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## Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales

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**Abstract.** Wildfires influence many temperate terrestrial ecosystems worldwide. Historical environmental heterogeneity created by wildfires has been altered by human activities and will be impacted by future climate change. Our ability to predict the impact of wildfire-created heterogeneity on biodiversity is limited because few studies have investigated variation in community composition (beta-diversity) in response to fire. Wildfires may influence beta-diversity through several ecological mechanisms. First, high-severity fires may decrease beta-diversity by homogenizing species composition when they create landscapes dominated by disturbance-tolerant or rapidly colonizing species. In contrast, mixed-severity fires may increase beta-diversity by creating mosaic landscapes containing habitats that support species with differing environmental tolerances and dispersal traits. Moreover, the effects of fire severity on beta-diversity may change depending on site conditions. Disturbance is hypothesized to increase local species richness at higher productivity and decrease local species richness at lower productivity, a process that can have important, but largely unexamined, consequences on beta-diversity in fire-prone ecosystems. We tested these hypotheses by comparing patterns of beta-diversity and species richness across 162 plant communities in three sites that span a large-scale gradient in climate and productivity in the Northern Rockies of Montana. Within each site, we used spatially explicit fire-severity data to stratify sampling across unburned forests and forests burned with mixed- and high-severity wildfires. We found that beta-diversity (community dispersion) of forbs was higher in mixed-severity compared to high-severity fire, regardless of productivity. Counter to our predictions, local species richness of forbs was higher in burned landscapes compared to unburned landscapes at the low-productivity site, but lower in burned landscapes at the high-productivity site. This pattern may be explained by rapid regeneration of woody plants after fire in high-productivity forests. Moreover, forbs and woody plants had disproportionately higher overall species richness in mixed-severity fire compared to high-severity fire, but only at the low-productivity site. These patterns suggest that mixed-severity fires promote higher landscape-level biodiversity in low-productivity sites by increasing species turnover across landscapes with a diverse mosaic of habitats. Our study illustrates the importance of understanding the mechanisms by which patterns of wildfire severity interact with environmental gradients to influence patterns of biodiversity across spatial scales.

**Key words:** beta-diversity; community assembly; disturbance severity; fire management; homogenization; landscape ecology; Northern Rockies Ecoregion; mixed-severity wildfire; plant community composition; net primary productivity; restoration ecology; spatial scale.

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## INTRODUCTION

Among the many threats posed to biodiversity by global change, shifts in natural disturbance regimes are likely to have some of the most profound impacts on ecological communities and the ecosystem services they provide (Turner 2010). Wildfire is a common disturbance that influences biodiversity in many ecosystems worldwide (Bowman et al. 2009). However, natural wildfire regimes have been altered by human activities, and, with increasing occurrence of droughts due to climate change (Pederson et al. 2010), greater numbers and intensities of fires are expected in many areas (Westerling et al. 2006, Thibault and Brown 2008, Bowman et al. 2009, Davidson et al. 2012). Concurrently, there is widespread interest in restoration of fire-prone landscapes in which natural wildfires have been suppressed by humans (Donovan and Brown 2007, Hessburg et al. 2015), where landscapes are typically defined as areas that contain a heterogeneous mix of biophysical settings, environmental conditions, or species composition (cf. Turner et al. 2001). A critical challenge at the interface of conservation and ecology is to understand why the effects of wildfire disturbance are highly variable, especially at the spatial scales most germane to conservation and management in naturally heterogeneous landscapes (McKenzie et al. 2011).

Although ecologists have excelled at investigating how individual species and local communities respond to wildfires (Turner et al. 2003, Baker 2009), different communities often show variable responses to disturbance (Chase 2007, Vellend et al. 2007, Tonkin and Death 2013, Vanschoenwinkel et al. 2013, Myers et al. 2015). One key mechanism by which fires may create contrasting patterns of biodiversity among landscapes is through spatial or temporal variation in fire severity (Collins and Stephens 2010; Fig. 1B). However, empirical studies of fire severity often focus on patterns of species richness at a single spatial scale, most often local species richness (alpha-diversity; Dodson and Peterson 2010, Abella and Springer 2015). In contrast, little is known about how the local effects of fires scale-up to influence landscape biodiversity by altering spatial variation in community composition (beta-diversity; Myers et al. 2015). From the

perspectives of both theory and management, it is critical to understand how variation in wildfire severity influences patterns of biodiversity across landscapes (Belote 2015). For example, fires that produce large patches of high-severity burns are often expected to homogenize species composition when disturbance-tolerant species dominate post-fire patches (Pausas and Verdú 2008), resulting in low beta-diversity among local communities (e.g., Chase 2007, Vellend et al. 2007, Myers and Harms 2011). Mixed-severity fires, in contrast, may increase beta-diversity through two non-mutually exclusive mechanisms. First, mixed-severity fires could increase beta-diversity by creating landscapes that contain a diverse mosaic of habitat types that support a larger pool of disturbance-tolerant and -intolerant species compared to landscapes with high-severity fire (Perry et al. 2011). Second, mixed-severity fire could have no influence on the size of the species pool but increase beta-diversity by increasing species sorting among habitats with contrasting environmental conditions created by variable fire severity.

