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Post-fire logging produces minimal persistent impacts on understory vegetation in northeastern Oregon, USA

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A B S T R A C T

Post-fire forest management commonly requires accepting some negative ecological impacts from management activities in order to achieve management objectives. Managers need to know, however, whether ecological impacts from post-fire management activities are transient or cause long-term ecosystem degradation. We studied the long-term response of understory vegetation to two post-fire logging treatments – commercial salvage logging with and without additional fuel reduction logging – on a long-term post-fire logging experiment in northeastern Oregon, USA. We sampled understory plant cover and species diversity on 10–11 sampling plots within each of nine experimental treatment units to see if post-fire logging treatments produced any lasting effects on understory plant cover, species diversity, community composition, or exotic species cover. Post-fire logging treatments produced no significant effects on understory vegetation cover, diversity, or community composition 15 years after treatment. We found no significant treatment effects on graminoid, forb, woody plant, or exotic plant cover and species richness, and differences among treatment means were generally small. Differences in treatment means were larger at the individual species level, but were only statistically significant for one native grass, California brome (*Bromus carinatus*), which responded differently to the two logging treatments. Multivariate analysis of understory plant communities across 91 sample plots found two major gradients in understory plant community composition, one correlated with regenerating forest (sapling) density and one correlated with residual overstory tree density, suggesting that initial fire severity (tree mortality) and post-fire regeneration may have greater long-term impacts on post-fire understory vegetation than post-fire logging. This study demonstrates that understory vegetation can be resilient to post-fire logging, particularly when best management practices, like logging over snow, are used to limit damage to soils and understory vegetation. Further research is needed to establish the generality of our results and to identify sources of variability in understory plant community responses to wildfire and post-fire logging. If further research confirms our findings, post-fire logging debates will be able to focus more on how to mitigate short-term disturbance impacts and manage fire-killed trees to meet wildlife habitat, fuel reduction, and economic objectives, and less on concerns over long-term ecosystem degradation.

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1. Introduction

Post-fire forest management commonly requires balancing competing social–ecological resource interests and deciding whether to accept short-term ecological impacts to achieve management objectives. For example, harvesting fire-killed trees quickly after wildfire can provide economic benefits to communities impacted by fire (Prestemon et al., 2006; Lowell et al., 2010), reduce future surface woody fuels (Ritchie et al., 2013; Peterson et al., 2015), hasten forest regeneration through artificial regeneration (Sessions et al., 2004; Newton et al., 2006), and promote long-term carbon sequestration in forest products (Apps et al., 1999; Stockman et al., 2012). However, fire-killed trees (standing and fallen) also provide habitat functions for a wide variety of organisms, influence soil carbon and nutrient cycling processes, and modify soil and surface microclimates for tree seedlings and understory vegetation (Harmon et al., 1986; Smith, 2000; Brown et al., 2003; Boulanger and Sirois, 2007; Hutto, 2008; Marañón-Jiménez et al., 2013). Given recent trends toward larger wildfires

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(Westerling et al., 2006; Dennison et al., 2014), there may increasingly be enough fire-killed trees on landscapes after large wildfires to meet wildlife habitat needs and also allow some harvesting to meet other resource objectives. In those cases, post-fire logging decisions will focus more on assessing and balancing the short- and long-term resource costs and benefits.

Logging is a form of disturbance (*sensu* White and Pickett, 1985), so we would expect post-fire logging to alter community structure and the physical environment to some extent. Indeed, previous studies have shown that post-fire logging can increase soil disturbance and erosion, alter the cover and composition of recovering native vegetation, damage natural tree regeneration, and increase surface woody fuels within 2–4 years after fire and logging (Klock, 1975; Stuart et al., 1993; McIver and Starr, 2001; Purdon et al., 2004; McIver and McNeil, 2006; Donato et al., 2006; Keyser et al., 2009; Ritchie et al., 2013; Slestak et al., 2015; Wagenbrenner et al., 2015). Disturbance impacts on forest ecosystems can diminish as ecosystems recover, however, so longer-term impacts of post-fire logging may differ from short-term impacts (e.g., Kurulok and Macdonald, 2007; Ritchie et al., 2013; Peterson et al., 2015). Longer-term studies of post-fire logging impacts are needed to determine whether post-fire logging produces only short-term disturbance impacts or if post-fire logging impacts exceed ecosystem resilience thresholds and alter trajectories of post-fire recovery and succession (Gunderson, 2000; Beschta et al., 2004; Brewer et al., 2012; Kishchuk et al., 2015).

In this study, we assessed possible long-term effects of post-fire logging treatments on understory vegetation recovery and succession by surveying understory vegetation cover and diversity on a previously established post-fire logging experiment. Our study was conducted 18 years after the wildfire and 15 years after logging treatments were completed. We assessed vegetation recovery in terms of understory plant cover, community composition, and species richness, asking if post-fire logging treatments produced persistent effects on understory plant cover and diversity, exotic plant cover and diversity, or plant community composition that were still detectable 15 years after treatment. Based on previous studies, we hypothesized that logged sites would support lower plant cover and plant species diversity than unlogged sites. However, we also anticipated that post-disturbance vegetation recovery processes would reduce or eliminate at least some of the impacts commonly observed shortly after treatment, helping us to identify areas of persistent negative impacts.

