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Short-term understory plant community responses to salvage logging in beetle-affected lodgepole pine forests☆

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ABSTRACT

Recent bark beetle outbreaks in western North American subalpine forests have prompted managers to salvage log some beetle-affected stands. We examined the short-term (i.e., two to three years post-treatment) consequences of such salvage logging on vascular understory plant (i.e., graminoid, forb, and shrub) communities. At 24 lodgepole pine (*Pinus contorta*) sites in Colorado, USA, that had been attacked by mountain pine beetles (*Dendroctonus ponderosae*), we evaluated how logging operations impacted understory plant species richness, cover, and composition by comparing paired unlogged and logged stands. At half of the sites, we also evaluated how logging-related slash management and site preparation activities impacted understory plant cover by comparing experimentally-implemented treatments. Average total species richness increased 18% following logging due to an increase in graminoids and forbs, while average total cover decreased 33% due to a decrease in shrubs. Experimental treatments showed that, within logged stands, average total and shrub cover were greatest where slash was retained on-site and lowest where slash was taken off-site and the soil was scarified. Average exotic species richness more than doubled after logging but values were low even in logged stands, while average exotic cover was unaffected by logging. Taken together, our results suggest that salvage logging following beetle outbreaks altered understory plant communities in the short-term by making them richer, sparser, more graminoid- and forb-dominated, less shrub-dominated, and somewhat more invaded by exotics. Our results also suggest that slash management and site preparation activities can impact the magnitude of some of the understory plant community changes brought about by logging.

1. Introduction

Recent bark beetle outbreaks have disturbed millions of hectares of subalpine forest across western North America (Raffa et al., 2008; Meddens et al., 2012). Much of the damage in these forests is attributable to mountain pine beetle (*Dendroctonus ponderosae*), which attacks lodgepole pine (*Pinus contorta*) and other pines, and spruce beetle (*Dendroctonus rufipennis*), which attacks Engelmann spruce (*Picea engelmannii*) and other spruces (Raffa et al., 2008; Meddens et al., 2012). The recent outbreaks have caused as much as 70% overstory tree mortality in some stands, with larger host trees preferentially killed (DeRose and Long, 2012; Kayes and Tinker, 2012; Hawkins et al., 2012; Derderian et al., 2016; Rhoades et al., 2016). Moreover, salvage logging operations have further disturbed a fair proportion of beetle-affected stands (Patriquin et al., 2007; Lewis 2009; Collins et al., 2010). Salvage logging removes dead and dying trees following disturbance to capture their economic value and to mitigate concerns about insufficient tree regeneration, elevated wildfire hazard, and threats to human safety. In light of the broader ongoing debate surrounding salvage logging (Lindenmayer and Noss, 2006; Stokstad, 2006; Lindenmayer et al., 2017), it is critical that the ecological consequences of post-outbreak logging be thoroughly understood.

A key uncertainty surrounding salvage logging is whether logging in stands that have already experienced a recent disturbance will affect ecological properties and processes differently than conventional logging in undisturbed stands (Lindenmayer and Noss, 2006). Yet while numerous studies have examined the impacts of conventional logging in western subalpine and other higher-elevation and higher-latitude

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forests (e.g., Troendle and King, 1985; Harvey and Bergeron, 1989; Jurgensen et al., 1992; Niemelä et al., 1993; Kreyling et al., 2008), fewer have examined the impacts of logging in the wake of bark beetle outbreaks (e.g., Cheng 1989; Collins et al., 2010, 2011, 2012; Griffin et al., 2013; Hood et al., 2017). Furthermore, while the impacts of post-fire logging have also been well-studied (e.g., Purdon et al., 2004; Donato et al., 2006; Kurulok and Macdonald, 2007; Peterson et al., 2009; Silins et al., 2009), these studies provide limited insight into the impacts of post-outbreak logging because the conditions that precede post-fire and post-outbreak logging are usually quite different. For example, prior to salvage logging, fire-affected stands are typically characterized by complete or nearly complete overstory tree mortality and understory plant, litter, and duff consumption (Peterson et al., 2009), whereas beetle-affected stands are typically characterized by a lesser degree of overstory tree mortality and intact understory plant, litter, and duff layers (Collins et al., 2011, 2012; Griffin et al., 2013). Additional research on the impacts of post-outbreak logging is needed so that managers can make informed decisions about how best to steward the vast expanse of beetle-affected western subalpine forest.

Vascular understory plant (i.e., graminoid, forb, and shrub) communities are integral components of western subalpine forests, as they contribute most of the plant diversity, support wildlife, and influence ecosystem processes such as nutrient cycling and tree regeneration (Peet, 1978, 1981; Deschamp et al., 1979; Fahey et al., 1985; Kreyling et al., 2008). In the absence of salvage logging, beetle-caused overstory tree mortality can increase the amount of light, water, and nutrients available to understory plants (Clow et al., 2011; Hubbard et al., 2013; Rhoades et al., 2016), in turn releasing the pre-existing understory plant community and increasing its overall cover (Stone and Wolfe, 1996; McMillin et al., 2003; Pec et al., 2015). New species can also establish following beetle outbreaks, especially those preferring open forest conditions such as graminoids, although establishment opportunities can be limited because beetle outbreaks do not expose mineral soil (Stone and Wolfe, 1996; Edwards et al., 2015; Pec et al., 2015). Salvage logging may further influence understory plant communities in a variety of ways. As with any mechanical forest treatment, it may immediately reduce understory plant richness and cover by physically uprooting or crushing plants (Roberts and Zhu, 2002). Compared to the more subtle increase in light due to beetle-induced overstory tree mortality, the dramatic increase in light due to overstory tree removal may also damage late-seral species requiring relatively closed forest conditions (Rumbaitis del Rio, 2006; Macdonald and Fenniak, 2007; Liu and Bao, 2014). Yet with few or no overstory trees in logged stands to compete with the understory plant community, its richness and cover may ultimately be stimulated, particularly for early-seral, open-forest species (Roberts and Zhu, 2002; Craig and Macdonald, 2009). Mineral soil exposure due to logging may also contribute to increases in richness and cover by facilitating establishment (Roberts and Zhu, 2002). Decisions about how to manage logging slash, and about whether to conduct site preparation activities such as soil scarification, may have further implications for understory plant communities in logged stands (Olsson and Staaf, 1995; Karlsson et al., 2002; Roberts and Zhu, 2002; Åström et al., 2005; Goodman and Hungate, 2006).