A second major challenge to scaling-up effects of disturbance at local scales is to understand how similar wildfires influence patterns of biodiversity across biogeographic regions with dissimilar environmental conditions. However, very few studies of local effects of fire are replicated across broad biogeographic areas that vary in environmental conditions such as climate and net primary productivity. Theoretical models suggest that the effects of disturbance on biodiversity may vary systematically with variation in net primary productivity (Huston 1979, 2014, Foster and Dickson 2004). Productivity may influence the effect of fires on biodiversity by altering competition for limiting resources. In high-productivity communities with high population-growth rates, fire may increase local species diversity by increasing mortality of competitors, thereby decreasing the strength of resource competition in disturbed relative to undisturbed communities (Foster et al. 2004, Huston 2014). In low-productivity communities with low population-growth rates, in contrast, fire may decrease local diversity by increasing mortality and rates of local extinctions in disturbed relative to undisturbed communities (Huston 2014). Alternatively, high-productivity

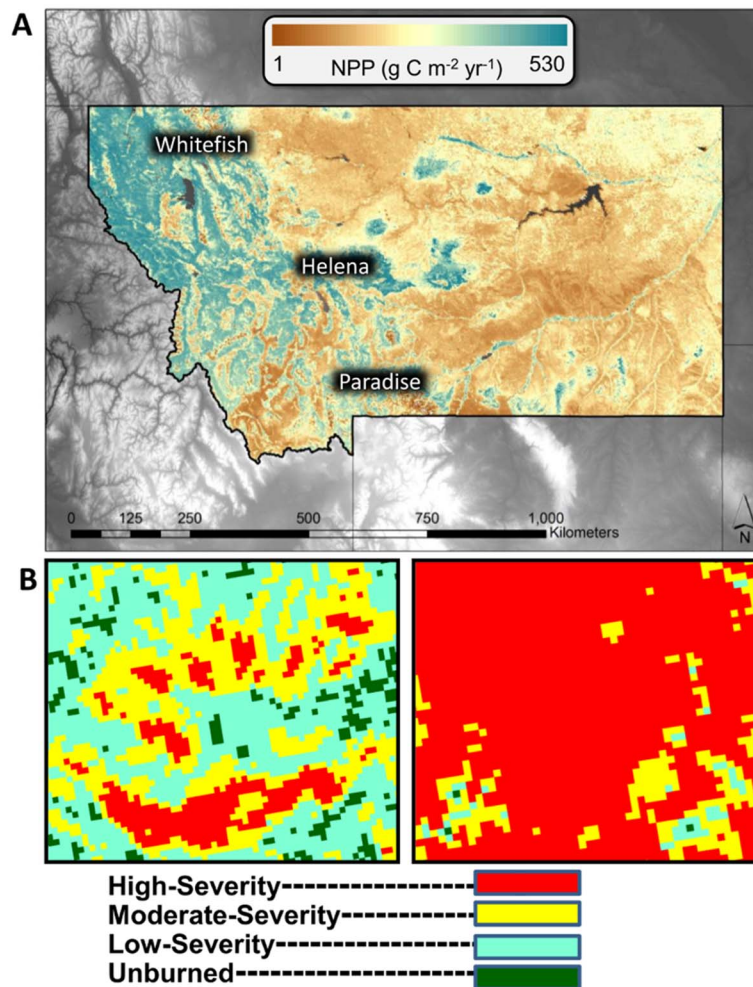


Fig. 1. Map of study regions in the Northern Rockies Ecoregion of western Montana. (A) Locations of study sites across a regional gradient in net primary productivity (NPP). (B) Maps showing examples of 15-ha landscapes with mixed-severity wildfires (bottom left) and high-severity wildfires (bottom right). The maximum distance among transects was 484 km. Fire-severity maps (30-m resolution) were generated using data from the Monitoring Trends in Burn Severity (MTBS) program (<http://www.mtbs.gov/>).

communities may rapidly develop a dense forest canopy following fire that could reduce local species diversity relative to low-productivity communities. The potential variability of wildfire effects across broad-scale environmental gradients presents one of the greatest challenges for predicting responses of biodiversity across spatial scales.

In this study, we examined how wildfire severity influences spatial patterns of plant species diversity across a large-scale gradient of climate and productivity in the Northern Rockies

Ecoregion (NRE) of the western United States. The NRE is an ideal region in which to investigate the interplay between fire severity and productivity on patterns of biodiversity across scales. First, the NRE boasts a strong regional gradient in net primary productivity (Fig. 1A) that varies along steep climate gradients influenced by mountainous terrain and orographically driven patterns of local and regional precipitation (Bassman et al. 2003, Belote and Aplet 2014). Second, wildfires are the primary driver of ecosystem change in the NRE (Bowman

et al. 2009) and vary strongly in their severity through space and time (Westerling et al. 2006, Kurz et al. 2008, Belote 2015). We used high-resolution fire-severity data (Eidenshink et al. 2007) to explicitly compare how high- and mixed-severity wildfires influenced diversity of three plant functional groups (forbs, graminoids, and woody plants) in landscapes representing a strong climate-driven gradient in productivity. We focused on two patterns that together provide insights into mechanisms that may influence changes in biodiversity across landscapes with contrasting wildfire severity and productivity. First, we examined how species richness varies with wildfire severity and productivity at local spatial scales. We hypothesized that communities that burned with high-severity fires would have low local species richness at low productivity but high local species richness at high productivity (Huston 2014). Second, we examined how beta-diversity (measured as community dispersion) and species composition vary with wildfire severity and productivity. Specifically, we hypothesized that beta-diversity would be higher across landscapes with mixed-severity fires compared to landscapes with high-severity fires, but that the strength of this pattern would vary depending on productivity. We conclude with a discussion of how these patterns provide insights into the maintenance of diversity within and among heterogeneous landscapes as well as implications for conservation in fire-prone ecosystems.