2. Materials and methods

2.1. Site description

The study area is located within the area burned by the 1996 Summit Fire, which burned about 16,000 ha in northeastern Oregon, USA (McIver and McNeil, 2006; McIver and Ottmar, 2007). Soils are mostly rocky, clay-loam to clay soils, but some soils also have a layer of Mt. Mazama ash (McIver and McNeil, 2006; McIver and Ottmar, 2007). Slopes in the study area ranged from 10 to 25 percent, with south to southwest aspects (McIver and Ottmar, 2007). Mean daily temperatures range from −2 °C in January to 18 °C in July, while mean annual precipitation is about 520 mm, much of which falls as snow between November and April (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu/explorer/, accessed on October 20, 2015).

The study area supports dry coniferous forests that were historically dominated by ponderosa pine (*Pinus ponderosa*), but with some Douglas-fir (*Psuedotsuga mensiezii*) and grand fir (*Abies grandis*) trees also present (McIver and McNeil, 2006). Historically, dry ponderosa pine forests in the region burned frequently and at predominantly low severity, with mean fire return intervals of 14–16 years reported for the period 1687–1900 (Heyerdahl et al., 2001). Like many dry coniferous forests in the region, reductions in fire frequency and extent and increases in logging and cattle grazing likely altered forest structure and fuels during the 20th Century, combining to produce denser stands with smaller trees and higher surface fuel loads than were typical historically (Hessburg and Agee, 2003; McIver and Ottmar, 2007). These altered stand structural conditions promote higher fire severity. Of the 8103 ha of the Summit Fire that burned on the Malheur National forest, 72% burned at high severity (>80% of overstory trees killed; McIver and Ottmar, 2007).

2.2. Experimental design and treatments

The original post-fire logging study included four treatment blocks with three treatment units per block. These 12 treatment units ranged in size from 6 to 16 ha. Treatment blocks were located in separate drainages, each with a perennial stream. We limited our sampling to the first three treatment blocks (9 treatment units) of the original study because the fourth block (Wray Creek) re-burned in the 2008 Sunshine wildfire. Ponderosa pine was the dominant overstory species in two of the treatment blocks. In the third block, ponderosa pine and Douglas-fir were codominant in one treatment unit, while Douglas-fir and grand fir were codominant in the other two units (McIver and Ottmar, 2007).

Three experimental treatments (control, commercial logging, and commercial plus fuel reduction logging) were randomly assigned to one treatment unit in each of the treatment blocks, using a complete randomized block design (McIver and Ottmar, 2007). The control treatment was not logged after fire. The commercial post-fire logging treatment called for removing about 2/3 of the dead merchantable trees, but leaving at least 17 snags/ha greater than 30 cm DBH. The commercial plus fuel reduction logging treatment called for removing most dead merchantable trees (retaining at least six snags/ha greater than 30 cm DBH) and also removing most non-merchantable small trees (10–29 cm DBH). The commercial logging treatment was designed to reflect typical logging operations, with retention of some wildlife snags, while the commercial plus fuel reduction logging treatment was designed to remove merchantable material and reduce residual woody fuel mass and future wildfire severity. Logging was conducted between October 1998 and August 1999, and was limited to periods with frozen or dry ground to minimize soil compaction and disturbance. Commercial treatment units were entered once (commercial timber sale), while fuel reduction treatment units were entered twice (commercial timber sale followed by a service contract to remove smaller trees). McIver and Ottmar (2007) provide additional details about the logging methods and subsequent forest regeneration activities.

2.3. Data collection

The original experiment used a grid of permanent sample plot centers (hereafter, grid points) placed at 50-m intervals in each treatment unit, leaving at least a 50-m buffer around the treatment unit boundary. Because of size differences, treatment units contained 14–47 grid points. For this study, we randomly selected 10–11 grid points from each unit for understory vegetation sampling in summer 2014. At each selected grid point, we established two parallel 10-m sampling transects, four meters apart and oriented parallel to the slope contour, thereby delineating a 40-m^2 (4-m by 10-m) rectangular sampling plot centered on the grid point.

We assessed plant cover, by species, using the line-point intercept (LPI) method, with LPI sampling points placed at 20-cm intervals along each of the two 10-m sampling transects for a total of 100 LPI sample points per plot. We calculated percent cover for each plant species on each plot as the percentage of LPI sampling points at which we observed the species. We then calculated plot-level plant cover estimates for all vascular plants, for exotic species, and for individual life forms (e.g., graminoids, forbs, shrubs, and trees) by summing the percent cover estimates for species in those groups. Finally, we summarized plot-level plant cover estimates to the treatment unit level.

We assessed plant species richness and plant community heterogeneity by conducting a complete census of understory vascular plant species within each 40-m^2 sampling plot. From this census, we calculated plant species richness for all vascular plants, for exotic species, and for three plant lifeforms – graminoids, forbs, and woody plants (shrubs and trees) – by counting the number of species observed within each group at each plot. We then calculated unit-level species richness as the number of unique species recorded across all sampling plots within a treatment unit. Finally, we estimated plant community heterogeneity (beta diversity *sensu* Whittaker, 1975) for each treatment unit as unit-level species richness divided by the mean plot-level species richness.

To characterize local stand structure at each sampling plot, we surveyed all mature trees (DBH $\geqslant$ 12.5 cm) and tree saplings (height > 1.35 m and DBH < 12.5 cm) within a circular plot with an 8-m radius around the plot center. For each sapling or tree, we recorded the species, DBH, and current status (alive or dead). We did not survey tree seedlings (height < 1.35 m). From these data, we calculated tree density (stems per ha) and basal area (m^2 per ha) for saplings alone, trees alone, and saplings and trees combined.

