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Post-spruce beetle timber salvage drives short-term surface fuel increases and understory vegetation shifts

Lucas R. Mattson[a,*], Jonathan D. Coop[a], Mike A. Battaglia[b], Antony S. Cheng[c], Jason S. Sibold[d], Sara Viner[a]

[a] School of Environment and Sustainability, Western Colorado University, Gunnison, CO 81231, United States
[b] Rocky Mountain Research Station, US Forest Service, Fort Collins, CO 80526, United States
[c] Colorado Forest Restoration Institute and Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, United States
[d] Department of Anthropology, Colorado State University, Fort Collins, CO 80523, United States

A R T I C L E I N F O

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A B S T R A C T

Recent, widespread spruce beetle (*Dendroctonus rufipennis*) outbreaks have driven extensive tree mortality across western North America. Post-disturbance forest management often includes salvage logging to capture economic value of dead timber, reduce fire hazard, and meet other social or ecological objectives. Little is known about effects of salvage logging on surface fuel loads or plant understory communities in Engelmann spruce (*Picea engelmannii*)-dominated forests. We sampled fine and coarse woody debris, ground cover, and plant species composition along transects in spruce-beetle impacted stands in southwestern Colorado, USA. Twenty stands had been subject to clearcut 1–2 years prior to sampling; 32 stands were unlogged controls.

Salvage logged stands exhibited altered surface fuels, ground cover, plant species cover, and community composition. Salvage increased 1-, 10-, and 100-hr fuels, and cover by bare ground and woody debris; cover by litter and cryptogams was reduced. Understory plant cover was reduced in salvaged stands, primarily due to losses of shrub cover. We found no difference in species diversity or richness between treated stands and controls. Salvage logging also drove shifts in plant community composition. Mean cover by non-native species was low, and not different, between control and salvage stands.

Our study characterizes short-term effects that will undoubtedly change substantially over longer periods, in particular due to anticipated tree seedling growth and movement of standing dead wood from the canopy to the surface. In the near term, abundant fine woody surface fuels at salvage sites could influence the likelihood and rate of spread of surface fires, though over time we expect surface fuels in untreated stands to increase to comparable or greater levels than in salvaged stands. Differences in vascular plant cover and composition imparted by salvage harvests is also expected to change over time, though whether treated and untreated communities diverge or converge is not known. As such, we recommend that salvage harvest effects be monitored over extended time frames in order to detect longer-term trends.

1. Introduction

Bark beetles are a native disturbance agent that affects more forested area in North America than wildfire, with major consequences for biota, ecological dynamics, ecosystem services, and land management (Raffa et al. 2008). Recent bark beetle outbreaks are considered to be the largest and most severe in recorded history (Bentz et al. 2010, Raffa et al. 2008). In the last several decades > 5 million ha of coniferous forests in western North America have experienced mortality from bark beetles (Romme et al.,1986; Meddens et al. 2012), leading to increased focus by land managers, and the extensive adoption of proactive and reactive land management interventions (Fettig et al. 2007).

In the southern Rocky Mountains, the spruce beetle (*Dendroctonus rufipennis*) is endemic to high-elevation, spruce-fir forest types, and has been considered the most disruptive insect of the subalpine forest zone (Veblen et al. 1991). Spruce beetles can profoundly shape patterns of subalpine forest composition and stand structure (Kulakowski and Veblen 2006), primarily directly through episodic, severe mature tree mortality, but also via indirect interactions with other disturbances such as fire and wind (Kulakowski et al. 2003). Engelmann spruce (*Picea engelmannii*) dominates high-elevation spruce-fir forests in the

* Corresponding author.
E-mail address: lucas.mattson@western.edu (L.R. Mattson).

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Rockies, and is the preferred host species for the spruce beetle (Schmid and Frye 1977). Historically, the pattern of spruce beetle outbreaks in the southern Rockies was characterized by a mosaic of patches of overstory tree mortality that would provide opportunities for ecological succession by releasing available resources to tree seedlings and other vegetation in the understory (Veblen et al. 1991). However, recent assessments have documented > 85% overstory mortality in Engelmann spruce stands impacted by spruce beetle infestations (DeRose and Long 2007; Dymerski et al. 2001; Temperli et al. 2014; Werner et al. 2006). Over the last two decades, approximately 436,000 ha of forests in Colorado have been impacted by spruce beetle (Colorado State Forest Service 2017). Prior to the current outbreak, the last major recorded spruce beetle outbreak in this region occurred in the 1940′s (Veblen et al. 1991; Bebi et al. 2003).

The spatial extent and severity of recent outbreaks has prompted the widespread adoption of post-disturbance land management activities (Griffin et al., 2013; Windmuller-Campione et al. 2017). One post-beetle infestation management prescription is a clearcut salvage harvest. Salvage logging is a reactive management practice that is implemented following disturbance, primarily to capture any remaining economic value of standing dead trees, but also to promote a suite of ecological and/or social objectives (Lindenmayer and Noss 2006). For example, objectives for salvage logging may also include wildfire hazard mitigation and increased human safety. In this regard salvage logging is intended to reduce potential crown fire by removing canopy fuels and breaking up the horizontal and vertical continuity of the dead canopy (Collins et al. 2012). The removal of tree boles is also intended to increase wildland firefighter safety by removing snags that may fall during fire suppression operations. Furthermore, the removal of the tree boles limits future coarse fuel loadings that could result in high fireline intensity, increased resistance to control, facilitate spread of fire through spotting, and extreme soil heating in the event of a fire. However, salvage logging may also increase fine woody surface fuel loadings. For instance, in mountain pine beetle (*Dendroctonus ponderosae*)-impacted lodgepole pine stands, studies have shown that within the first several years post-salvage, woody surface fuels can increase two to three times relative to non-salvaged stands (Collins et al. 2012; Hood et al. 2017; Griffin et al., 2013; Rhoades et al. 2018). Given important differences between site types and ecology of these systems, it is not clear how well findings from mountain pine beetle outbreaks in lodgepole pine forests apply to ecological change in spruce forests following spruce beetle outbreaks. Beyond increasing short-term fuel hazard, there is also concern that salvage logging may exert greater influences on ecosystem processes than the initial disturbances, and may reduce important biological legacies, including shifts in plant community composition, alterations of stand structure and complexity, and even impaired natural vegetation recovery (Lindenmayer and Noss 2006; Lindenmayer et al. 2017).

Tree mortality followed by salvage logging in spruce beetle-impacted forests is expected to alter the understory abiotic environment, particularly through increased solar radiation (Temperli et al. 2014), which is likely to drive shifts in understory species composition, though this has been the subject of sparse research. Jonášová and Prach (2008) found an increase in graminoid species following a salvage harvest in European spruce beetle (*Ips typographus*)-affected forests when compared to non-salvaged stands, However, there were substantial decreases in bryophytes and changes in vegetation composition. In a subalpine forest that had been affected by recent windthrow, Rumbaitis del Rio (2006) found an increase in graminoids and a decrease in shrubs and forbs as well as a decrease in richness, diversity, and cover in salvage logged stands. In lodgepole pine stands impacted by mountain pine beetle, Fornwalt et al. (2018) reported altered vegetative composition and cover in salvaged stands compared to unlogged stands. Species richness increased by 18% in salvaged stands, primarily driven by increased forbs and graminoid richness, while overall understory plant cover decreased by 33%, largely due to a decrease in shrubs, most notably *Vaccinium* species (Fornwalt et al. 2018). Rhoades et al. (2018) found that salvage logging drove major decreases in forb and shrub cover in a mountain pine beetle-impacted lodgepole pine forest. However, results may differ in spruce beetle-affected forests where conditions are generally wetter and support more understory species than lodgepole pine forests.

The purpose of our research is to fill gaps in scientific knowledge about the ecological impacts of salvage logging, especially given the lack of such knowledge for spruce-dominated forests of the southern Rocky Mountains, USA, and the growing prominence of salvage operations by land managers in this forest type and region. The effects of salvage logging on fuels and understory plant communities is expected to be most pronounced in the first few years following treatment (Collins et al. 2012; Fornwalt et al. 2018). As such, ecological research on the effects of salvage logging is essential to establish a baseline of evidence upon which land managers can draw to mitigate potentially undesired ecological outcomes throughout salvage treatment planning, design, and implementation phases. In particular, we were interested in examining salvage harvest effects on surface fuel loads, ground cover, and understory plant community richness and composition. We also contrasted the occurrence of non-native, invasive plant species in treated and untreated stands. Specifically, we hypothesized that salvage logging would lead to (***1***) increased surface fuels relative to untreated control stands, and (***2***) altered understory plant communities with reduced plant cover and species diversity.

2. Methods

2.1. Study area

Study sites were located on the Grand Mesa, Uncompahgre, and Gunnison (GMUG) National Forests in the La Garita Mountains of southwestern Colorado, with Lake City (38.0300° N, 107.3153° W) approximately representing the western boundary, and San Luis Peak (37.9869° N, 106.9314° W) the eastern boundary (Fig. 1). The La Garita Mountains are part of the San Juan Volcanic Field, and were formed by massive eruptions 40–35 million years ago (Steven & Lipman 1976). The majority of sample plots were located along Colorado State Highway 149 near Slumgullion Pass (Fig. 1).