## METHODS

### *Study site: The Northern Rockies Ecoregion (NRE)*

The NRE encompasses the Crown of the Continent and the Greater Yellowstone Ecosystem in Montana (Fig. 1A), two of the few remaining intact ecosystems in the lower 48 states (Prato and Fagre 2007). This region contains the world's oldest national park (Yellowstone) and is at the center of debates surrounding climate change, conservation of native biodiversity, fire management and forest restoration (Arno and Fiedler 2005, Baker et al. 2007, Prato and Fagre 2007). Historically, forests in the western U.S. were characterized by mixed-severity fire regimes (Fischer and Bradley 1987, Baker 2009), which create conditions that support

understory and early successional plant species within a mosaic of forest ages, habitat conditions, and successional stages (Hessburg and Agee 2003, Perry et al. 2011). More recently, however, there is evidence to suggest that fire severity may be increasing in parts of this region (e.g., Miller et al. 2009).

### *Plant community sampling across wildfire and productivity gradients*

We compared the effects of wildfire severity (unburned, mixed severity, high severity) on plant diversity across a large-scale gradient in climate and net primary productivity (Fig. 1A). Using remotely sensed estimates of fire perimeters and burn severity (Eidenshink et al. 2007), as well as net primary productivity (Zhao 2005), we selected three study sites with a similar recent history of wildfire that span a regional gradient of productivity: Helena (low productivity), Paradise (medium productivity), and Whitefish (high productivity; Table 1, Figs. 1A and 2). The broad biogeographic placement of these sites and the lack of multiple wildfires occurring at the same time precluded us from replicating the study at each productivity level. Although lack of replication is common when investigating broad-scale ecological patterns, we acknowledge that this limits our ability to attribute differences among the sites specifically to productivity and that future studies are needed to disentangle the influence of factors such as climate that covary with productivity among our study sites. The three sites include a variety of forest ecosystems in the region, including ponderosa-pine dominated forests and woodlands in Helena, lodgepole-pine and Douglas-fir forests in Paradise Valley, and western-larch, lodgepole-pine and mixed-conifer forests in Whitefish. Visually, it is clear that woody plants are recovering slowly, if at all, from high-severity fire in Helena, while young trees dominate high-severity burned areas in Whitefish (Fig. 2; Appendix: Table A2), suggesting that the pace of succession and influence of a woody overstory varies among the sites.

In each site, we identified a large wildfire perimeter within which a fire occurred between 2001 and 2007 (Table 1). Time-since-fire ranged from 6-12 years among the three sites, but did not vary systematically with productivity. To spatial-

Table 1. Characteristics of study sites along a gradient of climate and net primary productivity in the Northern Rockies Ecoregion, Montana, USA. Values for productivity, elevation, mean annual temperature and annual precipitation represent the mean of unburned transects within a site. Variances for climate and productivity are not reported here because the spatial resolution of the data ( $1 \times 1$  km grid cells) is generally much coarser than the spatial distances among transects within sites (median distance = 0.42 km). Productivity data was obtained from Moderate Resolution Imaging Spectroradiometer (MODIS) observations (<http://modis.gsfc.nasa.gov>) and bioclimatic variables were obtained from WorldClim (<http://www.worldclim.org/bioclim>; Hijmans et al. 2005).

Site	Lat., lon.	Prod. (g C m <sup>2</sup> /yr)	Elev. (m)	Temp. (°C)	Precip. (mm)	No. of plant species in unburned transects				Name of fire (year)
						forb	grass	woody	total	
Helena†	46.7, -111.7	467	1373	15.8	351	57	19	19	95	Jimtown (2003)
Paradise	45.2, -110.4	495	2248	-13.0	632	38	9	20	67	Wicked Creek (2007)
Whitefish	48.6, -114.3	595	1312	-2.2	684	49	10	23	82	Moose (2001)

Note: Lat. and lon. are latitude and longitude, respectively; Prod. is productivity, Elev. is elevation, Temp. is temperature, and Precip. is precipitation.

† Mean climate and productivity values after excluding two transects located just outside the central  $1 \times 1$ -km grid cells of the site.

ly stratify our sampling within each fire perimeter, we used data from the Monitoring Trends in Burn Severity (MTBS) program (<http://www.mtbs.gov/>) to identify two units (15-ha) that experienced high-severity fire and two units that experienced mixed-severity fire composed of a spatially diverse mix of fire severity (Appendix: Fig. A1). We established these 15-ha units to limit our travel time between sampling locations within extremely large fire perimeters (450 to

>29,000 ha) and to establish a nested block design where units were nested within sites. In close proximity to fire perimeters, we identified two additional units (15-ha) to serve as unburned controls (no wildfire within at least 60 years). The locations of all units were chosen to allow relatively easy access by roads. Within each unit, we randomly stratified nine line transects (25-m long) across similar geographic distances using a generalized random tessellation stratified (GRTS)

#### A) Helena: low productivity



#### B) Whitefish: high productivity



Fig. 2. Representative landscapes with high-severity fire in Helena (low productivity) and Whitefish (high productivity).

survey design function in the R *spsurvey* package ( $N = 162$  total transects: 18 transects for each level of fire severity in each site  $\times$  3 levels of fire severity  $\times$  3 sites). Within each mixed-severity fire unit, we used GRTS to stratify the nine transects equally across areas with low, medium, and high fire severity ( $N = 3$  transects for each fire severity in each unit) using the fire-severity categories defined by MTBS. In the field, we oriented all transects along topographic contours to minimize changes in elevation within transects. Within sites, mean distances among unburned transects ranged from 0.38–3.99 km (range = 0.02–7.64 km), mean distances among mixed-severity transects ranged from 0.37–0.52 km (range = 0.03–1.19 km), and mean distances among high-severity transects ranged from 0.83–1.02 km (range = 0.03–2.18 km). The maximum distance among all transects was 484 km (Fig. 1A).