2.4. Data analyses

We used non-metric multidimensional scaling (NMS, Kruskal, 1964; Mather, 1976) in PC-ORD (McCune and Mefford, 2011) to describe the multivariate structure of the understory plant communities, explore potential overstory–understory relationships in the plant communities, and assess post-fire logging treatment effects on understory community composition. These ordination analyses used species cover data from individual sampling plots within treatment units (n = 91) to capture plant community variability within and among treatment units. We used the ‘‘slow and thorough” autopilot mode for NMS in PC-ORD, using the Sorenson distance measure and 250 runs each with real and randomized data. The final solution had two dimensions. We used correlation analyses (Pearson’s r) to examine relationships among plot ordination scores, variables describing overstory structure, and the cover and species richness of understory plant life forms.

We assessed logging treatment effects on plant cover and species richness using linear mixed-effects statistical models (SAS PROC GLIMMIX, SAS Institute 2012). Model structure followed that for a standard randomized complete block experiment (Littell et al., 2006). All models included post-fire logging treatment as a categorical predictor variable with three treatment categories (commercial logging, commercial logging followed by fuel reduction logging, or no logging) and treatment block as a random variable. Response variables were summarized to the treatment unit level for analysis. Response variables tested included vascular plant cover; vascular plant species richness; plant cover and species richness by plant lifeform (shrubs and trees, forbs, and graminoids); plant cover and species richness of exotic plant species; understory plant community heterogeneity (β-diversity); and overstory stand structure (tree density and basal area). We also assessed treatment effects on mean cover of eight common understory species. We adopted a Type I error rate of 5% as our threshold for determining the statistical significance of treatment effects using Type III tests of model fixed effects.

3. Results

We sampled a total of 172 vascular plant species, including 119 forb, 34 grass and sedge, 13 shrub, and 6 tree species. Species richness on the untreated (control) treatment units averaged 34 species per plot (40 m^2) and 87 species per unit (Table 1). Forbs represented the largest life form group (21 species per plot), followed by grasses (9 species) and woody species (4 species; Table 1). Exotic species were common, with an average of 6 species encountered per plot. Projected live plant cover averaged 83% on the untreated treatment units, while absolute cover (which counts multiple species layers) averaged almost 139%. Grasses and sedges dominated the understory vegetation on untreated units with 96% absolute cover, followed by forbs (34% cover), and shrubs and trees (9% cover). Exotic species averaged 34% absolute cover, or about 25% of total plant cover. The most common understory species, based on frequency and total cover, included yarrow (*Achillea millefolium* L.), California brome (*Bromus carinatus* Hook. & Arn.), soft brome (*Bromus hordeaceus* L.), cheatgrass (*Bromus tectorum* L.), Geyer’s sedge (*Carex geyeri* Boott), pinegrass (*Calamagrostis rubescens* Buckley), grassy tarweed (*Madia gracilis* (S.) D.D. Keck), and common snowberry (*Symphoricarpos albus* (L.) S.F. Blake).

Multivariate analysis of the understory plant community produced a two dimensional solution with a final stress of 17.8 (instability < 0.0001) that explained 80% of the variance in the initial dataset (Fig. 1). Sample plot scores on the primary ordination axis (explaining 57% of the variance) were negatively correlated with total stand density (trees and saplings, $r = -0.62$, $P < 0.001$), sapling density ($r = -0.58$, $P < 0.001$), shrub cover and species richness, and forb cover and species richness, but were positively correlated with grass and sedge cover, grass and sedge species richness, and exotic plant cover (Fig. 2). Plant community composition represented by the secondary ordination axis (23% of variance) was more strongly associated with variation in residual overstory stand structure and highlighted differences among treatment blocks more than among logging treatments. Sample plot scores on the secondary ordination axis were positively correlated with residual tree density ($r = 0.35$, $P < 0.001$) and forb species richness ($r = 0.22$, $P = 0.037$), but negatively correlated with regenerating sapling density ($r = -0.29$, $P = 0.005$).

Post-fire logging treatments did not significantly affect understory vegetation cover or composition in this long-term study (Table 2). We found no significant treatment effects on graminoid, forb, woody plant, or exotic plant cover (Table 2, Fig. 3). We found some support ($P = 0.077$) for a logging treatment effect on total vascular plant cover, but the largest difference was between the two logging treatments, with the commercial logging treatment having the highest mean cover and the commercial plus fuel reduction logging treatment having the lowest mean cover (Fig. 3). Analysis of the plot ordination scores also revealed no significant treatment effects. Differences among treatment means were small in relative terms in addition to being not statistically significant. For example, mean total vascular plant cover ranged from 129% in the commercial plus fuel reduction logging treatment to 139% in the control treatment and 143% in the commercial logging treatment.