Elevations of studlots ranged from 3,050 to 3,500 m. Mean annual temperature in Lake City (2,640 m) is 4.3° C; mean annual precipitation is 37.5 cm (1981–2010 30-year means for all; Western Regional Climate Center, 2018; https://wrcc.dri.edu/). Weather conditions in 2017, when sampling was conducted, were warmer and drier than average; mean annual temperature was 6.5 °C, and total precipitation was 27.0 cm (Lake City Heights Weather; Personal Weather Station: KCO-LAKEC3 by Wunderground.com).

At the time of the beetle outbreak, subalpine forests across the study area were composed of closed-canopy, multi-aged stands with many trees ranging from 150 to 300 + years, with Engelmann spruce dominant in both the overstory and understory. Subalpine fir (*Abies lasiocarpa*), and mature quaking aspen (*Populus tremuloides*) were also minor components of these forests across the study area. The current spruce beetle outbreak was first noted on the GMUG in 2009, though it originated in the Rio Grande National Forest to the south several years earlier. Within six years of initial detection of beetle infestation, GMUG staff reported mortality of ca. 99% of all Engelmann spruce over 12.7 cm diameter at breast height (DBH; 1.37 m), and 83% of trees between 2.54 and 12.7 cm DBH (Arthur Haines, USFS, personal communication) within our study area. The salvage harvest prescription being implemented in this area called for removing all dead trees > 20 cm DBH, except for areas along highway 149, where all standing trees were removed for safety. Harvests were conducted during summer, fall, and winter seasons, and slash was piled and burned (Arthur Haines, USFS, personal communication).

Sampling locations were selected prior to salvage harvests using a

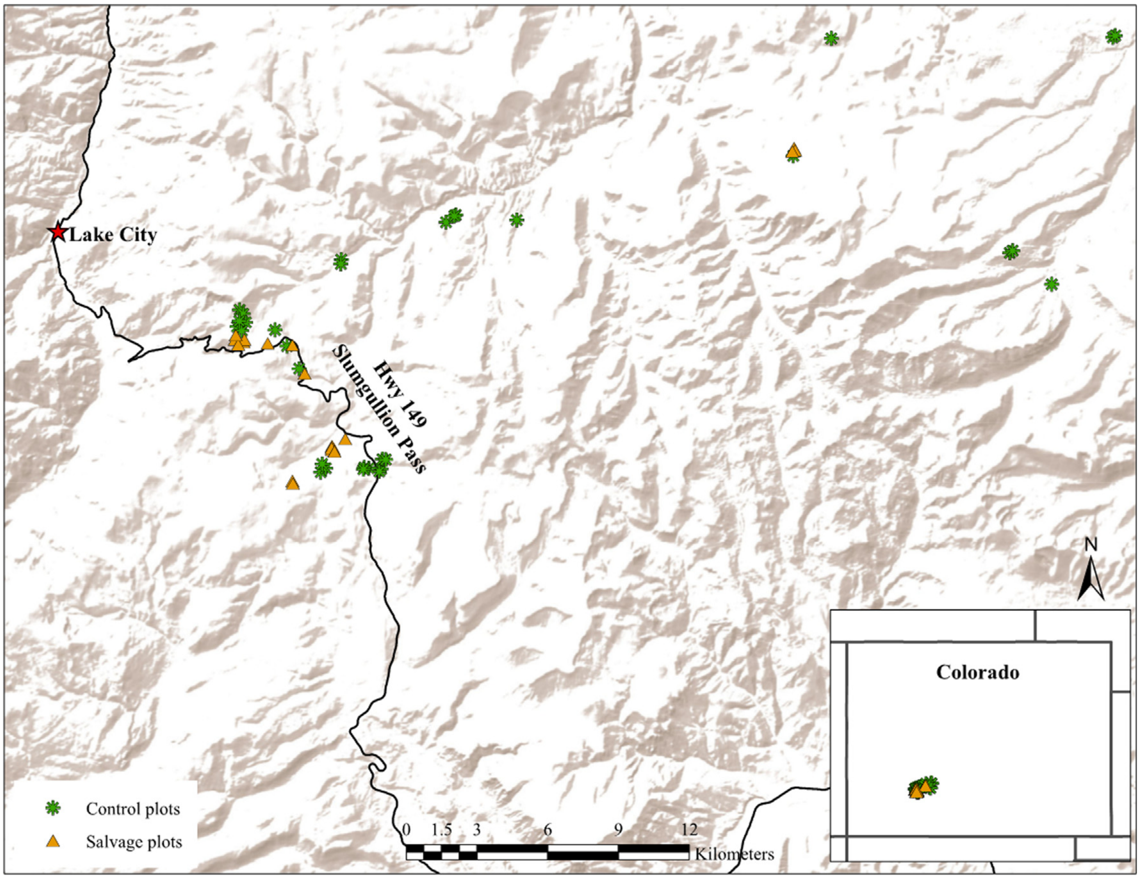

Fig. 1. Locations of sample plots; control and salvage units in the La Garita Mountains of southwest Colorado, USA.

GIS vegetation layer provided by the GMUG National Forests. The vegetation layer was used to identify areas that were either spruce dominant forest type or spruce-aspen mixed forest type. A management history GIS layer displaying currently planned salvage harvests, areas that had historically received a shelterwood prep cut (1980′s – 1990′s), and areas that had no recorded historical treatment or planned salvage were overlaid with the vegetation layer. Points were randomly generated within these polygons; 112 of these were located in the field and permanently marked for sampling to address a suite of salvage harvest-related ecological research questions. Of these, we sampled a total of 52 sites including 20 treatment plots that have been salvage logged, and 32 control plots that were not subject to recent management activities (Fig. 1). Of the treatment plots, 18 plots were classified as spruce dominant, one plot was classified as spruce/aspen mix, and one plot was classified as spruce/aspen/fir mix. Of the control plots 23 were classified as spruce dominant, seven were classified as spruce/aspen mix, and two were classified as spruce/fir/aspen mix. We note, however, that these classifications may mask considerable variation in the relative abundance of fir and aspen across all forest types (e.g., aspen and fir may have occurred up to 25% in stands classified as spruce dominant). Accordingly, to account for this variation, we included cover by aspen and fir as covariates in a series of statistical models, described below. All salvage harvests were completed 1–2 years prior to our sampling, between 2015 and 2016.

2.2. Field sampling methods

Understory fuels, ground cover, and vegetation were sampled during the growing season of 2017 between the months of May and September (Fig. 2). At each plot center we recorded slope, aspect, elevation and spatial location (UTM; NAD 83). Coordinates and elevation were recorded using an iPhone 7 with GAIA GPS software with a horizontal accuracy of ± 10 m (GAIA GPS, 2018). Prior to analysis, plot aspect was transformed using methods of Trimble and Weitzman (Beers et al. 1966) using the formula: sin (A + 45°) + 1, where A is equal to the azimuth of the prevailing slope.

Prior to salvage harvest (in 2015), data on forest overstories were collected within 0.05-ha, fixed-radius (12.62-m) plots. Within each sample plot, all trees were identified to species, DBH (diameter at breast height) was measured, and trees were assigned a mortality class code: (1) live-no hit (no sign of beetle damage), (2) imminent mortality (beetle damage evident), (3) dead (gray stage), (4) dead (no fine twigs, bark loose or gone), or (5) down, recent beetle kill (only downed spruce trees exhibiting clear evidence of mortality caused by recent bark beetles were recorded, no other downed species were recorded).

To gather data sufficient to test our hypotheses, we established three, 10.2-m transects from plot-center in each sample plot for measurements of fuels, ground cover, and understory vegetation, following the methods of Coop et al. (2017). The bearing of the first transect was random; the 2nd and 3rd transects were offset by 120° and 240°, respectively. We recorded the slope inclination of each transect and took a digital photo looking from the far end of each transect towards plot center. Surface fuel loads were classified by time-lag moisture classes using Brown's planar intersect method (Brown 1974). We recorded the occurrence of 1-hour fuels (twigs < 0.64 cm diameter) and 10-hour fuels (0.64–2.54 cm) along the last 2 m of each transect, 100-hour fuels (2.54–7.62 cm) along the last 5 m of each transect, and 1000-hour fuels (> 7.62 cm) along the entire length of each transect. Decay class was recorded for all 1000-hour fuels. We also recorded the depth of litter (needles and foliage, bark fragments, etc.) and duff at 2-m intervals along each transect. Vegetation was sampled using a point-line-intercept method at 0.3-m increments along each transect (for a total of 102