In summer 2013, we measured plant species abundances and composition in each transect using a point-intercept method. Every 10 cm along each 25-m transect, we held a pin flag vertically and recorded the identity of all plant species touching the flag, up to 1 m from the ground. We measured the abundance of each species as the total number of times a species touched the flag across all sampling points along the transect. If a plant could not be identified to species in the field, a specimen of the same species was collected at least 25 m away from the transect, pressed and dried, and identified to species in the lab. Each species was categorized into one of three functional groups: forbs, graminoids (grasses and sedges), or woody plants. Species accumulation curves within each site were similar among the three levels of fire severity (Appendix: Fig. A3).

### Statistical analyses

*Local species richness and diversity.*—For each site, we tested for effects of fire severity (unburned, mixed-severity fire, high-severity fire) on local species richness and diversity. We measured species diversity using Hurlbert's Probability of Interspecific Encounter (PIE), a sample-size independent measure of species evenness that accounts for variation in abundances among communities (Hurlbert 1971, Chase and Knight 2013). Hurlbert's PIE allowed

us to account for potential differences in species accumulation curves among the three levels of fire severity within each site (Appendix: Fig. A3). For each site, we first tested for the overall effect of fire severity on the richness and diversity of all plant species combined using separate mixed-effects MANOVA models with units as random effects. After confirming significant effects of fire severity on plant richness and diversity, we used separate mixed-effects MANOVA models to test for effects of fire severity on species richness and diversity of each functional group (forbs, graminoids, woody plants) at each site. Significant tests were followed by Tukey's HSD tests to determine differences among the three levels of fire severity. Richness and diversity measures were normally distributed for sites and for fire-severity levels within sites, except for forb diversity, which we squared-transformed.

*Beta-diversity and species composition.*—Beta-diversity can be defined in a variety of ways that each highlight different aspects of compositional similarity among communities (Anderson et al. 2011). For example, when comparing two communities, there can be significant differences in community composition between them without differences in species richness, and vice versa. Thus, we compared patterns of beta-diversity among the three levels of fire severity at each site (unburned, mixed-severity fire, high-severity fire) by calculating community dispersion, measured as the pairwise similarity in species composition among all transects within each level of fire severity. We calculated pairwise similarities using both an abundance-based (Bray-Curtis) and incidence-based (Jaccard) metric. We tested for differences in community dispersion using homogeneity of multivariate dispersions based on average distance-to-centroid values calculated using the 'betadisper' function in the R *vegan* package. Function 'betadisper' tests for differences in group homogeneities and is analogous to Levene's test of the equality of variances (Oksanen et al. 2009). We used ad hoc Tukey's tests to determine differences among fire-severity levels. Additionally, we tested for differences in overall species composition among fire severities using multivariate analysis of variance on community dissimilarities of each plant functional group at each site using the 'adonis' function in the R *vegan* package.

Function ‘adonis’ partitions dissimilarities for sources of variation (e.g., fire severity) and uses permutation tests to determine whether partitions are significant (Oksanen et al. 2009). We used ordination (non-metric multidimensional scaling) on the raw abundance data to visualize these patterns. For any significant differences in species composition among fire severities, we used similarity percentage analyses to determine which species, if any, contributed most strongly to the compositional differences using ‘simper’ function in the R vegan package. As with species richness and diversity, we performed separate analyses for forbs, graminoids, and woody plants. We obtained similar results for both metrics of beta-diversity and therefore present graphical results for the Jaccard metric in the Supporting Information.

## RESULTS

We observed 279 total plant species across all transects in the three sites, including 177 forb species, 47 graminoid species, and 55 woody species. Among the three sites, total plant species richness in unburned communities was highest in Helena (the site with the lowest productivity; 95 species in unburned transects; 168 species total), intermediate in Whitefish (the site with the highest productivity; 67 species in unburned transects; 120 species total), and lowest in Paradise (the site with medium productivity; 82 species in unburned transects; 114 species total; Table 1). Overall species composition in unburned communities differed significantly among the three sites (Appendix: Fig. A2).

### Local species richness and diversity

Fire severity had contrasting effects on local species richness and diversity among sites, and the magnitude and direction of the patterns differed among plant functional groups (Fig. 3, Table 1). In general, local species richness did not differ significantly between mixed-severity fires and high-severity fires. The only exceptions were for forbs in Paradise (Fig. 3B) and woody plants in Helena (Fig. 3C), both of which had higher local species richness in mixed-severity fires compared to high-severity fires. In contrast to forbs and woody plants, local species richness of graminoids did not differ strongly between

mixed-severity fires and high-severity fires (Fig. 3D–F). Counter to our predictions, forb species richness and diversity was higher in burned communities (both mixed- and high-severity) compared to unburned communities in Helena, but lower in burned communities in Whitefish (Fig. 3A, C, Table 1). Graminoid species richness and diversity was also higher in burned communities compared to unburned communities in Helena, but in contrast to forbs, fire did not influence graminoid richness or diversity in Whitefish (Fig. 3D, F, Table 1). In contrast to forbs and graminoids, woody species richness was lower in burned communities compared to unburned communities in both Helena and Paradise, and there was no effect of fire on species richness in Whitefish (Fig. 3G–I, Table 1). Overall, patterns of species diversity (Fig. 3) paralleled patterns of species richness, except that there were no differences in species diversity among fire severities for graminoids in Paradise or for woody plants in Helena.

