	Δ AICc	w_i
Shannon diversity	Soil fertility + Fire severity	4	234.10	0.00	0.55
	Soil fertility \times Fire severity	5	234.54	0.43	0.44
	Fire severity	3	243.37	9.27	0.00
	Soil fertility	3	244.31	10.2	0.00
Evenness	Soil fertility \times Fire severity	5	−107.45	0.00	0.89
	Soil fertility + Fire severity	4	−103.14	4.31	0.10
	Fire severity	3	−98.75	8.71	0.01
	Soil fertility	3	−85.00	22.50	0.00

Table A6. Correlation coefficients between six environmental variables and the first two DCA axes (see Fig. 3). *P* values are based on 999 permutations.

Environmental variable	DCA1	DCA2	R^2	<i>P</i>
Soil fertility	−0.56	−0.82	0.66	<0.001
Fire severity	0.40	−0.91	0.15	<0.001
Elevation	−0.99	0.06	0.70	<0.001
Solar radiation	−0.89	0.83	0.00	NS
Litter and duff	0.06	−0.84	0.03	NS
Overstory cover	−0.94	−0.32	0.01	NS

Table A7. Correlation coefficients environmental variables and the first two CCA axes (see Fig. 4). *P* values are based on 999 permutations.

Environmental variable	CCA1	CCA2	<i>F</i>	<i>P</i>
Soil fertility	−0.65	0.50	11.25	<0.001
Fire severity	0.02	0.80	8.13	<0.001
Elevation	−0.97	0.17	13.25	<0.001

SUPPLEMENT

Complete raw data set used for the community composition meta-analysis (*Ecological Archives*, <http://dx.doi.org/10.1890/ES14-00431.1.sm>).