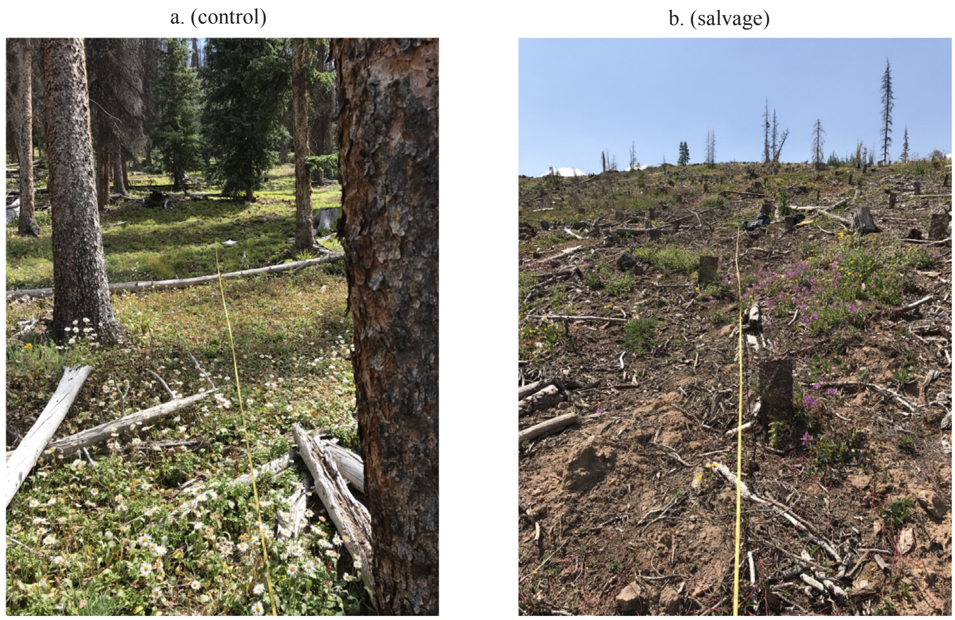

Fig. 2. Photographs of typical (a) control and (b) salvage plot in spruce beetle affected forest stands in our study area.

intercepts at each study plot); we recorded the species identity of all vascular plants < 1.37 m in height, ground cover type (litter, wood, bare soil, cryptogam, rock, or live plant), and the height of the highest live plant intercept point ("hit") on each transect. A complete list of all plant species encountered in samples is presented in Appendix A; nomenclature follows the USDA Plants Database (USDA, NRCS 2018).

2.3. Data analysis

We used equations from Brown (1974) to convert numbers of intersections of dead woody fuels to fuel mass at each site, using Brown's values for the spruce forest type. Values for slash were used at salvage sites, and non-slash for control sites. Sound or rotten values were used to calculate 1000-hour fuels. Measured depths of duff and litter were converted to mass using values from FIREMON database (Lutes et al. 2006), by multiplying the average depth by 44.05 $\mathrm{kg\,m^{-3}}$ and 88.10 $\mathrm{kg\,m^{-3}}$; these were then converted to $\mathrm{Mg\,ha^{-1}}$. Bulk density values for herbaceous and live woody (shrub) surface fuel volumes were similarly calculated from the vegetation point-line intercept transects (percent cover × height) and multiplied by 0.8 $\mathrm{kg\,m^{-3}}$ for herbs and 1.8 $\mathrm{kg\,m^{-3}}$ for shrubs (values from Lutes et al. 2006). Plant species coverages were calculated as the total number of "hits" along the three point-line-intercept transects at each plot, divided by the total number of sample points (1 0 2). We also calculated mean cover of each species within salvage and control units. Ground cover attributes, recorded at each vegetation sample intercept, were averaged across each sample plot. Understory plant species richness was calculated as the total number of species present in each plot; Shannon's diversity values were calculated using the diversity function in R package 'vegan' (Oksanen et al. 2016).

To test for effects of salvage logging on response variables of interest for ***hypothesis 1*** (fuel quantities and ground cover) and ***hypothesis 2*** (understory plant species cover, diversity and richness) we employed linear models. We developed two classes of models for each response variable as follows: model 1 tested for salvage treatment effects alone, while model 2 included salvage treatment, but also covariates representing pre-treatment differences in stand structure and history that might also influence surface fuels and vegetation. Covariates included historical logging (a binary variable indicating whether the stand had been subject to shelterwood prep cut between 1971 and 1990, summarized in Appendix B), elevation, and pre-treatment total (live + dead) basal area (BA) of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and quaking aspen (*Populus tremuloides*). Final response variables included in model 2 were chosen using a backward stepwise selection procedure to determine best-fitting model based on lowest Akaike information criterion (AIC) score. P-values were subsequently calculated for the final, best-fitting model. In nearly all cases, both classes of models identified similar magnitude of the effects of salvage harvest, described in the results below.

General patterns of plant community composition and their relationships to abiotic factors, including salvage timber harvest (***hypothesis 2***), were characterized by conducting a non-metric multidimensional scaling (NMS) using R package 'vegan' (Oksanen et al. 2016). The purpose of this analysis was to identify the strongest patterns in our plant species compositional data, and assess their relationships to environmental factors. In particular, we wished to assess how strongly salvage treatments were associated with shifts in understory plant species composition, relative to other sampled factors (e.g., elevation). We utilized Bray-Curtis (Sørensen) distance measure of absolute cover values of 86 plant species averaged across all three transects at each of the 52 sites (32 control, 20 salvage). We examined correlations between NMS axes, abiotic variables, and plant species coverages. We also tested for differences in plant community composition between control and salvage sites (hypothesis 2) using multiple response permutation procedures (MRPP). All analysis was conducted in R (R Core team 2017).

3. Results

3.1. Treatment effects to surface fuels and ground cover

We found strong influences of salvage logging on the quantity of some surface fuel classes (Fig. 3) and most ground cover types (Fig. 4) relative to untreated controls (Table 1).

Below, we report mean values ± 1 S.D., to characterize both net differences and also variability in untreated vs. salvaged stands from model 1 (salvage only). Relative to unlogged controls, salvage treatments showed roughly doubled 1-hr fuels (0.99 ± 1.00 vs. 1.97 ± 0.92 $\mathrm{Mg\,ha^{-1}}$ in controls vs. treatments; Table 1, Fig. 3a), and nearly tripled 10-hr fuels (2.37 ± 1.31 vs. 5.88 ± 2.73 $\mathrm{Mg\,ha^{-1}}$; Table 1, Fig. 3b). We also found greater quantities of 100-hr fuels in salvage units (2.94 ± 2.25 vs. 4.80 ± 2.49 $\mathrm{Mg\,ha^{-1}}$ in controls vs.

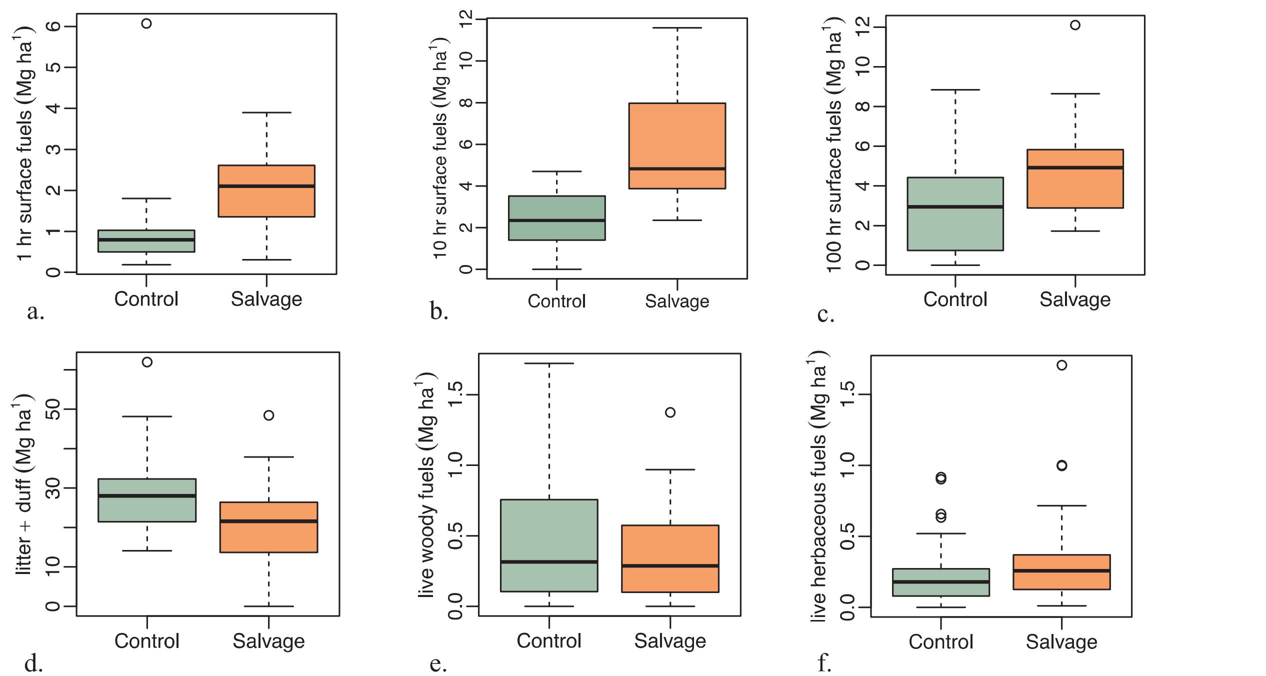

Fig. 3. Estimates of surface fuel parameters in control vs. salvage plots, including (a) 1-hr woody fuels, (b) 10-hr woody fuels, (c) 100-hr woody fuels, (d) litter + duff, (e) live woody (shrubby) fuels, and (f) live herbaceous fuels.

treatments; Table 1, Fig. 3c). 1000-hr fuels did not show a significant difference between control and salvage sites (26.96 ± 29.90 vs. 35.03 ± 27.96 Mg ha^{-1}; Table 1). Litter and duff surface fuels decreased in salvage plots (29.02 ± 10.91 vs. 21.96 ± 11.46 Mg ha^{-1}; Table 1, Fig. 3d). Live woody fuels were not significantly impacted by salvage treatments (0.48 ± 0.47 vs. 0.39 ± 0.36 Mg ha^{-1}; Table 1, Fig. 3e). We did not find significant differences in live herbaceous fuels between sample types (0.24 ± 0.24 vs. 0.38 ± 0.36 Mg ha^{-1}; Table 1, Fig. 3f).