### Community dispersion and species composition

Fire severity influenced community dispersion (mean distance to centroids) and overall species composition (Fig. 4, Table 2; Appendix: Fig. A4–5, Table A1). Community dispersion of forbs was lower in landscapes with high-severity fire compared to landscapes with mixed-severity fire at all three sites (Fig. 4). In Helena, community dispersion of forbs in landscapes with high-severity fire was also lower than in unburned landscapes. In contrast, community dispersion of graminoids and woody plants was not significantly affected by fire severity at any site. Fire severity also significantly influenced species composition at all sites (Appendix: Table A1, Fig. A4).

In general, communities with mixed- and high-severity fire had similar species composition, whereas unburned communities often differed compositionally from burned communities within a site. In Helena, for example, *Linaria dalmatica*, *Balsamorhiza sagittata*, and *Tragopogon dubius* most strongly contributed to compositional differences in forbs between unburned and burned communities, especially in landscapes that burned with high-severity fires. *Linaria dalmatica* and *T. dubius* are exotic species and were six and 22 times, respectively, more abundant in high-severity



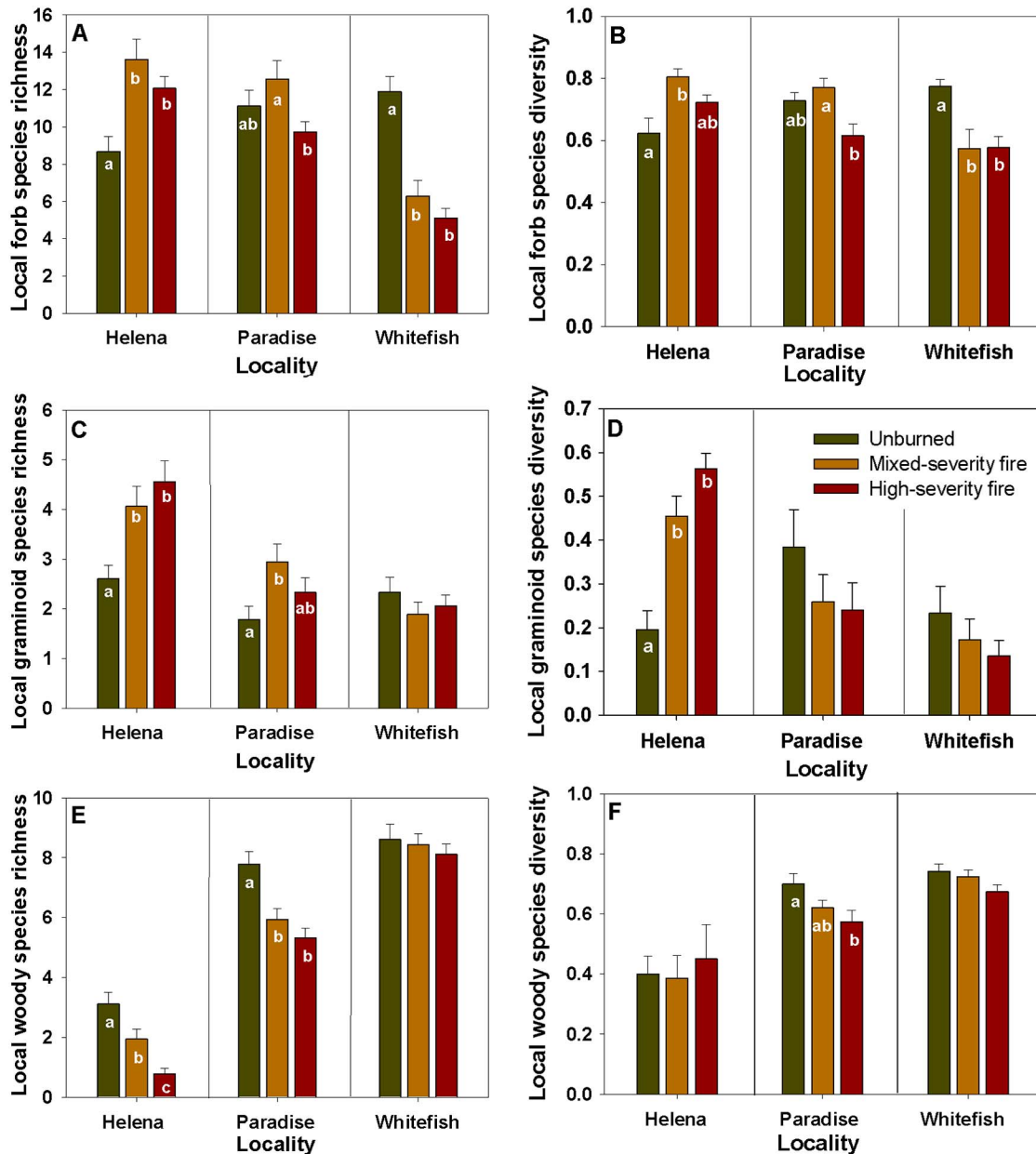


Fig. 3. Effects of wildfire severity on local species richness and diversity of forbs (A, B), graminoids (C, D), and woody plants (E, F) in Helena (low productivity), Paradise Valley (medium productivity), and Whitefish (high productivity). Bars represent means  $\pm 1$  standard error for unburned (green), mixed-severity fire (orange), and high-severity fire (red) communities ( $N = 18$  transects per burn level). Bars with different letters indicate significant differences ( $P < 0.05$ ) among levels of fire severity with a site based on Tukey's tests; missing letters indicate no differences among levels of fire severity with a site.

burns than unburned communities. *Balsamorhiza sagittata*, a native forb, was 28% more abundant in unburned than high-severity fire communities. In Paradise and Whitefish, compositional differ-

ences in forb communities among fire severities were driven by native species, such as *Chamerion angustifolium* (fireweed) in burned communities and *Fragaria virginiana* in unburned communities.