At the species level, we found that post-fire logging treatments significantly altered mean plant cover for only one of the eight common understory species examined (Fig. 4). Mean cover of California brome (*B. carinatus*) was significantly higher for the commercial logging treatment than for the fuel reduction treatment, but neither were significantly different from the control treatment (Fig. 4). The exotic brome grasses (*B. hordeaceus* and *B. tectorum*) and a native forb (*M. gracilis*) displayed a common, but statistically insignificant pattern with highest mean cover after commercial logging treatment, intermediate mean cover on the

Table 1
Summary of stand structure, species diversity, and plant cover, by treatment unit. Species diversity measures include species richness at the treatment unit (SR unit) and sample plot (SR plot) levels and beta diversity (Beta div.). Absolute plant cover is shown for all vascular plants (Total cover), different plant life forms (Grass, Forb, and Woody cover), and exotic species, using mean cover estimates from all sample plots within the treatment unit. Values in parentheses indicate standard errors of the means.

Block	Treatment	Site	Tree basal area (m^2/ha)	Tree density (ha^{-1})	Sapling density (ha^{-1})	SR unit	SR plot	Beta div.	Total cover (%)	Grass cover (%)	Forb cover (%)	Woody cover (%)	Exotic cover (%)
1	None	324	7.2	65	30	89	32	2.8	129	103	22	4	43
			(2.6)	(18)	(21)		(1)		(15)	(15)	(3)	(2)	(15)
	Commercial	327	1.8	15	154	82	29	2.8	141	118	18	4	77
			(1.5)	(11)	(64)		(2)		(7)	(2)	(2)	(2)	(9)
	Fuel	323	5.3	50	154	94	33	2.8	124	87	27	10	23
			(2.6)	(27)	(55)		(2)		(12)	(7)	(6)	(2)	(8)
2	None	422	0.2	15	597	79	35	2.2	151	96	40	15	25
			(0.2)	(11)	(106)		(2)		(9)	(3)	(5)	(3)	(6)
	Commercial	424	0.1	9	438	86	35	2.5	149	100	32	17	27
			(0.1)	(6)	(84)		(2)		(6)	(3)	(3)	(3)	(7)
	Fuel	421	0.2	15	468	70	31	2.3	131	94	30	7	27
			(0.2)	(15)	(99)		(2)		(6)	(3)	(3)	(2)	(7)
3	None	420	5.2	45	393	92	35	2.6	136	90	39	7	34
			(2.4)	(20)	(248)		(1)		(8)	(7)	(5)	(4)	(9)
	Commercial	418	0.0	0	279	81	34	2.4	140	86	49	5	24
			(0)	(0)	(67)		(2)		(11)	(8)	(6)	(1)	(8)
	Fuel	419	0.6	5	60	93	32	2.9	133	100	31	2	58
			(0.6)	(5)	(39)		(2)		(13)	(10)	(4)	(1)	(13)

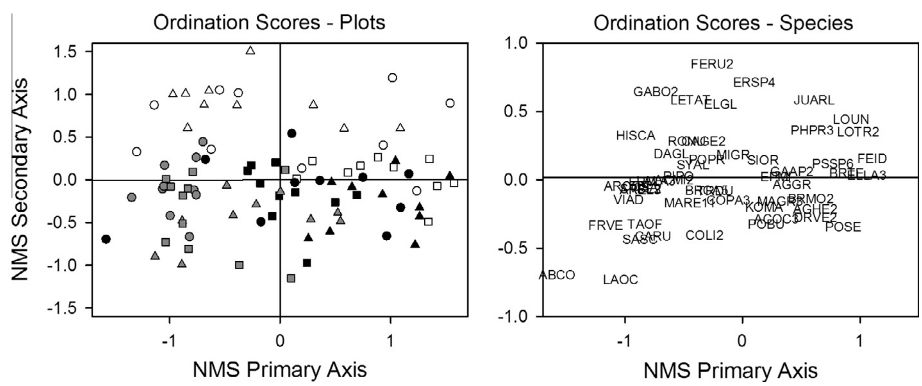

Fig. 1. Non-metric multidimensional scaling ordination results showing (a) plot ordination scores by treatment and block, and (b) species ordination scores for common species (found on 9 plots or more). Symbols for plots indicate no treatment (circles), commercial logging (squares), or fuel reduction logging (triangles), while symbol colors (white, gray, or black) correspond to treatment blocks. Species codes correspond to those in the USDA PLANTS database.

fuel reduction treatment, and lowest mean cover on the control treatment (Fig. 4).

Post-fire logging treatments also produced no significant effects on understory plant diversity. We found no significant treatment effects on species richness, regardless of the scale of observation (sample plot means or treatment unit) or the plant group (Table 2, Fig. 3). Similarly, we found no significant treatment effects on community heterogeneity within treatment units (β diversity). Unit-level species richness of exotic plants was somewhat higher on logged units than on unlogged units (Table 2), but the difference of less than three species per unit was not statistically significant ($P = 0.086$). Differences among treatment means were practically small as well as not statistically significant. For example, mean sample plot species richness ranged from 31.8 species for the commercial plus fuel reduction logging treatment to 34.0 species for the control treatment. Community heterogeneity among plots (β diversity) was the same in the commercial logging and control treatments, and only slightly higher in the fuel reduction treatment.

4. Discussion

In this study, we found that post-fire logging produced almost no persistent negative impacts on understory plant communities, suggesting that these understory plant communities were either not disturbed by post-fire logging or were resilient to post-fire logging as a disturbance. Contrary to our hypotheses, we found no significant effects of post-fire logging on total understory vegetation cover, plant life form cover, total plant diversity, or plant life form diversity 15 years after treatments (18 years after wildfire). The only statistically significant finding was for one grass species where the two logging treatments produced opposite effects on cover relative to the control treatment. With only three replicate treatment units per treatment, our study has relatively low power to differentiate among treatment means, which is a common problem with management studies. However, differences among treatment means in this study were relatively small, except for overstory tree density and mean cover of some individual species, and would probably not be considered meaningful to most forest managers even if they were deemed statistically significant.