In this study, we examined the short-term (i.e., two to three years post-treatment) response of understory plant communities to salvage logging in Colorado, USA, lodgepole pine forests attacked by mountain pine beetles. We accomplished this using two complementary approaches. First, we examined how salvage logging operations impacted understory plant species richness, cover, and composition by comparing paired unlogged and logged stands. Second, we investigated how experimentally-implemented slash management and site preparation alternatives for logged stands – retaining slash on the site, removing slash from the site, and removing slash from the site followed by mechanically scarifying the soil – further impacted the cover of understory plants.

2. Methods

2.1. Study areas and study sites

Our work was conducted at four large-scale (~1000 ha) study areas in subalpine forests of north-central Colorado. These study areas were established in support of a broad effort investigating the ecological impacts of a recent mountain pine beetle outbreak and post-outbreak management (Collins et al., 2011, 2012; Pelz et al., 2015). The Fraser Experimental Forest study area (39.92° N, 105.87° W) is located on the Arapaho National Forest, the State Forest study area (40.58° N, 105.99° W) is located on the State Forest State Park, and the Gore Pass study area (40.03° N, 106.61° W) and the Willow Creek Pass study area (40.39° N, 106.14° W) are located on the Routt National Forest. Prior to the mountain pine beetle outbreak, forest overstories at the study areas were mature and dominated by lodgepole pine (Collins et al., 2011, 2012; Pelz et al., 2015). Engelmann spruce, subalpine fir (*Abies lasiocarpa*), and aspen (*Populus tremuloides*) were also often present (Collins et al., 2011, 2012; Pelz et al., 2015). Pre-outbreak understories were likely relatively sparse and depauperate, akin to those described for other nearby study areas (Peet, 1981; Huckaby and Moir, 1998; Selmants and Knight, 2003); closed-forest species such as blueberry (*Vaccinium* spp.) and heartleaf arnica (*Arnica cordifolia*) were likely dominant. Average elevations of the study areas range from ~2750 to ~2850 m. The climate at the study areas is continental, with average annual precipitation ranging from ~550 to ~700 mm and mean annual temperature ranging from ~1.9 to ~2.6 °C (PRISM, 2016).

Widespread mortality of lodgepole pine trees due to mountain pine beetles began at the study areas between 1998 and 2002, with around 70% of the overstory basal area ultimately killed on average (Collins et al., 2011, 2012; Pelz et al., 2015). Salvage logging operations occurred in select beetle-affected stands at the Fraser Experimental Forest study area in the winter of 2007–2008, and at the State Forest, Gore Pass and Willow Creek Pass study areas in the winter of 2008–2009. Beetle-killed trees were generally in the “gray stage” at the time of logging, meaning that they had generally shed their needles. Logging operations were conducted by clearcut whole tree harvesting using tracked feller bunchers and rubber-tired skidders, with trees transported to landings over snow to minimize ground disturbance. Slash was piled at the landings. Site preparation activities like mechanical soil scarification were not conducted following logging.

Six study sites were established at each of the four study areas, yielding a total of 24 sites (Fig. 1). Each site consisted of a single pair of unlogged and salvage logged stands. Unlogged and logged stand pairs were carefully selected to be comparable in elevation, slope, aspect, and pre-logging overstory composition; see Collins et al. (2012) for additional information on stand selection procedures and the comparability of unlogged and logged stands. Logged stands ranged from 5 to 30 ha in area and were located 400 m or less from their unlogged counterparts. Unfortunately, the expansiveness of the mountain pine beetle outbreak precluded us from also locating comparable control stands (i.e., unattacked and unlogged stands) at the study sites.

2.2. Data collection and analysis

2.2.1. Salvage logging

We examined the effects of salvage logging operations by collecting observational data at all 24 study sites. Data were collected during the summers of 2010 and 2011, about ten years after the onset of the beetle outbreak and two to three years after logging. Data collection at each site occurred in eight 50-m^2 circular plots (4.0 m radius), with four plots in the unlogged stand and four plots in the logged stand (Fig. 2). Plot centers were situated at the ends of permanently-marked 100-m long transects (Collins et al., 2011, 2012; Pelz et al., 2015), the locations (latitude, longitude, and elevation) of which were captured using a hand-held Global Positioning System receiver.

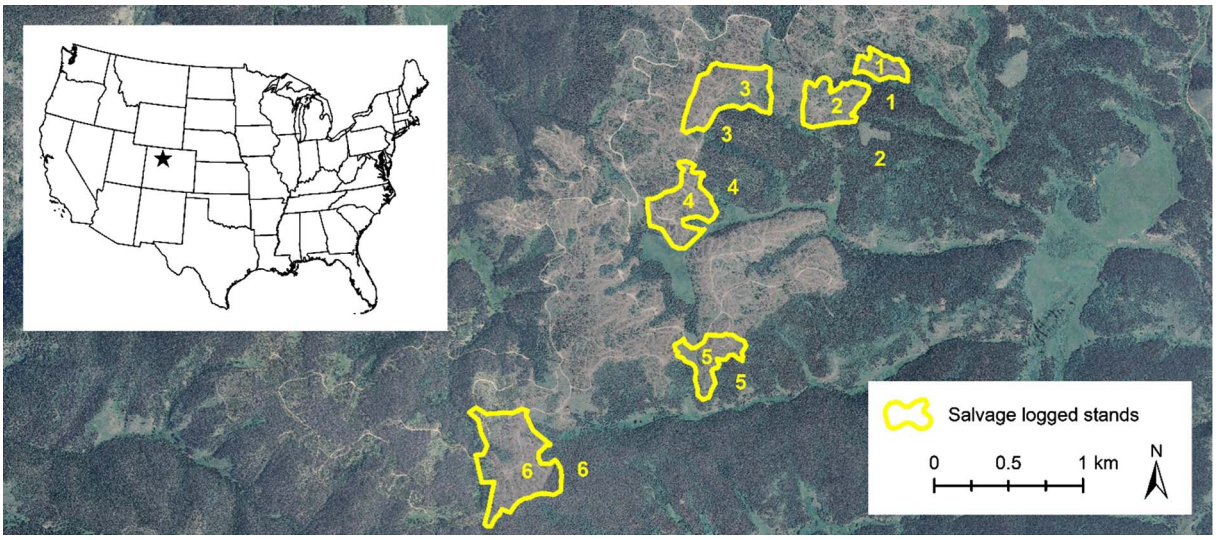

Fig. 1. Aerial photograph of the mountain pine beetle-impacted study area at Gore Pass (40.03° N, 106.61° W), illustrating the location of the study area's six unlogged and salvage logged stand pairs (i.e., study sites). Gore Pass is one of the four large-scale (~1000 ha) study areas established in north-central Colorado, USA.