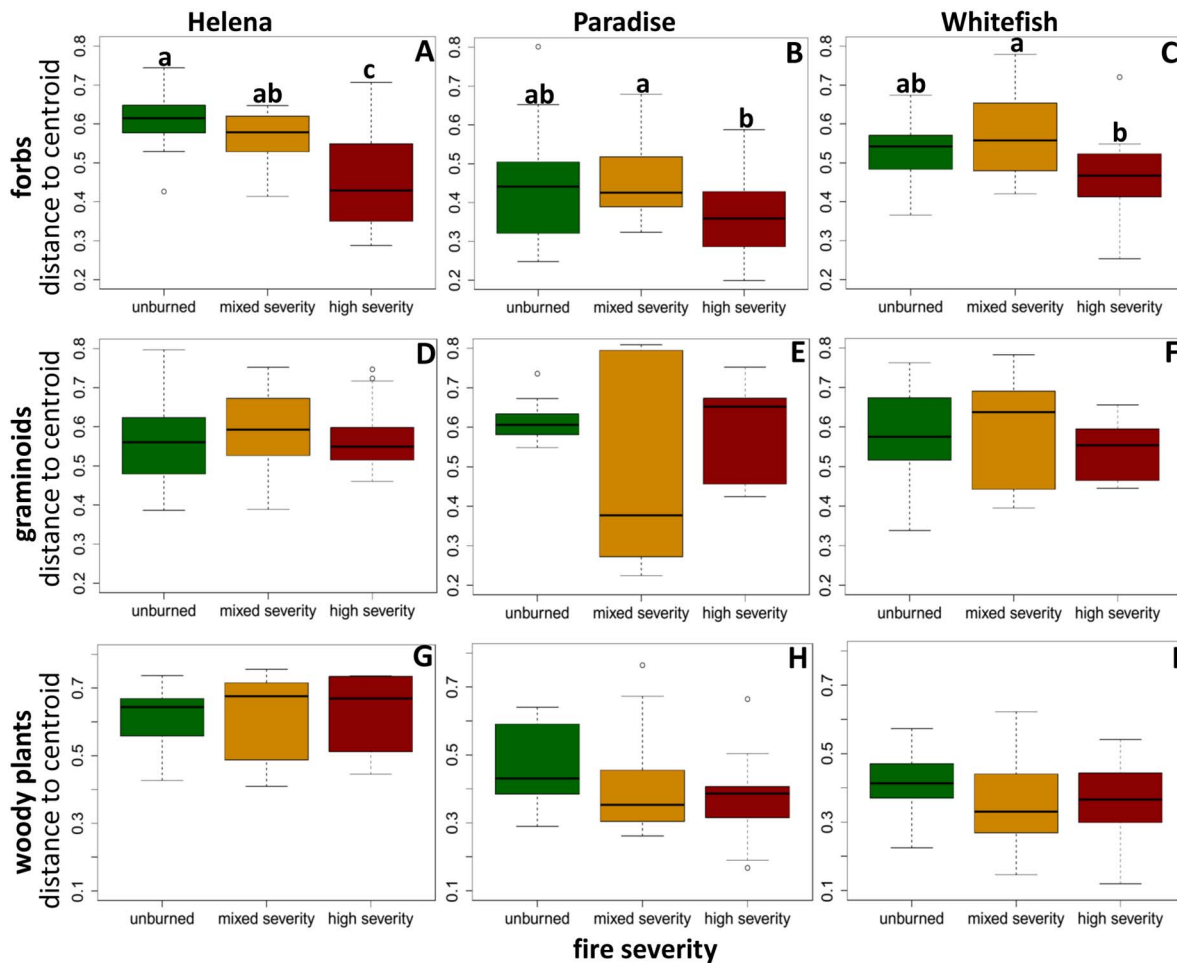


Fig. 4. Boxplots of the effects of wildfire severity on community dispersion (distance-to-centroids) of forbs, graminoids, and woody plants in Helena (low productivity), Paradise Valley (medium productivity), and Whitefish (high productivity). Letters above bars indicate significant differences in community dispersion ( $P < 0.05$ ) among levels of fire severity within a site based on Tukey's tests; missing letters indicate no differences among levels of fire severity within a site. Distance-to-centroids were calculated using Bray-Curtis dissimilarities.

Exceptions to this general pattern included the forb and woody plant communities in Whitefish, where mixed-severity fire, high-severity fire, and unburned transects each supported different assemblages of forb and woody species.