Our results differ from the many studies that identified significant short-term effects of post-fire logging on understory vegetation (e.g., Sexton, 1998; Purdon et al., 2004; Kurulok and Macdonald, 2007; Hebblewhite et al., 2009; Leverkus et al., 2014; Wagenbrenner et al., 2015), but are consistent with previous studies that found that post-fire logging effects diminished over time (Kurulok and Macdonald, 2007; Keyser et al., 2009). Our study shows that post-fire logging does not necessarily produce long-term ecosystem degradation or alternative recovery pathways

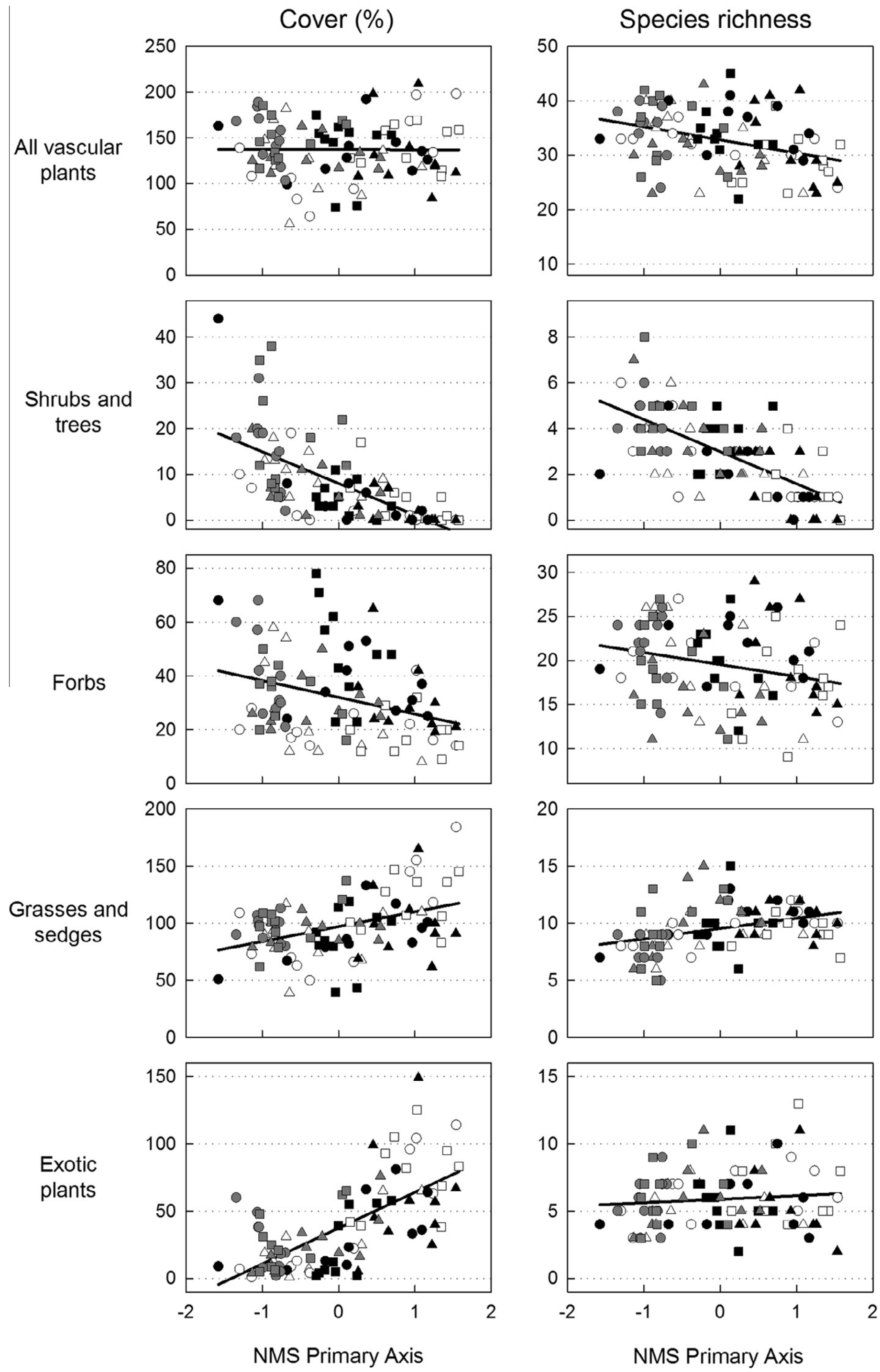

Fig. 2. Correlations between plot scores on primary NMS ordination axis and cover and species richness for all vascular plants, shrubs, forbs, grasses, and exotic plants at the plot level.

(Lindenmayer and Ough, 2006; Lindenmayer et al., 2008; Kishchuk et al., 2015).