We characterized overstory conditions in each plot by measuring diameter at breast height (DBH; breast height = 1.4 m), species, and live or dead status for all trees over breast height tall. We also measured overstory canopy cover at breast height using a convex spherical densiometer, with measurements taken at plot center in each of the four cardinal directions and averaged.

We measured the cover of vascular understory plants in each plot, as well as of ground cover components such as mineral soil, moss, lichen, litter, duff, fine wood (< 7.6 cm diameter), and coarse wood (> 7.6 cm diameter), using four 1-m^2 (1 m × 1 m) quadrats. The quadrats were placed 2 m from plot center in the cardinal directions. We used the point intercept method to make observations at 100 regularly-spaced points per quadrat. We recorded all understory plant species (varieties and subspecies were not distinguished) and ground cover components observed at the 100 points, and we tallied observations for each species and ground cover component to determine its percent cover in the quadrat. We then calculated a plot-level cover value for each species and ground cover component as the average of the quadrat values. Additionally, we recorded the presence of all understory plant species in the entire 50-m^2 plot. If the identity of a plant was unknown, a specimen was collected for later identification. Most unknown plants were ultimately identified to species; however, in some instances they were only identified to genus (or in a very few instances, they were only identified to family or were not identified at all) because key morphological characteristics were not sufficiently developed. Pussytoes (*Antennaria* spp.), sedge (*Carex* spp.), rose (*Rosa* spp.), and blueberry were by far the most apt to be identified only to genus, and so for consistency across plots, we analyzed them at this level. Hereafter they are also referred to as species. We determined the growth form (i.e., graminoid, forb, or shrub) and nativity (i.e., native or exotic to the continental United States) of all species using The PLANTS Database, local botanical keys, and our personal knowledge (Weber and Wittman, 2012; Ackerfield, 2015; USDA NRCS, 2016). Nomenclature follows The PLANTS Database (USDA NRCS, 2016).

We compared unlogged and salvage logged stands for a variety of overstory, ground cover, and understory plant attributes using generalized linear mixed models (GLMM) in SAS 9.4 (SAS Institute Inc., Cary, North Carolina, USA). Overstory attributes were live density, dead density, live basal area, dead basal area, and canopy cover, while ground cover attributes were the cover of mineral soil, moss and lichens, litter and duff, fine wood, and coarse wood. Understory plant attributes were total species richness (species 50 m^{-2}) and total cover, as well as species richness and cover within functional groups defined by growth form and nativity. We modeled each attribute against the fixed effect treatment (i.e., unlogged or logged) using the appropriate distribution and link function (e.g., a negative binomial distribution with a logarithmic link function for richness attributes). We identified the stand as the experimental unit, treating the multiple plots per stand

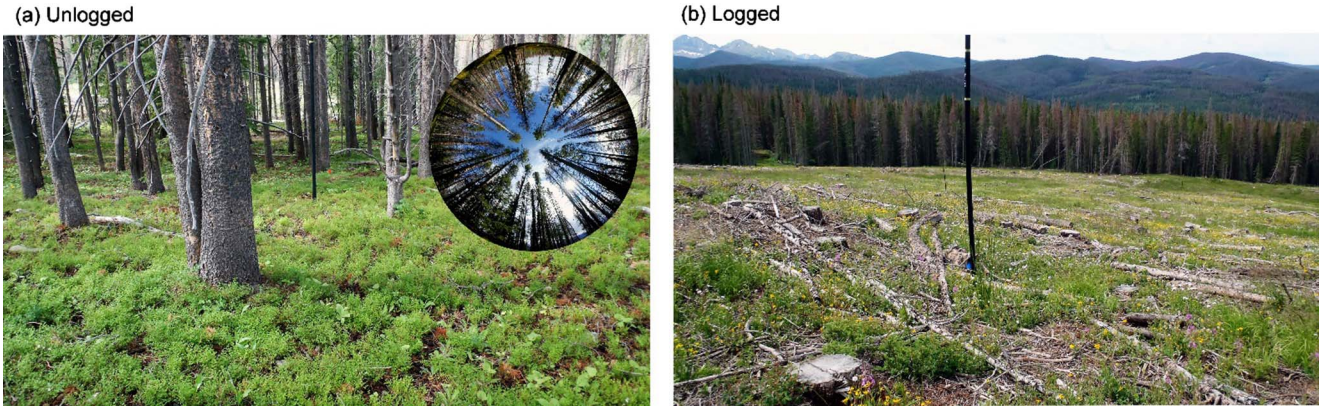

Fig. 2. Photographs of a representative (a) unlogged and (b) salvage logged plot in paired beetle-affected lodgepole pine stands at the State Forest study area (40.58° N, 105.99° W). The inset in (a) is a hemispherical photograph depicting the condition of the overstory canopy.

as subsamples by including the random effect treatment (nested within study site nested within study area). We accounted for the pairing of unlogged and logged stands at the study sites by including the random effect study site (nested within study area). We assessed statistical significance in these and all other analyses at $\alpha = 0.050$.

We used non-metric multi-dimensional scaling (NMS) ordination and permutational multivariate analysis of variance (PERMANOVA) procedures in PC-ORD 6.17 (MjM Software Design, Gleneden Beach, Oregon, USA) to investigate whether unlogged and salvage logged stands differed in overall understory plant community composition. These analyses were conducted following the recommendations of McCune and Grace (2002). We used stand-level species cover data, which we calculated by averaging plot-level values; species present in a plot but not in the plot's quadrats were assigned a nominal cover of 0.1% for these calculations. Species occurring in < 5% of the stands were subsequently omitted to reduce noise in the dataset. To conduct the NMS ordination, we first assessed the dimensionality of the dataset by running 250 ordinations with real data and 250 ordinations with randomized data using a step-down in dimensionality procedure and a random starting configuration. Each run used the Sørensen distance measure, a maximum of 500 iterations, and a stability criterion of 0.00001. The optimal preliminary configuration was identified as the one that had a significant p-value and that minimized the number of dimensions in the solution while also minimizing stress (a measure of "badness of fit"). Then, we conducted a final ordination run with the optimal preliminary configuration used as the starting configuration. Last, we rigidly rotated the final configuration to align treatment with axis one, and we calculated the Pearson's R^2 correlation between ordination axes and treatment, location attributes (latitude, longitude, and elevation), overstory attributes (live density, dead density, live basal area, dead basal area, and canopy cover), and ground cover attributes (cover of mineral soil, moss and lichens, litter and duff, fine wood, and coarse wood). An axis was correlated with an attribute if $R^2 > 0.200$. We conducted our PERMANOVA by designating treatment as the grouping factor and study site as the blocking factor.