## DISCUSSION

Patterns of biodiversity within and among ecological communities often show variable responses to fire disturbance (e.g., Suding and Gross 2006, Pausas and Verdú 2008, Myers and Harms 2011, Myers et al. 2015). This variability

can emerge through a variety of mechanisms including variation in fire severity, ecosystem productivity, and how biodiversity responds to fire at different spatial scales. However, few studies examine these factors in concert. Here, we found that spatial patterns of plant diversity varied across landscapes with contrasting fire severity and environmental conditions, including net primary productivity. In support of the hypothesis that mixed-severity fire increases beta-diversity, we found that community dispersion of forbs was higher in landscapes with mixed-severity fire compared to landscapes with

Table 2. Results from analyses testing effects of fire severity (unburned, mixed-severity, high-severity fire) on biodiversity patterns of forbs, graminoids, and woody plants at Helena (low productivity), Paradise Valley (medium productivity), and Whitefish (high productivity). Local species richness and diversity (Hurlbert's PIE) were analyzed using mixed-model ANOVA with units as random effects. Degrees of freedom for species richness and diversity were 2 (numerator) and 50 (total) for each test ( $N = 18$  total transects for each level of fire severity in each site). Results from mixed-model MANOVAs that combined both response variables were significant for all three sites ( $P < 0.03$ ). Beta-diversity (community dispersion) was analyzed using homogeneity of multivariate dispersions based on average distance-to-centroid values with both an abundance-based (Bray-Curtis dissimilarity) and an incidence-based (Jaccard dissimilarity) metric. Degrees of freedom (DF) for community dispersion differ from species richness and diversity because not all transects had all plant functional groups present ( $N = 9$ – $18$  total transects for each level of fire severity in each site).  $P$  values  $< 0.05$  are highlighted in bold.

Site	Species richness		Species diversity		DF	Community dispersion			
	F	P	F	P		Bray-Curtis		Jaccard	
						F	P	F	P
Helena									
Forbs	10.45	<b>0.0002</b>	7.12	<b>0.0017</b>	2, 51	12.64	<b>&lt;0.0001</b>	10.33	<b>0.0002</b>
Graminoids	8.18	<b>0.0009</b>	17.19	<b>&lt;0.0001</b>	2, 51	0.019	0.83	0.23	0.80
Woody	17.44	<b>&lt;0.0001</b>	0.21	0.81	2, 42	0.086	0.92	0.01	0.99
Paradise									
Forbs	2.91	0.064	7.31	<b>0.0016</b>	2, 51	3.02	<b>0.050</b>	3.23	<b>0.048</b>
Graminoids	3.42	<b>0.041</b>	1.30	0.28	2, 48	2.89	0.058	4.08	<b>0.023</b>
Woody	13.18	<b>&lt;0.0001</b>	3.67	<b>0.032</b>	2, 51	2.79	0.071	2.76	0.073
Whitefish									
Forbs	23.31	<b>&lt;0.0001</b>	9.26	<b>0.0004</b>	2, 51	4.84	<b>0.012</b>	4.85	<b>0.012</b>
Graminoids	0.75	0.48	0.98	0.38	2, 51	0.92	0.41	1.70	0.19
Woody	0.36	0.70	2.34	0.11	2, 51	1.34	0.27	1.32	0.28

high-severity fires, irrespective of site. We also examined the extent to which changes in local diversity may contribute to patterns of beta-diversity. In contrast to the hypothesis that disturbance decreases local diversity at low productivity and increases local diversity at high productivity (e.g., Huston 2014), we found the opposite result, whereby local species richness of forbs was higher in burned compared to unburned landscapes in Helena and lower in burned compared to unburned landscapes in Whitefish. Local richness of woody plants in Helena, in contrast, was lower in burned compared to unburned landscapes and similar between burned and unburned landscapes in Whitefish. Together, these patterns suggest several possible mechanisms that may influence variation in biodiversity across landscapes with contrasting wildfire severity and regions with contrasting climate and productivity.

#### *Beta-diversity is higher in landscapes with mixed-severity wildfire*

Mixed-severity fires may increase beta-diversi-

ty by creating landscapes that contain a mosaic of habitats that support disturbance-tolerant and -intolerant species. By definition, mixed-severity fires produce more heterogeneous post-fire conditions compared to high-severity fires (Agee 1996, Perry et al. 2011, Belote 2015). Burning conditions of mixed-severity fires produce heterogeneity at widely varying scales from sub-meter mortality of plants and combustion of litter to multi-hectare removal of canopy coverage and increases in light. In turn, environmental heterogeneity can increase species sorting that results in clumped distributions of species across habitats (Myers et al. 2015), leading to high beta-diversity among local communities with contrasting disturbance. By comparison, high-severity fires can decrease species sorting by homogenizing the species composition of local communities, leading to low beta-diversity among communities dominated by disturbance-tolerant species (Chase 2007). In the forests of our study region, for example, high-severity wildfires are often stand-replacing events that lead to strong shifts from communities dominated by late-succession-

al to early-successional plant species (Swanson et al. 2010). In addition, high beta-diversity can result from dispersal limitation or stochastic colonization and extinction dynamics (Hubbell 2001). Although both of these processes may contribute to the high forb beta-diversity we observed in landscapes with mixed-severity fire, they are less likely to explain why community dispersion of forbs was consistently higher in mixed-severity fires compared to high-severity fires across three geographically widespread sites that differ in overall plant species composition (Appendix: Fig. A1) and broad-scale environmental conditions such as productivity (Table 1).