The minimal post-fire logging impacts we observed are likely attributable to the extended recovery period between logging treatment completion and our study, and not just a lack of initial impacts. Ground-based logging systems can damage or kill vegetation and disturb soils (e.g., compaction, exposing bare soil) and may influence colonization by new species and individuals, including exotic species (Klock, 1975; McIver and Starr, 2001; Wagenbrenner et al., 2015). The logging treatments in this study displaced or compacted an average of 15% of the soil surface in commercial logging units and 19% of the soil surface in the fuel reduction logging units (McIver and McNeil, 2006), similar to other studies of ground-based post-fire logging impacts on soils (Klock, 1975; McIver and Starr, 2001; Wagenbrenner et al., 2015). Potential soil impacts were likely reduced by management prescriptions that called for hand-felling of trees and limited logging operations to periods of dry or frozen ground (McIver and McNeil, 2006). However, with the amount of soil surface disturbed, the logging treatments almost certainly produced short-term reductions in

Table 2
Post-fire logging treatment effects on plant cover, non-plant cover, species richness, plant community heterogeneity, plant community composition (NMS scores), and overstory structure. For each response, we list the least-square means (and SE) for each treatment and the type III test (*F*, *P*) for significant treatment effect. Degrees of freedom are the same for all tests (numerator DF = 2, denominator DF = 4, block DF = 2).

Response	Group	Not logged (mean)	Salvage only (mean)	Salvage & fuel (mean)	SE	Model F	Model P
Plant cover (%)	All plants	138.7	143.4	129.1	4.4	5.21	0.077
	Graminoids	96.2	101.4	93.8	6.2	0.35	0.725
	Forbs	33.8	33.2	29.2	6.1	0.34	0.729
	Shrubs & Trees	8.7	8.8	6.2	3.4	0.32	0.742
	Exotic plants	34.0	42.5	36.2	12.2	0.12	0.891
Non-plant cover (%)	Bare soil	1.4	3.1	2.6	1.2	0.52	0.630
	Litter	83.2	78.4	76.8	4.1	1.75	0.284
	Rock	3.3	4.5	4.4	2.6	0.09	0.918
	Wood	9.1	7.4	8.0	1.9	0.21	0.819
Species richness (unit level)	All plants	86.7	83.0	85.7	5.1	0.16	0.857
	Graminoids	20.0	20.0	21.7	1.7	0.89	0.478
	Forbs	57.0	53.0	55.0	4.2	0.29	0.765
	Shrubs & Trees	9.7	10.0	9.0	1.6	0.10	0.909
	Exotic plants	13.3	17.3	14.7	1.2	4.48	0.095
Species richness (plot level)	All plants	34.0	32.6	31.8	1.3	0.77	0.523
	Graminoids	9.3	9.5	9.7	0.5	0.14	0.876
	Forbs	21.0	18.9	18.8	1.1	1.00	0.445
	Shrubs & Trees	3.7	4.2	3.3	0.9	0.58	0.600
	Exotic plants	5.8	6.2	5.6	0.3	2.20	0.227
Beta diversity	All plants	2.6	2.6	2.7	0.17	0.55	0.617
	Graminoids	2.1	2.1	2.2	0.16	1.75	0.284
	Forbs	2.7	2.8	2.9	0.15	0.90	0.421
	Shrubs & Trees	2.8	2.5	3.2	0.55	0.51	0.633
	Exotic plants	2.3	2.8	2.7	0.21	2.91	0.166
NMS	NMS axis 1	0.16	−0.11	−0.05	0.31	0.26	0.785
	NMS axis 2	0.13	−0.18	0.05	0.29	0.99	0.449
Stand structure	Stand basal area	5.4	1.8	2.8	1.1	3.55	0.130
	Sapling density	308	287	227	126	0.43	0.680
	Tree density	41	8	23	12	3.96	0.113

understory vegetation cover and plot-level species richness similar to those reported by previous studies (Sexton, 1998; Purdon et al., 2004; Kurulok and Macdonald, 2007; Hebblewhite et al., 2009; Leverkus et al., 2014; Wagenbrenner et al., 2015).

Recent studies have shown that understory plant communities in dry coniferous forests are resilient to high severity disturbance (Abella and Fornwalt, 2015; Morgan et al., 2015). Plant species have varying adaptive traits for responding to fire and other disturbances that can influence disturbance effects on plant communities and plant community responses after disturbances (Gill, 1981; Noble and Slatyer, 1980; Rowe, 1983). The species pool in this study is derived from dry coniferous forests of the interior Pacific Northwest that historically supported high frequency, low severity fire regimes (Heyerdahl et al., 2001). The traits that allowed these species to persist in a region of frequent fire disturbances (e.g., resprouting, rapid growth, long-distance seed dispersal) are not necessarily fire-specific adaptations (Bradshaw et al., 2011) and could also allow them to persist through other disturbances, like logging.

Our results also show the potential importance of residual and regenerating forest structure on post-fire plant communities. We found two distinct gradients in plant community composition at the individual plot scale – the primary gradient was correlated with regenerating forest density, while the secondary gradient was correlated with residual tree density. These patterns are similar to those found in savanna and woodland ecosystems, where grass, forb, and shrub abundance commonly vary with local tree canopy cover (McPherson, 1997; Peterson et al., 2007). In ponderosa pine forests, overstory trees (including larger saplings) can influence understory biomass production and species composition through above- and belowground competition for resources (Moir, 1966; Riegel et al., 1992, 1995). Wildfires can initiate successional changes in these understory plant communities by reducing the abundance of fire-sensitive plant species; reducing resource competition from overstory trees; and facilitating colonization by new species, particularly ruderal species. However, plant communities may also resist successional changes as fire adaptations (e.g., sprouting shrubs) allow much of the pre-fire plant community to persist (Abella and Fornwalt, 2015). Persistence of pre-fire soil properties (e.g., nutrients, water-holding capacity) may also promote persistence of pre-fire plant communities. The differentiation in plant community composition described by the secondary ordination axis in this study (correlated with residual tree density) likely reflects a gradient in fire severity, which influenced tree survivorship, and an associated gradient in belowground resource availability governed by post-fire soil properties and belowground resource competition from residual trees.