We performed an indicator species analysis (ISA) in PC-ORD to identify understory plant species that were indicative of unlogged and salvage logged stands. Our ISA utilized stand-level species cover data, as described above. Treatment was designated as the grouping factor and study site was designated as the blocking factor. We considered a species to be an indicator of a treatment if it had a significant p-value and an indicator value ≥ 25 (Bakker, 2008).

2.2.2. Salvage logging-related slash management and site preparation activities

We examined the effects of common logging-related slash management and site preparation activities by installing experimental treatments at 12 of the 24 study sites (three sites per study area). We installed three "action" alternatives in the logged stand at each site: whole tree harvest (WTH), with slash taken off-site; stem only harvest (SOH), with slash retained on-site; and whole tree harvest followed by mechanical soil scarification (SCA). Treatments were installed in the summer of 2009 in 900-m^2 (30-m × 30-m) plots, with each treatment replicated once per site. The plots were aligned in a row and were separated by a 10 m buffer. WTH treatments, the de facto treatment for our logged stands, aimed to minimize fire hazard by reducing woody surface fuels. SOH treatments were designed to increase snow retention and soil moisture by increasing surface roughness. They were implemented by manually returning slash to plots. The intention of SCA treatments was to enhance tree regeneration by exposing a mineral soil seedbed and removing competing understory plants. Scarification was done with bulldozers, which passed over plots twice (one pass in each of two perpendicular directions). We installed a 900-m^2 plot of a fourth treatment, an unlogged treatment (UNL), in the unlogged stand at each study site to represent the "no-action" alternative.

In each 900-m^2 plot, we measured the cover of understory plant species and ground cover components within four randomly-located 1-m^2 (1 m × 1 m) quadrats. Measurements were conducted in the summer of 2011, two years after the experimental treatments were installed, and utilized the methodology described above to obtain a plot-level cover value for each species and ground cover component.

We used GLMM in SAS to test for treatment effects on ground cover (cover of mineral soil, moss and lichens, litter and duff, fine wood, and coarse wood) and understory plant (total cover and cover within growth form and nativity functional groups) attributes. As described above, we modeled each attribute against the fixed effect treatment using the appropriate distribution and link function. Study site (nested within study area) and stand (nested within study site) were included in the models as random effects. The former random effect accounted for the pairing of unlogged and logged stands at the study sites, while the latter accounted for the location of the UNL treatment in the unlogged stands and the WTH, SOH, and SCA treatments in the logged stands. When model results for an attribute indicated an overall treatment effect, we conducted pairwise comparisons using least squares means with a Tukey adjustment. All pairwise comparisons were conducted, although our primary comparisons of interest were those between the WTH, SOH, and SCA treatments.

3. Results

3.1. Salvage logging

Post-outbreak salvage logging altered overstory structure, as evidenced by measurements conducted in logged and unlogged stands two to three years after logging occurred (Table 1). Logging reduced live density and live basal area 91 and 83%, respectively, such that density in logged stands averaged only 89 stems ha^{-1} and basal area averaged only 2 m^2 ha^{-1}. Dead density and dead basal area were reduced even more by logging, by 99 and 87%, respectively. Meanwhile, canopy cover declined 91%, from an average of 74% in unlogged stands to an average of 7% in logged stands.

Salvage logging also altered ground cover components (Table 1). Mineral soil cover increased following logging, from an average of 1% in unlogged stands to an average of 3% in logged stands, while the combined cover of litter and duff decreased, from an average of 83 to 64%. Fine wood cover and coarse wood cover both increased following logging, with the former increasing from an average of 10 to 36% and the latter increasing from an average of 3 to 7%.

The impacts of salvage logging on total understory plant species richness and cover, and on species richness and cover by growth form, were variable (Figs. 3 and 4). Logging increased total richness 18%; an average of 17 species were found per 50 m^2 in unlogged stands, while

Table 1
Overstory (trees > 1.4 m tall) and ground cover attributes at 24 sites of paired beetle-affected unlogged and salvage logged stands. Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. P-values in bold indicate that unlogged and logged stands were different ($\alpha = 0.050$) for that attribute.

Attribute	P-value	Unlogged	Logged
Overstory			
Live density (stems ha^{-1})	**0.001**	1006 (387, 2617)	89 (34, 236)
Dead density (stems ha^{-1})	< **0.001**	807 (238, 2741)	5 (1, 19)
Live basal area (m^2 ha^{-1})	< **0.001**	14.5 (11.5, 18.4)	2.5 (1.1, 5.6)
Dead basal area (m^2 ha^{-1})	< **0.001**	23.2 (19.7, 27.4)	3.0 (1.4, 6.6)
Canopy cover (%)	< **0.001**	73.7 (46.0, 118.1)	6.7 (4.1, 11.0)
Ground cover			
Mineral soil cover (%)	< **0.001**	0.6 (0.3, 1.0)	2.6 (1.6, 4.3)
Moss and lichen cover (%)	< **0.001**	1.1 (0.7, 1.8)	0.3 (0.1, 0.5)
Litter and duff cover (%)	< **0.001**	82.7 (78.3, 87.3)	63.8 (60.4, 67.5)
Fine wood cover (%)	< **0.001**	9.9 (8.8, 11.3)	35.5 (31.7, 39.8)
Coarse wood cover (%)	< **0.001**	2.7 (2.0, 3.6)	7.2 (5.4, 9.5)

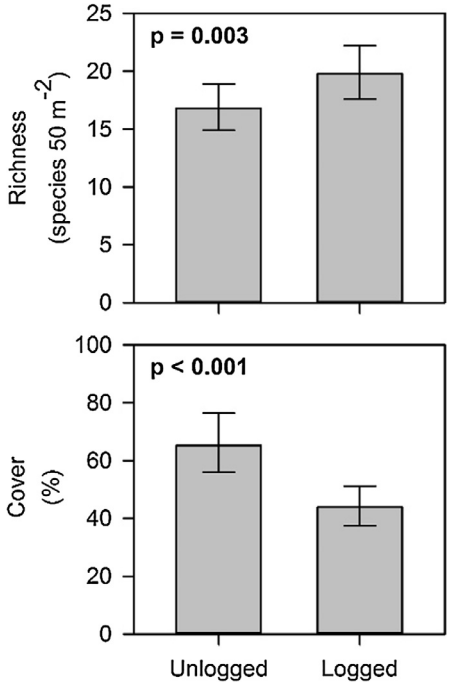

Fig. 3. Total understory plant species richness and cover at 24 sites of paired beetle-affected unlogged and salvage logged stands. Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. Bolded p-values indicate that unlogged and logged stands were different ($\alpha = 0.050$) for that attribute.