Bare ground percent cover increased in salvage stands (2.94% ± 3.70 vs. 12.47% ± 12.47; Table 1, Fig. 4a). The percentage of woody ground cover also increased in salvage stands (19.38% ± 8.76 vs. 39.05% ± 12.64; Table 1, Fig. 4b). Cryptogam percent cover decreased in salvaged stands (10.94% ± 8.37 vs. 3.53% ± 5.18; Table 1). The percentage of litter as a ground cover was also reduced in salvage units (64.47% ± 11.97 vs. 43.15% ± 8.18; Table 1, Fig. 4c).

Models that included covariates (model 2, Table 1) also indicated moderate influences of elevation, stand history, and forest composition on some fuels measures. In most cases the salvage alone and covariant model led to similar interpretations; however, in some instances the two models showed different results. Notably, model 2 indicated that 1-hr fuels were more strongly positively associated with historical logging than by recent salvage harvests (Table 1).

3.2. Treatment effects on vegetation composition and structure

We found differences in plant cover, but not species diversity, between control plots and salvage plots. Understory vegetation cover was significantly greater in control plots than salvage plots (63.08% ± 33.85 vs. 33.27% ± 17.80, Table 1, Fig. 4a). Shannon's diversity showed no significant difference between control and salvage plots (1.83 ± 0.45 vs. 1.74 ± 0.44, Table 1, Fig. 4b); nor did species richness (10.31 ± 4.25 vs. 8.80 ± 3.35, Table 1, Fig. 4c). We found some difference in cover by functional groups between salvage and control plots. There was a significant decrease in cover of shrubs in salvage plots (17.86% ± 15.40 in controls vs. 7.05% ± 5.76 in salvaged stands; Table 1, Fig. 4d). However, we did not find a significant difference in forb (32.75% ± 28.17 vs. 21.45% ± 12.89; Table 1, Fig. 4e) nor graminoid cover (9.5% ± 11.25 vs. 5.9% ± 6.07; Table 1, Fig. 4f). Of the most abundant 15 vascular plant species in subalpine forest understories, 14 were more abundant in control plots (Table 2).

Linear models that included covariates suggested that plant cover was also influenced by environmental covariates. Forb cover was negatively related to salvage harvest but positively related to elevation (Table 1). Graminoid cover was positively influenced by historical logging, but negatively related to the pre-treatment basal area of subalpine fir (Table 1). Models that included environmental covariates indicated that total vascular plant cover and species richness may have

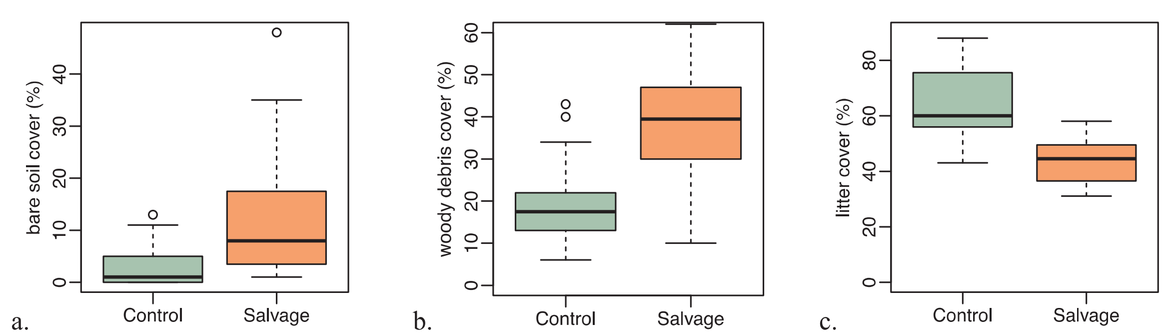

Fig. 4. Estimates of ground cover percentages in control vs. salvage plots, including percent cover of (a) bare ground, (b) woody debris, and (c) litter.

Table 1
Linear model results for fuels and vegetation variables collected at study plots. ***Model 1, salvage only*** is a linear model with treatment (salvage vs. control) as the only predictor. ***Model 2, salvage + covariates*** is the best fitting model, as determined by lowest AIC score, that included treatment and environmental covariates. AIC scores are shown for both classes of model. ABLA is subalpine fir (*Abies lasiocarpa*); PIEN is Engelmann spruce (*Picea engelmannii*); POTR is quaking aspen (*Populus tremuloides*). BA represents pre-treatment total live and dead basal area. Values in cells are linear model coefficients; empty cells indicates the variable was not included in the best-fitting model.

Variable	Model	Intercept	Salvage	Elevation	Historical Logging	ABLA BA	PIEN BA	POTR BA	R^2	df	AIC
1-hr fuels Mg ha^{-1}	1. Salvage only	0.98***	0.99***						0.19	50	148.8
	2. Salvage + covariates	0.91***	0.51^{NS}		1.00**	−0.11^{NS}			0.32	48	141.1
10-hr fuels Mg ha^{-1}	1. Salvage only	2.37***	3.47***						0.42	50	222.8
	2. Salvage + covariates	2.21***	2.99***		0.98^{NS}				0.43	49	222.6
100-hr fuels Mg ha^{-1}	1. Salvage only	2.94***	1.86**						0.12	50	240.3
	2. Salvage + covariates	2.94***	1.86**						0.12	50	241.3
1000-hr fuels Mg ha^{-1}	1. Salvage only	26.96***	8.01^{NS}						0.00	50	500.3
	2. Salvage + covariates	31.84***				4.29^{NS}		−1.33*	0.09	49	496.6
Litter & duff Mg ha^{-1}	1. Salvage only	29.02***	−7.06*						0.07	50	402.1
	2. Salvage + covariates	21.70***	−6.70*				0.24**		0.20	49	359.2
Live woody fuels Mg ha^{-1}	1. Salvage only	0.48***	−0.09^{NS}						0.01	50	63.5
	2. Salvage + covariates	0.51***			−0.18^{NS}				0.02	50	61.8
Herbaceous fuels Mg ha^{-1}	1. Salvage only	0.24***	0.15^{NS}						0.03	50	32.7
	2. Salvage + covariates	0.24***	0.15^{NS}						0.03	50	32.7
Bare ground cover	1. Salvage only	2.94*	9.54***						0.23	49	364.1
	2. Salvage + covariates	2.94*	9.54***						0.23	49	364.1
Cryptogam cover	1. Salvage only	10.94***	−7.34**						0.18	49	352.6
	2. Salvage + covariates	10.94***	−7.34**						0.18	49	352.6
Woody cover	1. Salvage only	19.38***	19.68***						0.47	50	395.1
	2. Salvage + covariates	19.38***	19.68***						0.47	50	395.1
Litter cover	1. Salvage only	64.47***	−21.32***						0.48	50	397.9
	2. Salvage + covariates	–32.30	–22.95***	0.03*				0.49^{NS}	0.52	48	396.1
Understory plant cover	1. Salvage only	63.08***	−26.81**						0.16	50	501.1
	2. Salvage + covariates	66.69***	−41.19***		25.08**			−1.79**	0.38	48	487.6
Understory Shannon's diversity	1. Salvage only	1.83***	−0.09^{NS}						−0.0	50	67.8
	2. Salvage + covariates	1.82***	−0.22^{NS}		0.29^{NS}	−0.06^{NS}			0.06	48	66.0
Understory species richness	1. Salvage only	10.31***	−1.51^{NS}						0.01	50	295.6
	2. Salvage + covariates	10.15***	−3.09*		3.32*	−0.50^{NS}			0.12	48	291.4
Shrub cover	1. Salvage only	17.88***	−10.83**						0.14	50	415.3
	2. Salvage + covariates	19.20***	−11.81**			2.03*		−0.66*	0.23	48	411.1
Forb cover	1. Salvage only	32.75***	−11.30^{NS}						0.03	50	480.1
	2. Salvage + covariates	−124.41 ·	−21.03**	0.04*	14.49^{NS}	−2.86^{NS}	0.32^{NS}		0.27	46	469.5
Graminoid cover	1. Salvage only	9.50***	−3.60^{NS}						0.01	50	383.9
	2. Salvage + covariates	75.50**		−0.02*	7.63*	−1.86*			0.22	47	377.5

^{NS} $P > 0.05$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

been elevated by recent salvage logging, but reduced by historical logging (Table 1).