Exotic plant cover and species richness was high throughout our study site, but logging treatment had only a small effect on total exotic plant cover and species richness, similar to a study in the Black Hills (Keyser et al., 2009). Stand-replacing wildfires can provide favorable habitat for exotic plant species (Crawford et al., 2001), particularly on dry sites with high incident radiation (Dodson and Root, 2015). High fire severity, low post-fire tree cover, and southerly slope aspects likely explain the high cover and species richness of exotic plant species observed in this study, though soil disturbance during treatment may have further facilitated establishment of some exotic species. Given the inverse correlation between exotic plant cover and sapling density, we expect exotic plant cover to decline in the future as regenerating forest stands continue to grow. The dominant exotic plant species in this study, cheatgrass (*B. tectorum*), has been shown to be sensitive to shading from overstory trees, understory shrubs, and litter, lending further support to this expectation. However, almost 30% of our plots (28 out of 91) had no saplings or trees 15 years after logging treatments and tree planting, suggesting either slow tree seedling

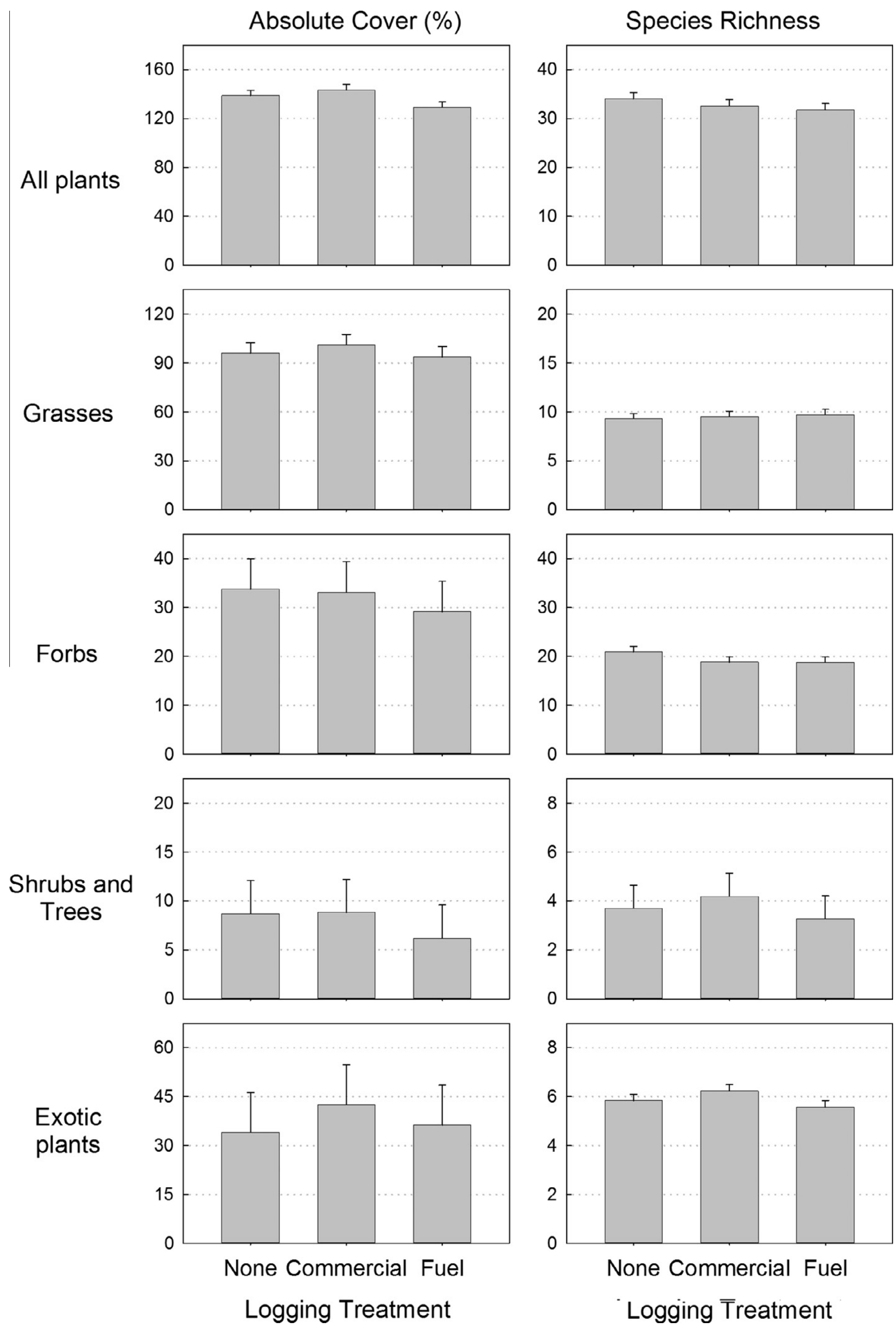

Fig. 3. Post-fire logging treatment effects on vascular plant cover and species richness. Post-fire logging treatments include no logging ("None"), commercial logging ("Commercial"), and fuel reduction logging ("Fuel"). Graphs show means and standard errors for absolute plant percent cover (left column) and species richness (right column) at the plot level (40 m^2 area) for all vascular plants, grasses, forbs, woody plants, and exotic plant species. Mean and standard errors are derived from model least-square means estimates.

growth rates or local regeneration failures in parts of the study area. Such areas may remain as early successional habitat for an extended period, with exotic plants, grasses, and forbs remaining abundant until trees or shrubs become established (Swanson et al., 2011).