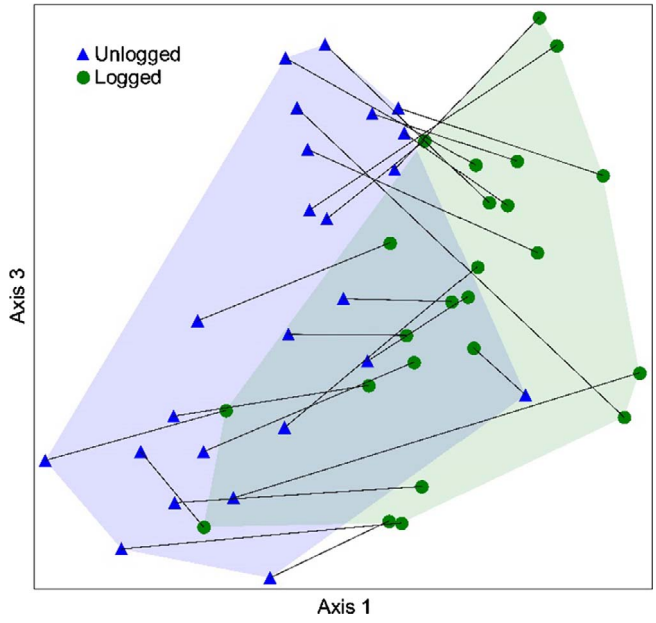

Fig. 5. Axis one versus three of a nonmetric multidimensional scaling ordination of understory plant community composition at 24 sites of paired beetle-affected unlogged and salvage logged stands. Unlogged stands are grouped by a shaded blue convex hull and logged stands are grouped by a shaded green convex hull, while unlogged and logged stand pairs are connected by vectors.

an average of 20 species were found in logged stands. The increase in total richness was driven by the response of graminoids and forbs, which increased 61 and 17% in richness following logging, respectively. Shrub richness was unaffected by logging. Meanwhile, logging decreased total cover by a third, from an average of 65% in unlogged stands to an average of 44% in logged stands. Shrub cover decreased nearly 60% following logging, from an average of 26 to 11%, and drove the reduction in total cover as forb cover was unaffected by logging and graminoid cover increased 63%.

Salvage logging increased exotic plant species richness but not exotic plant cover (Fig. 4). In unlogged stands we found an average of 1 exotic species 50 m^{-2}, while in logged stands we found an average of 2 species 50 m^{-2}. Exotic cover averaged 1% across all stands.

The NMS ordination procedure produced a three dimensional solution that explained 87% of the variation in the understory plant community composition dataset (stress = 11.487; Fig. 5). Axes one, two, and three accounted for 30, 19, and 38% of the variation, respectively. Unlogged and salvage logged stands appeared fairly

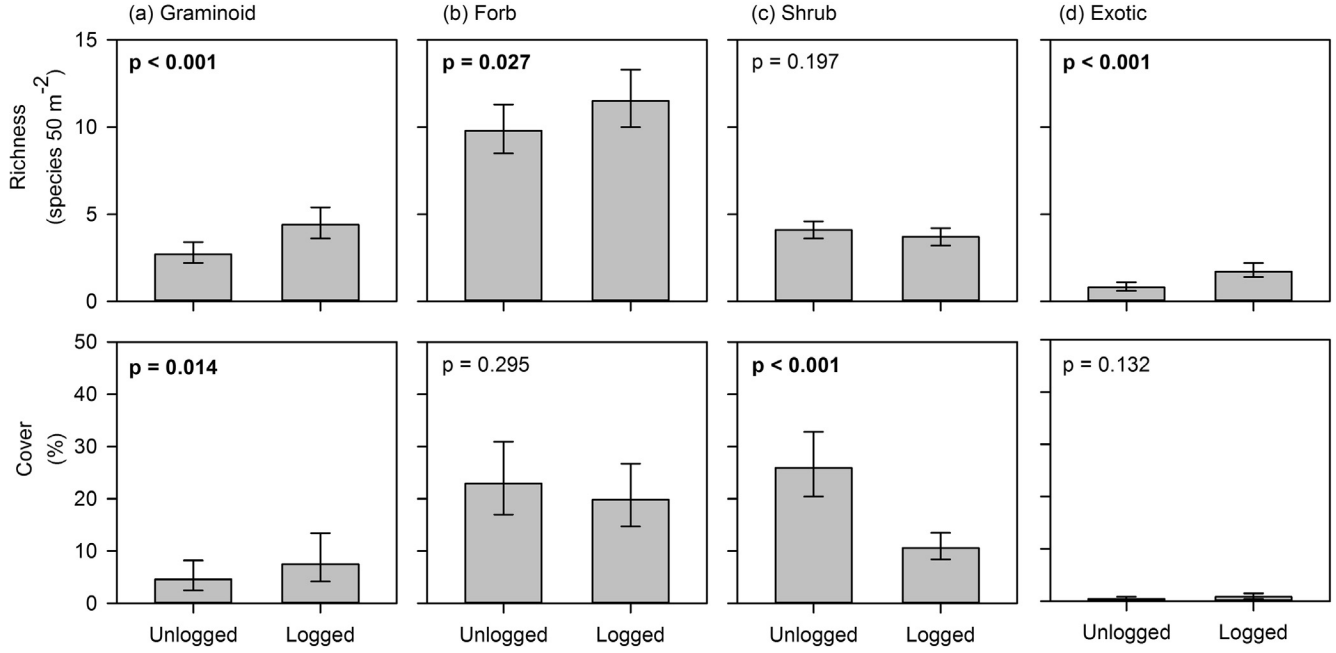

Fig. 4. Species richness and cover of (a) graminoids, (b) forbs, (c) shrubs, and (d) exotic plants at 24 sites of paired beetle-affected unlogged and salvage logged stands. Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. P-values in bold indicate that unlogged and logged stands were different ($\alpha = 0.050$) for that attribute.

Table 2
Pearson's R^2 correlations between treatment, location, overstory, and ground cover attributes and nonmetric multidimensional scaling ordination axes for understory plant community composition at 24 sites of paired beetle-affected unlogged and salvage logged stands. Bolded values indicate R^2 correlations > 0.200; the sign indicates the nature of the relationship.