Non-metric multidimensional scaling (NMS) produced a three dimensional solution (Fig. 5) with a stress of 0.14 (14%).

NMS 2 represented a shift between untreated controls and salvage samples (Pearson's r = 0.34) (Table 3); positive axis values were

Table 2
Mean percent cover of the most abundant 15 understory species in all plots sampled and Pearson's *r* correlations between species and NMS ordination axes for understory plant community composition at 52 plots in spruce beetle affected control and salvage stands in southwest Colorado. Correlation coefficients with an absolute value < 0.2 are indicated by bold font. Positive values represent a shift towards salvaged sites along NMS axes.

			Percent cover		Pearson's *r*		
Species	Common name	Scientific name	Control	Salvage	NMS1	NMS 2	NMS 3
VAMY2	whortleberry	*Vaccinium myrtillus*	11.5	6.5	**0.67**	−0.15	0.13
FRVI	Virginia strawberry	*Fragaria virginiana*	7.0	8.0	**0.45**	−0.01	**−0.60**
ERSP4	Aspen fleabane	*Erigeron speciosus*	3.9	3.3	**0.32**	0.07	0.11
CASI12	dryspike sedge	*Carex siccata*	3.7	3.6	**−0.27**	0.02	**−0.47**
ARCO9	heartleaf arnica	*Arnica cordifolia*	3.9	2.1	**0.50**	−0.06	−0.15
CHAN9	fireweed	*Chamerion angustifolium*	3.3	2.5	0.07	**0.42**	−0.13
PIEN	Engelmann spruce (seedlings and saplings)	*Picea engelmannii*	2.5	1.5	**0.37**	0.13	**−0.35**
ORPA3	Parry's goldenrod	*Oreochrysum parryi*	2.2	1.3	0.18	−0.01	**−0.34**
ARUV	kinnikinnick	*Arctostaphylos uva-ursi*	2.8	0.0	**−0.58**	**−0.27**	**−0.21**
ACMI2	yarrow	*Achillea millefolium*	1.5	0.8	**0.21**	−0.11	**−0.23**
JUCO6	common juniper	*Juniperus communis*	1.8	0.1	−0.15	**−0.56**	0.06
POPU3	Jacob's ladder	*Polemonium pulcherrimum*	1.8	0.1	0.11	0.05	**−0.44**
CACA4	bluejoint	*Calamagrostis canadensis*	1.4	0.3	−0.07	−0.08	0.15
CARO5	Ross' sedge	*Carex rossii*	1.2	0.4	**−0.22**	0.16	−0.11
BRCI2	fringed brome	*Bromus ciliatus*	1.1	0.1	−0.02	−0.02	**−0.36**

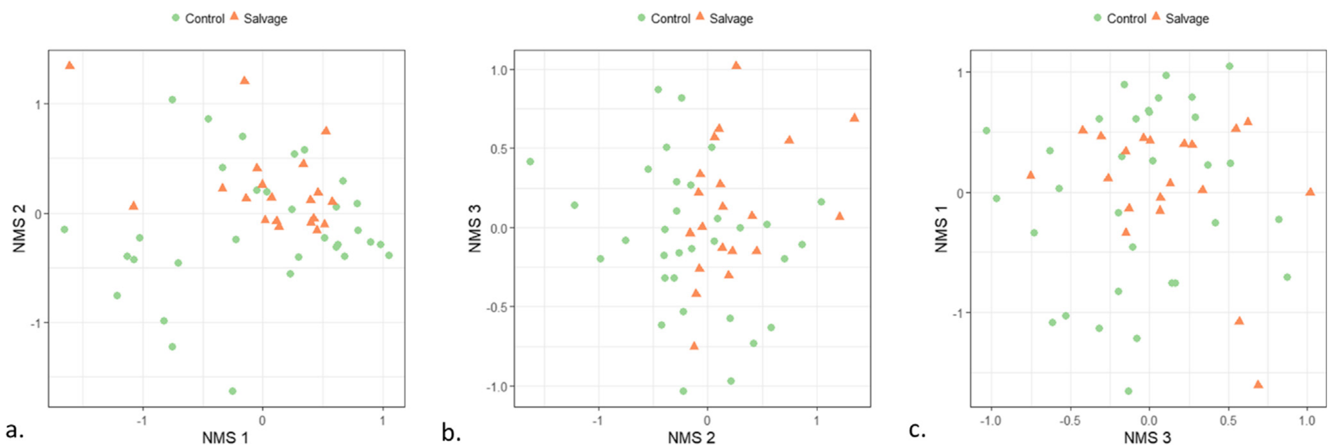

Fig. 5. Non-metric multidimensional scaling (NMS) ordination of control and salvage plots: (a) NMS axis 1 & 2, (b) NMS axis 2 & 3, and (c) NMS axis 3 & 1. Green circles represent control sites; orange triangles represent salvage sites.

Table 3
Correlations (Pearson's *r*) between treatment, location, pre-treatment overstory, ground cover attributes, and NMS axes for understory plant community composition. Correlation coefficients with an absolute value < 0.2 are indicated by bold font.

Attribute	NMS 1	NMS 2	NMS 3
Treatment	0.06	**0.34**	0.20
Location			
UTM E	**−0.41**	−0.10	−0.01
UTM N	**−0.40**	**−0.24**	−0.18
Elevation (m)	**0.61**	**0.51**	−0.00
Slope (%)	0.07	0.07	0.03
Aspect	−0.05	−0.05	0.06
Overstory (Live + Dead BA)			
Picea engelmannii	0.17	**0.32**	**−0.29**
Abies lasiocarpa	0.05	**−0.25**	0.20
Populus tremuloides	**−0.45**	**−0.21**	**0.21**
Ground cover			
Bare ground cover (%)	−0.16	**0.40**	**0.31**
Litter cover (%)	0.17	**−0.35**	**−0.27**
Wood cover (%)	−0.04	0.17	−0.05
Cryptogam cover (%)	0.01	−0.13	**0.23**
Plant functional group			
Shrub	**0.46**	**−0.43**	0.06
Forb	**0.40**	0.07	**−0.56**
Graminoid	**−0.33**	0.05	**−0.42**

associated with salvaged plots. NMS 1 and NMS 2 were both positively linked to elevation (Table 3). On average, salvage plots occurred approximately 70 m higher in elevation than control plots (3,391 m vs. 3,311 m, respectively). Pre-treatment Engelmann spruce basal area (live + dead) was positively correlated with NMS 2 and negatively correlated with NMS 3 (Table 3). Subalpine fir was negatively correlated with NMS 2; quaking aspen was negatively correlated to NMS 1 and NMS 2, and positively correlated to NMS 3 (Table 3). Bare ground cover, higher in salvage units (Fig. 4a), was positively correlated to NMS 2 and NMS 3 (Table 3). Litter cover, significantly decreased in salvage units (Fig. 4c), was negatively correlated to NMS 2 and NMS 3 (Table 3). Shrub cover, significantly reduced in salvage plots (Fig. 6d), was also negatively correlated to NMS 2 and positively correlated with NMS 1 (Table 3). Forb cover was positively correlated with NMS 1 and negatively correlated with NMS 3 (Table 3). Graminoid cover was negatively correlated with NMS 1 and NMS 3 (Table 3).

Ordination revealed shifts in plant community composition associated with salvage harvests as well as other environmental factors (Table 2). Whortleberry (*Vaccinium myrtillus*) was strongly positively correlated with NMS 1 (r = 0.67, Table 2). Aspen fleabane (*Erigeron speciosus*), heartleaf arnica (*Arnica cordifolia*), Engelmann spruce, and yarrow (*Achillea millefolium*) were also positively correlated to NMS 1 (Table 2). Virginia strawberry (*Fragaria virginiana*) was positively correlated with NMS 1 (r = 0.45, Table 2) and negatively correlated with NMS 3 (r = −0.60, Table 2). Kinnikinnick (*Arctostaphylos uva-ursi*), an understory shrub that was absent in salvage units, was negatively correlated with NMS 1 (r = −0.58, Table 2), NMS 2 (r = −0.27, Table 2), and NMS 3 (r = −0.21, Table 2). Common juniper (*Juniperus communis*), another understory shrub that was reduced in salvage units, was negatively correlated to NMS 2 (r = −0.56, Table 2). Fireweed (*Chamerion angustifolium*) was positively correlated with NMS 2 (r = 0.42, Table 2).

Our MRPP test confirmed differences in plant communities between control and salvage stands producing a delta of 0.696 for salvage plots and a delta of 0.813 for control plots (A = 0.023, $P < 0.001$).

Across all samples we identified two non-native species classified as introduced (USDA, NRCS, 2018): crested wheatgrass (*Agropyron cristatum*) and Canada thistle (*Cirsium arvense*). We also identified four potentially non-native species of uncertain origin (classified as both native and introduced in the lower 48; USDA, NRCS, 2018): yarrow (*Achillea millefolium*), field chickweed (*Cerastium arvense*), Kentucky bluegrass (*Poa pratensis*), and common dandelion (*Taraxacum officinale*). Cover by non-native species averaged 0.46% in controls and 0.49% in salvage stands, and did not differ significantly. A complete list of species percent cover and presence in control and salvage plots is provided in Appendix A.