We hypothesized that the effect of fire severity on beta-diversity would vary among biogeographically disparate sites that differ in climate and productivity. For example, post-fire beta-diversity could decrease with productivity (Evans et al. 2008, Stegen et al. 2013) if high-severity fires increase local diversity in high-productivity landscapes but not in low-productivity landscapes. In contrast, beta-diversity could increase with productivity (Chase and Leibold 2002, Chase 2010, Belote et al. 2011) if high-severity fires decrease local diversity in low-productivity landscapes but not in high-productivity landscapes. However, we found little support for this hypothesis. Instead, we found that fire severity had similar effects on community dispersion of forbs in sites that ranged from low-productivity ponderosa pine forests in Helena to high-productivity mixed-conifer forests in Whitefish. Given their relatively short stature, short lifespan, and diverse interactions with other trophic levels (e.g., pollinators, seed dispersers, mycorrhizal fungi), forbs might respond consistently and strongly to the variation in environmental conditions produced by mixed-severity fires across broad-scale climate and productivity gradients. In contrast, community dispersion of graminoids and woody plants was uninfluenced by fire severity at any of the sites, suggesting smaller changes in abundances of graminoid and woody species in response to mixed-severity fires. In Helena, for example, a few rare species (e.g., *Abies lasiocarpa*, *Pseudotsuga menziesii*) strongly contributed to species turnover of woody plants in landscapes with mixed-severity fire, but otherwise the woody communities were similar in composition and dispersion in landscapes with mixed-severity and high-severity wildfires.

#### *Contrasting effects of wildfire on species richness at low versus high productivity*

Our results do not support the hypothesis that disturbance increases local diversity at high productivity (Huston 1979, 2014, Foster and Dickson 2004). We found that local species richness of forbs was higher in burned compared to unburned landscapes in Helena and lower in burned compared to unburned landscapes in Whitefish. These patterns were likely influenced by differences in post-fire recruitment and population growth rates of woody species between sites. In the high-precipitation, high-productivity mixed-conifer forests of Whitefish, post-fire landscapes are typically dominated by high densities of regenerating lodgepole pine, western larch, and other conifers (Fig. 2). Increased competition from large-stature woody species for limiting resources (e.g., light, soil nutrients and space) likely reduces species richness of small-stature forbs. By contrast, in the low-precipitation, low-productivity ponderosa-pine forests and woodlands of Helena, post-fire landscapes have little to no tree regeneration (Fig. 2), likely resulting in decreased resource competition between woody species and forbs. In addition, species richness of woody plants decreased with fire in Helena (Fig. 3E), suggesting that decreased competition from woody species may explain higher local diversity of forbs in landscapes in mixed-severity fire (Figs. 3A and 4). Although the lack of replication of productivity levels within sites limits our ability to infer underlying mechanisms, our results highlight the need for biogeographically replicated experiments and observational studies that are designed to untangle how factors such as climate and productivity interact with wildfires across biogeographic gradients. For example, our observational study did not cover the full range of variation in productivity found within this region. Additional studies in sites at the extremes of the productivity gradient will provide important insights into how the relationship between herbaceous plant diversity and disturbance changes across biogeographic gradients.

Several additional factors may contribute to the higher species richness of herbaceous communities in burned landscapes in Helena. First, the Helena site supports a larger species pool of herbaceous plants (forbs and graminoids). The

Helena site is located at the interface of two major floristic regions (Rocky Mountains and Great Plains) and thus supports species whose geographic distributions overlap at climatic and topographic boundaries (Omernik 1987). Second, the Helena site has likely experienced a more frequent, but low-severity, fire regime (Fischer and Bradley 1987). Species pools at the Helena site may include more fire-tolerant species that persist following fire, as well as ruderal species that depend on increased resource availability immediately following fire. This combination of fire-tolerant species and fire-dependent ruderal species may contribute to diverse local assemblages of species with different traits and adaptations to fire. In contrast, the Paradise and Whitefish sites were historically characterized by stand-replacing, mixed-severity fires with longer return intervals (Fischer and Bradley 1987). These disturbance regimes may result in little temporal overlap between environmental conditions that support species that occur in mature forests as well as species that have strong fidelity to post-fire conditions. Third, although we selected our study sites to minimize differences in time-since-fire, sites vary in their rate of forest succession and biomass recovery following fire. In particular, many of the transects in the Whitefish site are currently in the stem-exclusion stage of forest succession where intense competition between trees leads to thinning of stands through competitive exclusion (Franklin et al. 2002). We would expect the diversity of herbaceous plants to vary through time as these forests undergo ecological succession.

#### *Implications for management and restoration of fire-prone ecosystems*

Our results have implications for management and restoration of fire-prone ecosystems. Although wildfires have shaped the ecology of forests in western North America for millennia, fire suppression—in combination with climate change, housing development, and timber harvesting—have put ecosystems at risk of regime shifts (*sensu* Westerling et al. 2011). Concurrently, billions of public dollars are spent on fire control annually and on restoration treatments intended to restore fire's role on the landscape (Donovan and Brown 2007, Schoennagel and Nelson 2010) without a clear understanding of

how fire may influence biodiversity and resulting ecosystem services across spatial scales. Our results suggest that heterogeneous conditions produced by mixed-severity fires are likely to support the highest numbers of plant species at landscape scales by increasing spatial variation in community composition (beta-diversity) across landscapes. At the same time, our results suggest that fire effects on plant species diversity are conditional upon a suite of complex factors (e.g., functional-group composition, climate, productivity, species pools), and more work is needed to understand the mechanisms underlying our observed patterns. Importantly, our study suggests that post-fire tree recovery in productive landscapes may suppress understory species diversity at local and landscape scales. In some cases, managers are thinning dense forests to reduce fire risk and accelerate forest development, which may have effects on forb communities. To the extent that shifts in plant diversity increase with environmental change, it will be critical to continue to investigate the ways in which the effects of fires on species diversity and ecosystems depend on landscape context and spatial scale.

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## SUPPLEMENTAL MATERIAL

### ECOLOGICAL ARCHIVES

The Appendix is available online: <http://dx.doi.org/10.1890/ES15-00438.1.sm>