Attribute	Axis 1	Axis 2	Axis 3
Treatment			
Unlogged (1) or logged (2)	**0.413 (+)**	0.000	0.000
Location			
Latitude (°)	0.061	0.140	0.002
Longitude (°)	0.027	0.173	0.141
Elevation (m)	0.125	0.102	**0.272 (−)**
Overstory			
Live density (stems ha^{-1})	**0.208 (−)**	0.096	0.065
Dead density (stems ha^{-1})	**0.354 (−)**	0.057	0.027
Live basal area (m^2 ha^{-1})	**0.266 (−)**	0.004	0.050
Dead basal area (m^2 ha^{-1})	**0.429 (−)**	0.001	0.004
Canopy cover (%)	**0.440 (−)**	0.017	0.10
Ground cover			
Mineral soil cover (%)	**0.214 (+)**	0.029	0.004
Moss and lichen cover (%)	0.111	0.000	0.106
Litter and duff cover (%)	**0.267 (−)**	0.126	0.016
Fine wood cover (%)	**0.383 (+)**	0.006	0.006
Coarse wood cover (%)	0.153	0.040	0.006

separated in ordination space along axis one, suggesting they differed in their overall composition. This visual assessment was corroborated by the PERMANOVA results comparing unlogged and logged stands ($p < 0.001$), and by the correlation between axis one and treatment (Table 2). Axis one was also correlated with several treatment-influenced overstory and ground cover attributes. Axis two was not correlated with any of the examined attributes, and axis three was correlated with elevation.

Of the 113 understory plant species examined via ISA, eight were identified as indicators of unlogged stands and seven were identified as indicators of salvage logged stands (Table 3). Species indicative of unlogged stands were all native forbs and shrubs. Among them was blueberry, which was found in nearly all study stands, but which had cover values that were considerably higher in stands that were unlogged (17%) than in those that were logged (6%). Indicators of unlogged stands also included sidebells wintergreen (*Orthilia secunda*) and greenflowered wintergreen (*Pyrola chlorantha*); while the average cover of these two species was very low (< 1%) for both unlogged and logged stands, they were nonetheless much more frequently encountered in the former (58 and 63% of stands, respectively) than the latter (21 and 25% of stands, respectively). Meanwhile, species indicative of logged stands were native graminoids and native and exotic forbs. They included rough bentgrass (*Agrostis scabra*), which averaged very low cover (< 1%) in both unlogged and logged stands, but was less common in those that were unlogged (4% of stands) than in those that were logged (29% of stands). Canada thistle (*Cirsium arvense*) and common dandelion (*Taraxacum officinale*) were also indicators of logged stands. Like rough bentgrass, these exotic forbs also averaged very low cover (1% or less) regardless of treatment, but they were documented less frequently in unlogged stands (21 and 83% of stands, respectively) than logged stands (75 and 100% of stands).

3.2. Salvage logging-related slash management and site preparation activities

Experimental slash management and site preparation treatments differentially influenced ground cover components (Table 4). Among the three action alternatives, mineral soil cover was greater for SCA treatments than for WTH and SOH treatments; mineral soil cover averaged 6% for the former treatment and 1% for the latter two treatments. The combined cover of litter and duff did not differ among the three action alternatives, averaging 48%. Fine wood cover was greater for SOH treatments than for WTH treatments, while coarse wood cover was greater for SOH treatments than for WTH and SCA treatments. Differences in coarse wood cover among the three action alternatives were especially dramatic, with values for SOH treatments averaging 25% and values for WTH and SCA treatments averaging 7 and 9%, respectively.

Slash management and site preparation treatments also influenced total understory plant cover and shrub cover, but not other understory plant cover attributes (Figs. 6 and 7). Among the three action alternatives, total cover was 44% greater for SOH treatments than for SCA treatments; it averaged 68% for the former and 47% for the latter. WTH treatments contained an intermediate amount of total cover, with

Table 3
Understory plant indicator species at 24 sites of paired beetle-affected unlogged and salvage logged stands. A species was an indicator if it had a significant p-value ($\alpha = 0.050$) and an indicator value ≥ 25.

Species	Cover (%)		% of stands		Indicator value		P-value
	Unlogged	Logged	Unlogged	Logged	Unlogged	Logged	
Unlogged							
Heartleaf arnica (*Arnica cordifolia*)	10.7	4.9	100	96	65	33	0.004
Autumn dwarf gentian (*Gentianella amarella*)	0.1	0.0	50	25	37	7	0.045
Common juniper (*Juniperus communis*)	3.3	0.6	96	83	63	29	0.049
Sidebells wintergreen (*Orthilia secunda*)	0.2	0.0	58	21	53	2	< 0.001
Oregon boxleaf (*Paxistima myrsinites*)	1.0	0.3	75	54	54	15	0.005
Greenflowered wintergreen (*Pyrola chlorantha*)	0.1	0.0	63	25	55	3	0.001
Russet buffaloberry (*Shepherdia canadensis*)	2.4	1.2	63	46	46	12	0.010
Blueberry (*Vaccinium* spp.)[a]	17.1	6.0	100	96	76	23	< 0.001
Logged							
Rough bentgrass (*Agrostis scabra*)	0.0	0.0	4	29	0	29	0.017
California brome (*Bromus carinatus*)	0.0	0.1	0	38	0	38	0.003
Sedge (*Carex* spp.)[b]	7.3	7.1	92	100	33	64	0.012
Fireweed (*Chamerion angustifolium*)	1.9	2.7	96	100	35	63	0.012
Canada thistle (*Cirsium arvense*)	0.0	0.2	21	75	3	65	< 0.001
Tiny trumpet (*Collomia linearis*)	0.0	0.1	8	33	0	32	0.008
Common dandelion (*Taraxacum officinale*)	0.5	0.7	83	100	30	64	0.017

[a] Primarily grouse whortleberry (*V. scoparium*), along with dwarf bilberry (*V. cespitosum*) and whortleberry (*V. myrtillus*).
[b] Primarily Geyer's sedge (*C. geyeri*) and Ross' sedge (*C. rossii*).

Table 4
Ground cover attributes in response to four experimental logging-related slash management and site preparation treatments in beetle-affected lodgepole pine stands. Treatments were replicated at 12 study sites and included: UNL = unlogged; WTH = whole tree harvest, with slash taken off-site; SOH = stem only harvest, with slash retained on-site; and SCA = whole tree harvest followed by soil scarification. Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. For attributes with a significant overall treatment effect (α = 0.050; p-values in bold), individual treatments that do not share letters are different based on Tukey-adjusted pairwise comparisons.