4. Discussion

Recent salvage harvest treatments in spruce-beetle impacted stands resulted in changes in surface fuel loads, ground cover, and understory vegetation compared to untreated stands in our study area. We found support for our ***hypothesis (1)***, that salvage logging would elevate surface fuels, and ***hypothesis (2)***, that salvage logging would alter understory plant communities. Fine woody surface fuels (1, 10, and 100-hr) were increased in salvage units. However, we did not observe strong differences in coarse woody surface fuels (1000-hr) or live woody and herbaceous fuels in salvage units. Increases of surface fuels following salvage harvest has been documented in other studies in montane forests (Collins et al. 2012; Hood et al. 2017), and is thus not unexpected as a consequence of salvage harvest operations, which tend to remove the merchantable part of tree boles and leave the remaining woody debris on site. Our models also identified a potential increase in 1-hr surface fuels imparted by previous timber harvest (occurring between 1971 and 1990). This increase may have been driven by breaking branches when trees were cut and yarded to landing under older logging techniques that have changed over the last several decades. Litter

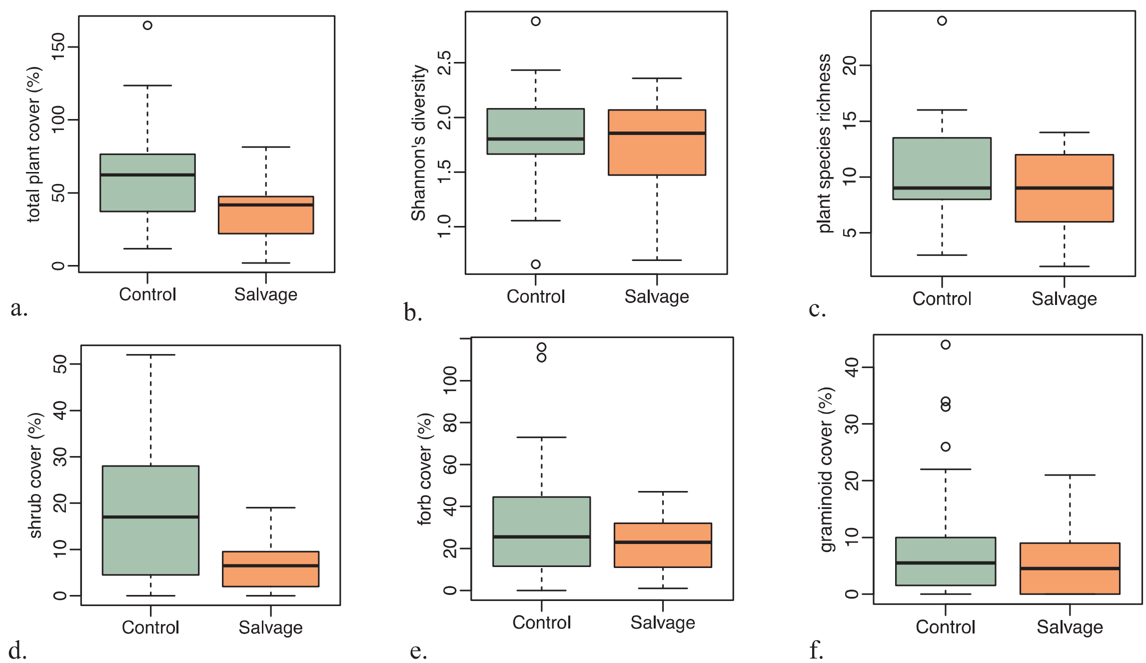

Fig. 6. Vegetation structure and composition in untreated control vs. salvage treatments, including (a) total vascular plant cover, (b) Shannon's diversity, (c) species richness, (d) shrub cover, (e) forb cover, and (f) graminoid cover.

and duff as a surface fuel component were reduced in salvage plots, which we attribute to mechanical impacts of logging activities on the surface, and/or the mixing of litter and duff into the soil during salvage operations that took place during snow-free seasons. Future research might consider the effects of different logging technologies and timing, especially differences between winter and summer operations on surface disturbance, as differences in mixing of plant biomass into the soil may be substantial.

Elevated quantities of woody surface fuels in salvaged stands would be expected to increase the intensity, flame length, and rate of spread of surface fires in the early years following treatment (Hood et al. 2017). These surface fires may be more intense and quicker moving than canopy fires (Rothermel 1972; Hicke et al. 2012) and could still result in negative impacts from fire. For example, following the 2013 West Fork Fire in southwest Colorado, Carlson et al. (2017) found that increased surface fuels imparted by beetle-induced mortality may have led to increased severity at the ground level that negatively affected vegetation recovery. However, Rhoades et al. (2018) reported that conifer seedlings experienced total mortality from wildfire in both salvaged and untreated lodgepole pine stands impacted by mountain pine beetle, suggesting that there was sufficient fuel loads in either treatment to cause mortality in these fire-intolerant species. We also note that our measures of surface fuels show high variance (as reflected in the standard deviations presented in the results, which are frequently greater than mean values); patchiness of surface fuels could potentially reduce some of the potential for rapid fire spread in salvaged stands. However, where fire mitigation is provided as an objective of salvage logging, managers may need to balance the tradeoffs of undertaking follow up treatments (e.g., broadcast burning) to reduce accumulations of surface fuels following logging activity with the potential loss of seedlings or residual trees.

Fine surface fuels are expected to increase over time in unlogged stands as branches and standing dead trees fall. Jenkins et al. (2008) projected increases of fine fuels from ca. 6 to 8 Mg ha^{-1} over two decades during a spruce beetle epidemic. Given our sampling relatively soon after the epidemic in our study area (with current dead and down fine fuel loads totaling 6.3 Mg ha^{-1} in unlogged stands), we might also project similar changes to occur. In beetle-impacted lodgepole pine stands, Collins et al. (2012) predicted that fine surface fuel loads in untreated stands would reach levels equal to those observed immediately post-salvage 80–100 years following beetle infestation. Furthermore, in salvaged sites, reduced inputs and decomposition are expected to lead to lower levels than observed in unlogged stands within ca. two decades (Collins et al. 2012). However, decomposition may be more rapid in mesic spruce-fir than drier lodgepole pine stands. Further, fine fuels in the salvage units we sampled averaged 12.7 Mg ha^{-1}, which is beyond the quantities predicted to accumulate in non-managed spruce stands over 150 years following beetle impacts (Jenkins et al. 2008). These differences again point toward the need for longer-term assessments and comparisons between mountain pine beetle and spruce beetle-affected systems.

Larger diameter dead and down woody debris (1000-hr fuels) is also expected to increase over time in untreated stands as standing dead trees fall. Jenkins et al. (2008) project increases from ca. 30 to 50 Mg ha^{-1} over 2–4 decades following initial beetle impacts. These projections also align with our measures (27 and 35 Mg ha^{-1} in control and salvage stands). However, such increases will be strongly limited in salvage treatments where most standing dead trees have been removed (Collins et al., 2012; Griffin et al., 2013; Hood et al., 2017). As such, although salvage harvests reduce canopy fuels in the short term but lead to increases in fine surface fuels, their primary fire hazard reduction may lie in the removal of larger surface fuels that would otherwise accumulate as trees fall over time in the non-salvaged stands. The rate of such changes and their dependence on forest type and site conditions is not well known, but may be increasingly relevant to informed fuel management during salvage operations, impelled by anticipated influences of climate change on previously climate-limited fire regimes (e.g., Abatzoglou and Williams 2016).

Increases in bare soil at salvaged sites present both potential opportunities and concerns for management. An essential component for successful spruce regeneration is exposed mineral soil (Windmuller-Campione et al. 2017), and the increases we found at salvage logged sites might aid in natural spruce regeneration where live tree seed sources occur within expected seed dispersal distances. However, increased bare soil could also lead to undesirable increases in erosion. Associated with this increase in exposed soil, we also observed a significant decrease in litter and cryptogam cover at salvage plots, both of which could potentially impede erosion. Cryptogam recovery is slow and their presence is a sign of a mature forest, although the effects of this loss are not fully understood (Kreyling et al. 2008). The decrease in cryptogams found at our site parallels findings of Jonášová and Prach (2008) who reported an immediate and drastic decline in mosses after salvage logging that they suggested would require several decades to recover (Jonášová and Prach, 2008).

Bare soil may also elevate the risk of establishment by non-native plant species, and both Canada thistle and common dandelion occurred more frequently in salvage plots than non-salvage plots. Canada thistle occurred in 20% of our salvage plots and 6.25% of our control plots. Canada thistle is an opportunistic, shade-intolerant species that takes advantage of disturbed areas and should be carefully monitored, as increases may lead to negative consequences for native biota (Guggisberg et al. 2012; Wright & Tinker 2012). However, non-native cover was not markedly different in salvage (0.49%) vs. control plots (0.40%), and was very low in both. Low non-native cover values are consistent with those reported from salvage-logged lodgepole pine stands (Fornwalt et al., 2018) and subalpine wildfires in Colorado (Coop et al. 2010), suggesting that these high-elevation systems are to some extent buffered from invasion by non-native plants.