Despite the high cover of exotic species (25% of total plant cover), native diversity was high. The average of 32 species per plot (40-m^2) observed in this study is similar to the pre-treatment species richness for much larger plots in ponderosa pine forests of Montana (36 species per 1000-m^2) plot (Metlen and Fiedler, 2006). This result supports previous reports that stand-replacing wildfire can result in diverse and abundant understories, even in areas which historically supported primarily high frequency, low severity fire regimes (Swanson et al., 2011; Abella and Fornwalt, 2015).

5. Conclusions

This study shows that post-fire logging can be conducted in ways that avoid long-term impacts on recovering vegetation and on ecosystem processes that are influenced by vegetation cover,

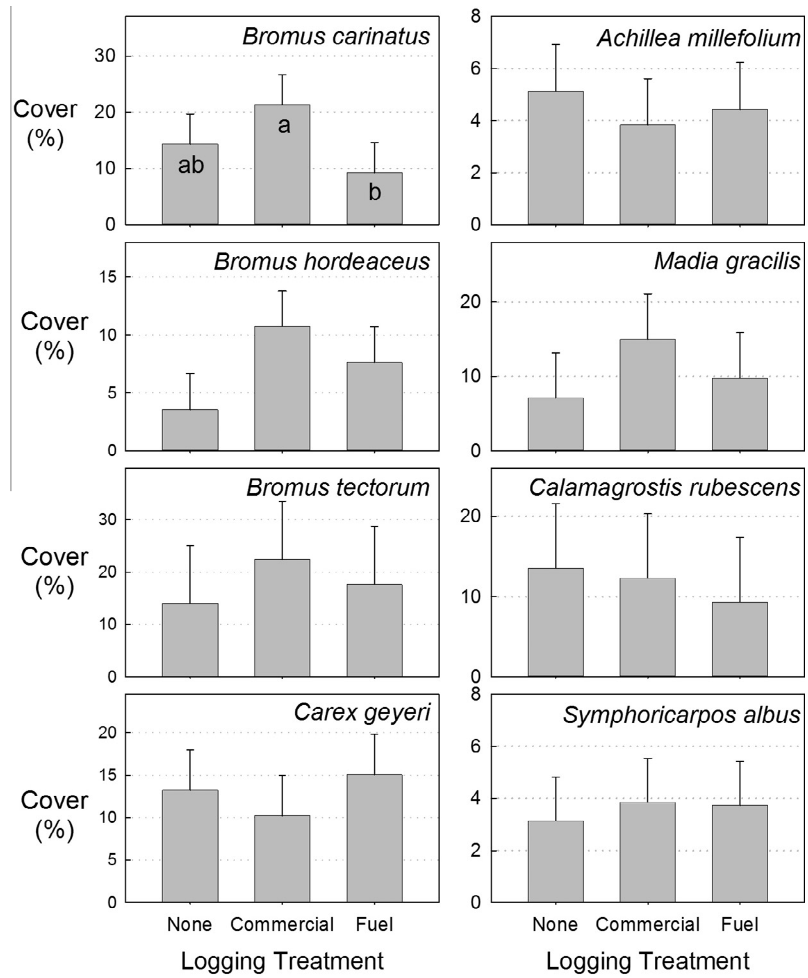

Fig. 4. Post-fire logging treatment effects on mean cover of common understory species. Bars display least-square means and standard errors for each species in each treatment. For species with a significant treatment effect, lower case letters (a and b) show results of pairwise tests for significant differences; bars (means) with the same letter are not significantly different.

like soil erosion. Post-fire logging is a form of disturbance, but the plant attributes that enable plant species to persist through wildfires (e.g., sprouting), or recolonize sites after wildfires (e.g., long-distance dispersal or persistence in the soil seed bank), appear to also convey resilience to post-fire logging. Best management practices that limit damage to soils, like logging over snow or frozen ground, may also limit damage to vegetation and encourage rapid recovery following logging disturbance.

Further research is needed to assess the consistency of these results across a range of forest types, and to examine longer-term impacts of post-fire logging on wildlife communities, soil properties, and ecosystem processes. Some of this work could be accomplished by resampling sites previously used to assess short-term impacts of post-fire logging. A more time-consuming, but more informative, approach would be to actively incorporate management studies with untreated control areas and long-term monitoring into new post-fire logging projects. Such studies can add expenses to projects, but the information generated could help reduce future post-fire management conflicts by providing better scientific information on which to base decisions about when and where to conduct post-fire logging. If further research confirms our findings, post-fire logging debates will be able to focus more on how to mitigate short-term disturbance impacts and manage fire-killed trees to meet wildlife habitat, fuel reduction, and economic recovery objectives, and less on concerns over long-term ecosystem degradation.

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