Attribute	P-value	UNL	WTH	SOH	SCA
Mineral soil cover (%)	< **0.001**	0.4 (0.1, 1.5) [a]	1.3 (0.5, 3.4) [a]	0.7 (0.2, 2.2) [a]	6.3 (2.7, 15.0) [b]
Moss and lichen cover (%)	0.053	0.6 (0.2, 1.7)	0.1 (0.0, 0.6)	0.2 (0.1, 0.9)	0.0 (0.0, 0.5)
Litter and duff cover (%)	< **0.001**	74.2 (65.2, 84.5) [a]	49.3 (42.9, 56.7) [b]	50.8 (44.0, 58.7) [b]	44.8 (38.9, 51.6) [b]
Fine wood cover (%)	< **0.001**	12.8 (9.7, 17.0) [a]	30.2 (23.5, 38.8) [b]	46.3 (36.0, 59.6) [c]	32.3 (25.2, 41.5) [bc]
Coarse wood cover (%)	< **0.001**	3.3 (1.9, 5.7) [a]	6.6 (4.0, 10.9) [ab]	25.3 (15.8, 40.5) [c]	8.9 (5.5, 14.4) [b]

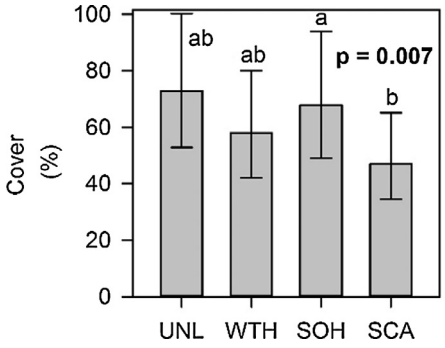

Fig. 6. Total understory plant cover in response to four experimental logging-related slash management and site preparation treatments in beetle-affected lodgepole pine stands. Treatments were replicated at 12 study sites and included: unlogged (UNL); whole tree harvest, with slash taken off-site (WTH); stem only harvest, with slash retained on-site (SOH); and whole tree harvest followed by soil scarification (SCA). Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. The bolded p-value indicates that treatment had a significant overall effect (α = 0.050). Individual treatments that do not share letters are different based on Tukey-adjusted pairwise comparisons.

values that were comparable to both SOH and SCA treatments. Similarly, shrub cover was 120% greater for SOH treatments than for SCA treatments, while shrub cover for WTH treatments was intermediate.

4. Discussion

4.1. Salvage logging and logging-related slash management and site preparation activities

Post-outbreak salvage logging operations modestly increased total understory plant species richness, from an average of 17 species 50 m^{-2} to an average of 20 species. Our ISA results suggest that this increase was due to the post-logging recruitment of new graminoid and forb species, coupled with the persistence of most pre-logging species. Conventional logging in undisturbed higher-latitude and higher-elevation forests has been shown to produce similar patterns (Haeussler et al., 2002; Roberts and Zhu, 2002; Pykälä, 2004). Species that recruited into logged stands tended to be those that prefer early-seral, open-forest environments (e.g., rough bentgrass), and thus were likely capitalizing on the dramatically elevated light and mineral soil levels brought about by logging operations. Meanwhile, persistence of pre-logging species may reflect the fact that subalpine forests in our study areas are adapted to stand-replacing wildfires (Schoennagel et al., 2004), and the traits that enable species to persist after such fires may also enable them to persist after disturbances such as logging (Stickney, 1986; Anderson and Romme, 1991; Romme et al., 2016). Persistence of pre-logging species may also reflect the fact that logging operations in our study areas occurred in the winter when the ground was covered by snow, which may have minimized physical damage from logging equipment (Wolf et al., 2008). It is important to note, however, that our ISA results also suggest that some pre-logging species were eliminated from some logged stands, at least at the scale of our sampling. These species tended to have low cover even in unlogged stands, and tended to require late-seral, closed-forest environments (e.g., sidebells wintergreen and greenflowered wintergreen).

In contrast to the modest increase in total understory plant species richness, total understory plant cover decreased substantially two to three years following salvage logging, from an average of 65% to an average of 44%. This decline was mostly attributable to a loss of shrub cover, particularly blueberry cover. As our ISA results show, blueberry was found in nearly all unlogged and logged stands but its cover

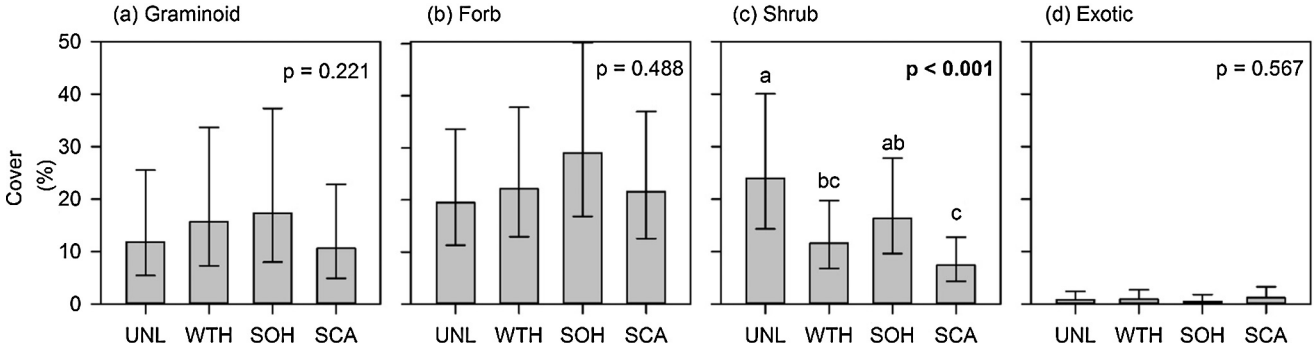

Fig. 7. Cover of (a) graminoids, (b) forbs, (c) shrubs, and (d) exotic plants in response to four experimental logging-related slash management and site preparation treatments in beetle-affected lodgepole pine stands. Treatments were replicated at 12 study sites and included: unlogged (UNL); whole tree harvest, with slash taken off-site (WTH); stem only harvest, with slash retained on-site (SOH); and whole tree harvest followed by soil scarification (SCA). Presented are estimated means (and lower and upper 95% confidence interval bounds) from generalized linear mixed model analyses. For attributes with a significant overall treatment effect (α = 0.050; p-values in bold), individual treatments that do not share letters are different based on Tukey-adjusted pairwise comparisons.

averaged 17% in the former and 6% in the latter. Blueberry is susceptible to both direct and indirect logging damage because it has a shallow root system and is intolerant of exposed growing conditions (Atlegrim and Sjoberg, 1996; Selmants and Knight, 2003; Palviainen et al., 2005). We suspect that exposure is driving the loss of blueberry cover that we documented, as snow presumably protected blueberry from being physically damaged during logging, and we we often observed dead but otherwise intact blueberry plants in our logged stands. Decreases in total cover due to decreases in closed-forest species like blueberry also occurred following conventional logging in western subalpine and other higher-elevation and higher-latitude forests (Roberts and Zhu, 2002; Macdonald and Fenniak, 2007; Liu and Bao, 2014), following post-windthrow and post-outbreak salvage logging (Rumbaitis del Rio, 2006; Griffin et al., 2013), as well as following stand-replacing wildfire (Turner et al., 1999). Understory plant cover losses in beetle-affected logged stands could have negative implications for wildlife and for on-site nutrient and water retention (Deschamp et al., 1979; Collins and Urness, 1983; Rhoades et al., 2016), yet positive implications for tree regeneration (Cortini and Comeau, 2008; Gärtner et al., 2011).