One to two years post-harvest, understory plant cover was nearly halved in salvage treatments compared to untreated controls. In particular, shrub cover decreased from 18% in control plots to 7% in salvage plots. This reduction is also consistent with findings from salvaged spruce and lodgepole pine forests in northern Colorado (Rumbaitis del Rio 2006; Fornwalt et al. 2018; Rhoades et al. 2018), and may be due to direct mechanical damage associated with logging activities or drier conditions associated with increased insolation and reduced snow cover in large, salvage-logged openings. In contrast with research by Fornwalt et al. (2018) in lodgepole pine forests, *Vaccinium* species were still present on a majority of our study sites, though cover was approximately halved. However, two other forest shrubs that were frequent in controls, kinnikinnick and russet buffaloberry (*Shepherdia canadensis*), were absent in sampled salvage sites. Neither graminoid nor forb cover was significantly altered by salvage logging across our study sites. However, increased bare soil and light availability would be expected to present opportunities for expansion, as has been found in other studies of salvage logging impacts (Rumbaitis del Rio 2006; Fornwalt et al. 2018). It may be that not enough time has elapsed post-salvage for these groups to take advantage of altered conditions, and it will be important to continue to monitor salvaged stands for such changes. A graminoid-dominated understory may hinder the establishment of spruce seedlings, which could slow the recovery of the forest canopy. However, some herbaceous vegetation in control and salvage plots alike could also offer some protection and shading to spruce seedlings without substantially reducing available soil moisture (Alexander 1987).

In general, we found many of the same vascular plant species in both control and salvage stands, and we did not observe changes in diversity. However, in addition to the two shrub species described above, alpine milkvetch (*Astragalus alpinus*) and alpine fescue (*Festuca brachyphylla*) were also absent from salvage plots. In contrast, of the most abundant 15 species, Virginia strawberry was the only one that showed greater coverage in salvage plots, likely due to its capacity for rapid vegetative expansion via stolons. The extent to which understory vegetation cover and diversity may have been altered by spruce beetle impacts, relative to pre-disturbance conditions, is beyond the scope of this study. However, general patterns of community composition in both salvage and control samples are broadly consistent with those reported from this region by Johnston et al. (2001) prior to the current beetle epidemic, with dominance typically by whortleberry and a suite of native forbs and graminoids.

5. Conclusions and management implications

Given the potential role for human land-use (e.g., fire suppression) and a warmer and drier climate to exacerbate bark beetle activity (Kulakowski & Veblen 2006; Bentz et al. 2010; Hart et al. 2014; Raffa et al. 2008), large-scale beetle outbreaks and attendant post-outbreak management appear poised to increase across many high-elevation and high-latitude forests. Because salvage logging is a frequent land management response to recent and ongoing high-severity disturbances, land managers require information on the ecological consequences of these activities. Our research demonstrates short-term modifications to surface fuels, ground cover, and understory vegetative composition resulting from salvage operations. These changes are expected to influence ecological functions, in particular the potential effects of wildfire and the capacity for sites to maintain and recover forest understory plant species. Short-term increases in surface fuels may be undesirable for managers conducting salvage logging operations to mitigate fire hazard. Likewise, increases in bare soil may also be considered a negative consequence of management, particularly if these increases lead to increased opportunity for soil erosion or the establishment of non-native plant species. These changes could potentially be mitigated through changes in the extent and timing of salvage logging activities or post-logging slash management.

Short-duration studies may overestimate the impact of salvage logging, and ecological responses may vary as a function of forest community composition and the severity of the initial disturbance and post-disturbance salvage (Royo et al. 2016). Therefore, it will be important to continue to develop empirical research that examines the diversity and resiliency of different components of ecological systems as functions of ecological factors, intensity of logging operations, and time (Peterson & Leach 2008). We recommend that our protocols be repeated at ca. five year intervals to provide additional time for successional processes to be expressed. Such follow-up sampling would track future changes and contribute to the relatively sparse body of literature on changes to fuels and understory vegetation in salvage-logged spruce forests in western North America. Important attributes to include in further monitoring included changes in fuel loads as dead trees in unmanaged sites begin to fall and move fuels from the canopy to the surface. Future vegetation surveys may also provide insight into the capacity for common understory species to recover, or ongoing compositional changes, such as expected increases of graminoid cover or changes by non-native invasive species such as Canada thistle.

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Appendix A

Checklist of plant species that we encountered at sample sites in the La Garita mountains, southwest Colorado. Scientific names, common names, plant species code, and lifeforms are listed following USDA Plants (htpp://plants.usda.gov/). Frequency (occurrence in sample plots) and percent cover are shown for control and salvage treatments.

Scientific name	Common Name	Family	Code	Lifeform	Frequency (%)		Cover (%)	
					Control	Salvage	Control	Salvage
Abies lasiocarpa	subalpine fir	Pinaceae	ABLA	Tree (native)	12.5	5	0.52	0.05
Aconitum columbianum	Columbian monkshood	Ranunculaceae	ACCO4	Forb (native)	6.3	0	0.09	0
Achillea millefolium	yarrow	Asteraceae	ACMI2	Forb (uncertain)	40.6	25	1.53	0.83
Agropyron cristatum	crested wheatgrass	Poaceae	AGCR	Graminoid (introduced)	6.3	0	0.06	0
Agoseris glauca	pale agoseris	Asteraceae	AGGL	Forb (native)	3.1	0	0.03	0
Androsace chamaejasme	sweetflower rockjasmine	Primulaceae	ANCH	Forb (native)	0	10	0	0.1
Antennaria parvifolia	small-leaf pussytoes	Asteraceae	ANPA4	Forb (native)	0	5	0	0.05
Antennaria rosea	rosy pussytoes	Asteraceae	ANRO2	Forb (native)	3.1	0	0.03	0
Androsace septentrionalis	pygmyflower rockjasmine	Primulaceae	ANSE4	Forb (native)	3.1	0	0.03	0
Arnica cordifolia	heartleaf arnica	Asteraceae	ARCO9	Forb (native)	53.1	75	3.89	2.06
Arenaria lanuginosa var. *saxosa*	spreading sandwort	Caryophyllaceae	ARLAS	Forb (native)	3.1	0	0.09	0
Arnica parryi	Parry's arnica	Asteraceae	ARPA13	Forb (native)	0	5	0	0.25
Arctostaphylos uva-ursi	kinnikinnick	Ericaceae	ARUV	Shrub / Subshrub (native)	28.1	0	2.85	0
Astragalus alpinus	alpine milkvetch	Fabaceae	ASAL7	Forb (native)	21.9	0	1.1	0
Astragalus miser	timber milkvetch	Fabaceae	ASMI9	Forb (native)	3.1	0	0.03	0
Bromus ciliatus	fringed brome	Poaceae	BRCI2	Graminoid (native)	15.6	10	1.07	0.1
Bromus porteri	Porter brome	Poaceae	BRPO2	Graminoid (native)	9.4	0	0.21	0
Calamagrostis canadensis	bluejoint	Poaceae	CACA4	Graminoid (native)	34.4	20	1.44	0.29
Campanula rotundifolia	bluebell bellflower	Campanulaceae	CARO2	Forb (native)	0	5	0	0.05
Carex spp.	sedge	Cyperaceae	CAREX	Graminoid (native)	3.1	5	0.03	0.05
Carex rossii	Ross' sedge	Cyperaceae	CARO5	Graminoid (native)	34.4	30	1.19	0.44
Carex siccata	dryspike sedge	Cyperaceae	CASI12	Graminoid (native)	46.9	55	3.68	3.63
Cerastium arvense	field chickweed	Caryophyllaceae	CEAR4	Forb (uncertain)	6.3	5	0.06	0.05
Chamerion angustifolium	fireweed	Onagraceae	CHAN9	Forb (native)	40.6	60	3.34	2.55
Cirsium arvense	Canada thistle	Asteraceae	CIAR4	Forb (introduced)	6.3	20	0.4	0.49
Clematis columbiana	rock clematis	Ranunculaceae	CLCO2	Vine (native)	3.1	0	0.03	0
Conioselinum scopulorum	Rocky Mountain hemlockparsley	Apiaceae	COSC2	Forb (native)	3.1	0	0.03	0
Draba aurea	golden draba	Brassicaceae	DRAU	Forb (native)	6.3	0	0.15	0
Epilobium ciliatum	fringed willowherb	Onagraceae	EPCI	Forb (native)	0	5	0	0.05
Erysimum capitatum	sanddune wallflower	Brassicaceae	ERCA14	Forb (native)	0	5	0	0.1
Erigeron coulteri	large mountain fleabane	Asteraceae	ERCO6	Forb (native)	6.3	0	0.43	0
Erigeron divergens	spreading fleabane	Asteraceae	ERDI4	Forb (native)	3.1	0	0.03	0
Erigeron eximius	sprucefir fleabane	Asteraceae	EREX4	Forb (native)	12.5	0	0.52	0
Erigeron formosissimus	beautiful fleabane	Asteraceae	ERFO3	Forb (native)	3.1	0	0.03	0
Erigeron spp.	fleabane	Asteraceae	ERIGE2	Forb (native)	15.6	0	0.43	0
Erigeron speciosus	aspen fleabane	Asteraceae	ERSP4	Forb (native)	34.4	50	3.89	3.33
Erigeron subtrinervis	threenerve fleabane	Asteraceae	ERSU2	Forb (native)	3.1	0	0.06	0
Festuca brachyphylla	alpine fescue	Poaceae	FEBR	Graminoid (native)	25	0	0.4	0
Festuca spp.	fescue	Poaceae	FESTU	Graminoid (native)	3.1	0	0.03	0
Festuca thurberi	Thurber's fescue	Poaceae	FETH	Graminoid (native)	9.4	0	0.18	0
Fragaria virginiana	Virginia strawberry	Rosaceae	FRVI	Forb (native)	65.6	85	6.99	8.04
Geranium richardsonii	Richardson's geranium	Geraniaceae	GERI	Forb (native)	3.1	0	0.09	0
Hordeum jubatum	foxtail barley	Poaceae	HOJU	Graminoid (native)	9.4	5	0.28	0.34
Juniperus communis	common juniper	Cupressaceae	JUCO6	Shrub (native)	34.4	10	1.78	0.15
Koeleria macrantha	prairie Junegrass	Poaceae	KOMA	Graminoid (native)	9.4	10	0.18	0.39
Lonicera involucrata	twinberry honeysuckle	Caprifoliaceae	LOIN5	Shrub (native)	3.1	0	0.03	0
Lupinus argenteus	silvery lupine	Fabaceae	LUAR3	Forb (native)	3.1	0	0.12	0
Maianthemum stellatum	starry false lily of the valley	Liliaceae	MAST4	Forb (native)	3.1	0	0.03	0
Mertensia ciliata	tall fringed bluebells	Boraginaceae	MECI3	Forb (native)	3.1	0	0.58	0
Noccaea fendleri ssp. *Glauca*	alpine pennycress	Brassicaceae	NOMOM	Forb (native)	0	10	0	0.2
Oreochrysum parryi	Parry's goldenrod	Asteraceae	ORPA3	Forb (native)	50	55	2.18	1.32
Packera werneriifolia	hoary groundsel	Asteraceae	PAWE4	Forb (native)	21.9	10	0.37	0.2
Pedicularis sp.	lousewort	Scrophulariaceae	PEDIC	Forb (native)	3.1	0	0.03	0
Penstemon whippleanus	Whipple's penstemon	Scrophulariaceae	PEWH	Forb (native)	0	5	0	0.05
Phacelia alba	white phacelia	Hydrophyllaceae	PHAL9	Forb (native)	0	5	0	0.1
Phacelia sericea	silky phacelia	Hydrophyllaceae	PHSE	Forb (native)	0	5	0	0.05
Picea engelmannii	Engelmann spruce	Pinaceae	PIEN	Tree (native)	68.8	45	2.45	1.52
Poa cusickii	Cusick's bluegrass	Poaceae	POCU3	Graminoid (native)	3.1	0	0.09	0
Potentilla fruticosa	shrubby cinquefoil	Rosaceae	POFR4	Shrub (native)	3.1	0	0.18	0
Potentilla gracilis	slender cinquefoil	Rosaceae	POGR9	Forb (native)	21.9	5	0.46	0.1
Poa nemoralis spp. *Interior*	wood bluegrass	Poaceae	PONEI2	Graminoid (native)	0	5	0	0.05
Poa pratensis	Kentucky bluegrass	Poaceae	POPR	Graminoid (uncertain)	3.1	0	0.03	0
Polemonium pulcherrimum	Jacob's-ladder	Polemoniaceae	POPU3	Forb (native)	18.8	10	1.78	0.1
Poa secunda	Sandberg bluegrass	Poaceae	POSE	Graminoid (native)	3.1	15	0.15	0.54
Populus tremuloides	quaking aspen	Salicaceae	POTR5	Tree (native)	25	15	0.55	0.44
Pseudocymopterus montanus	alpine false springparsley	Apiaceae	PSMO	Forb (native)	12.5	10	0.34	0.2
Pyrola asarifolia	liverleaf wintergreen	Pyrolaceae	PYAS	Shrub / Subshrub (native)	6.3	0	0.06	0
Ranunculus macounii	Macoun's buttercup	Ranunculaceae	RAMA2	Forb (native)	3.1	0	0.03	0
Ribes montigenum	gooseberry currant	Grossulariaceae	RIMO2	Shrub (native)	6.3	0	0.21	0
Ribes wolfii	Wolf's currant	Grossulariaceae	RIWO	Shrub (native)	9.4	5	0.18	0.05
Salix glauca	grayleaf willow	Salicaceae	SAGL	Shrub / Tree (native)	3.1	0	0.03	0
Sambucus racemosa	red elderberry	Caprifoliaceae	SARA2	Shrub / Tree (native)	9.4	10	0.28	0.15
Senecio fremontii	dwarf mountain ragwort	Asteraceae	SEFR3	Forb (native)	0	5	0	0.05
Senicio wootonii	Wooton’s ragwort	Asteraceae	SEWO	Forb (native)	3.1	0	0.03	0
Shepherdia canadensis	russet buffaloberry	Elaeagnaceae	SHCA	Shrub (native)	18.8	0	1.01	0

Solidago multiradiata	Rocky Mountain goldenrod	Asteraceae	SOMU	Forb (native)	9.4	15	0.12	0.15
Stellaria longipes	longstalk starwort	Caryophyllaceae	STLO2	Forb (native)	3.1	5	0.03	0.05
Taraxacum officinale	common dandelion	Asteraceae	TAOF	Forb (uncertain)	18.8	30	0.7	0.49
Taraxacum officinale ssp. *ceratophorum*	horned dandelion	Asteraceae	TAOFC	Forb (native)	0	5	0	0.05
Thalictrum fendleri	Fendler's meadow-rue	Ranunculaceae	THFE	Forb (native)	3.1	0	0.06	0
Trifolium parryi	Parry's clover	Fabaceae	TRPA5	Forb (native)	3.1	0	0.95	0
Unknown	Unknown	Unknown	unknown	Unknown (Unknown)	31.3	40	0.58	0.54
Unknown	Unknown	Uknown	FORB1	Forb (Unknown)	3.1	0	0.31	0
Vaccinium myrtillus	whortleberry	Ericaceae	VAMY2	Shrub (native)	46.9	85	11.52	6.52
Zigadenus elegans	mountain deathcamas	Liliaceae	ZIEL2	Forb (native)	9.4	0	0.12	0

Appendix B

A list of all sample plots showing current and historical management. Shelterwood cuts were carried out between 1971 and 1991.

Plot ID	Treatment (current)	Treatment (historical)
CC109BCTLP	Control	Unmanaged
CC109CTLP	Control	Unmanaged
CC41BCTLP	Control	Unmanaged
CC41CTLP	Control	Unmanaged
CP24BCTLP	Control	Unmanaged
CP24CTLP	Control	Unmanaged
DL29BCTLP	Control	Unmanaged
DL29CTLP	Control	Unmanaged
ES16CTLP	Control	Unmanaged
ES19CTLP	Control	Unmanaged
EV34CTLP	Control	Unmanaged
LP44CTLP	Control	Unmanaged
MC200CTLP	Control	Unmanaged
MC37BCTLP	Control	Unmanaged
MC37CTLP	Control	Unmanaged
PC82CTLP	Control	Unmanaged
SC10BCTLP	Control	Unmanaged
SC10CTLP	Control	Unmanaged
SC13BCTLP	Control	Unmanaged
SC48BCTLP	Control	Unmanaged
SC48CTLP	Control	Unmanaged
LG47CTLP	Control	Shelterwood
RB0CTLP	Control	Shelterwood
RB2CTLP	Control	Shelterwood
RS3CTLP	Control	Unmanaged
WP9CTLP	Control	Shelterwood
WY2CTLP	Control	Unmanaged
WY7CTLP	Control	Unmanaged
WY12CTLP	Control	Unmanaged
WY10CTLP	Control	Unmanaged
RS6CTLP	Control	Unmanaged
RB8CTLP	Control	Shelterwood
RB15PLT	Salvage	Shelterwood
RB1PLT	Salvage	Shelterwood
Plot ID	Treatment (current)	Treatment (historical)
RB1PLTB	Salvage	Shelterwood
RB3PLT	Salvage	Shelterwood
RB4PLT	Salvage	Shelterwood
RB5PLTB	Salvage	Shelterwood
RB6PLT	Salvage	Shelterwood
RB7PLT	Salvage	Shelterwood
RB9PLT	Salvage	Shelterwood
RS11PLT	Salvage	Unmanaged
sRS12PLT	Salvage	Unmanaged
RS6PLT	Salvage	Shelterwood
WP1PLT	Salvage	Shelterwood
WP9PLT	Salvage	Shelterwood
WY12PLT	Salvage	Unmanaged
WY17PLT	Salvage	Unmanaged
WY1PLT	Salvage	Unmanaged
WY4PLT	Salvage	Unmanaged
WP6PLT	Salvage	Shelterwood
WY8PLT	Salvage	Unmanaged

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