Our experimental treatments demonstrated that slash management and site preparation decisions can further affect total understory plant and shrub cover in salvage logged stands. Total and shrub cover for the three action alternatives were aligned on a gradient, with values greatest for SOH treatments where slash was retained on-site, intermediate for WTH treatments were slash was taken off-site, and lowest for SCA treatments where slash was taken off-site and the soil was scarified. Elevated total and shrub cover values in SOH treatments could be because the slash increased snow retention and soil moisture as intended (Matonis et al., 2014); it could also be because the slash provided closed-forest understory plants such as blueberry with protection from elevated light levels (Åström et al., 2005). Meanwhile, lowered total and shrub cover values for SCA treatments suggest that mechanical scarification was effective at removing understory plants as intended, although whether it was likewise successful at its ultimate goal of enhancing tree regeneration remains to be evaluated.

Exotic plants are generally uncommon in western subalpine forests, yet nonetheless they tend to capitalize on disturbance to some degree (Lindgren et al., 2006; Rumbaitis del Rio, 2006; Kreyling et al., 2008; Wright and Tinker, 2012; Fornwalt et al., 2017). Our results from unlogged and salvage logged stands support this generalization. We found that exotic richness more than doubled after logging but values were low even in logged stands (averaging 2 species $50\,m^{-2}$), and exotic cover did not likewise increase. Of the exotic species we encountered, the Colorado List B noxious weed Canada thistle warrants continued attention as it was particularly responsive to logging; this species was found in 21% of unlogged stands and in 75% of logged stands, albeit with generally negligible cover. It should be noted that our work was conducted only in the logged stands themselves, and not in and alongside the roads and landings that serviced the logged stands. As Buckley et al. (2003) have shown, roads and landings are apt to be more heavily invaded due to their extremely high degree of disturbance.

Salvage logging altered the overall composition of the understory plant community, as indicated by the NMS ordination, the PERMANOVA results comparing composition in unlogged and logged stands, and the correlation between NMS axis one and treatment. This compositional change undoubtedly reflects both the increase in total richness (driven by the recruitment of open-forest graminoids and forbs) and the decrease in total cover (driven by the reduction of closed-forest shrubs), as discussed above. Axis one was further correlated with several overstory and ground cover attributes. Correlations with axis one were particularly strong for the attribute overstory canopy cover ($R^2 = 0.440$), supporting the notion that logging-induced increases in light were probably a principal driver of the understory community changes we observed.

4.2. Conclusions and implications

Recent bark beetle outbreaks in western North American subalpine forests have prompted managers to salvage log some beetle-affected stands (Patriquin et al., 2007; Lewis, 2009; Collins et al., 2010). We found that logging operations in Colorado lodgepole pine forests following a mountain pine beetle outbreak altered understory plant communities in the short-term by making them richer, sparser, more graminoid- and forb-dominated, less shrub-dominated, and somewhat more invaded by exotics. We also found that experimental slash management and site preparation activities impacted the magnitude of some of these changes. Our findings add to a relatively small but growing body of literature on the ecological consequences of post-outbreak logging (e.g., Cheng, 1989; Collins et al., 2010, 2011, 2012; Griffin et al., 2013; Hood et al., 2017), and should be of interest to managers deciding how best to steward beetle-affected forests such as those we studied.

One of the key uncertainties surrounding salvage logging is whether its ecological consequences are similar to, or different from, those of conventional logging in undisturbed stands (Lindenmayer and Noss, 2006). Several studies conducted shortly following conventional logging in western subalpine and other higher-elevation or higher-latitude forests have produced findings consistent with ours (e.g., Haeussler et al., 2002; Roberts and Zhu, 2002; Pykälä, 2004; Palviainen et al., 2005; Macdonald and Fenniak, 2007), suggesting that conventional and post-outbreak logging might not be fundamentally different from an understory plant perspective. This could be because in many ways, the conditions preceding conventional and post-outbreak logging are themselves not fundamentally different. Some or even many overstory trees in a stand typically remain alive following beetle outbreaks, and those that were killed typically die and shed their needles over a period of several years (Klutsch et al., 2009; Kayes and Tinker, 2012; Hawkins et al., 2012). Furthermore, understory plants and litter and duff layers typically remain intact (Stone and Wolfe, 1996; Klutsch et al., 2009). The work of Collins et al. (2010) lends some support to our interpretation; they examined tree seedling recruitment following conventional and post-outbreak logging using 27 years of survey records from a Colorado subalpine watershed, and found that the two forms of logging did not differ in either the density or the composition of recruits.

Our findings provide only a short-term snapshot of the understory condition following bark beetle outbreaks and post-outbreak salvage logging, yet nonetheless they serve as a useful starting point for making predictions about future conditions. We predict that, in unlogged and logged beetle-affected stands such as those we studied, understory plant communities may remain distinct for many decades owing to continued differences in overstory structure (Collins et al., 2011, 2012). Graminoid and forb richness and graminoid cover in logged stands may remain elevated relative to unlogged stands (Selmants and Knight, 2003; Kreyling et al., 2008; Lang et al., 2009), while forb cover in logged stands may soon exceed that in unlogged stands (Selmants and Knight, 2003; Craig and Macdonald, 2009; Rhoades and Fornwalt, 2015). Shrub cover in logged stands may also increase with time, although it may not become comparable to unlogged stands for decades owing to the slow growth and the preferred environmental conditions of blueberry (Selmants and Knight, 2003; Rhoades and Fornwalt, 2015). Shrub recovery may be expedited in logged stands where slash was retained, and delayed in logged stands where slash was removed and the soil was subsequently scarified (Selmants and Knight, 2003). Exotic plants such as Canada thistle may remain, and possibly even expand, in logged stands relative to unlogged stands, although they may not become a major component of the understory community (Selmants and Knight, 2003; Kreyling et al., 2008; Rhoades and Fornwalt, 2015). We hope to conduct future measurements in our stands so that we can develop more informed predictions about how post-outbreak salvage logging will shape understory plant communities in the decades to come.

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