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Short-term resistance of ecosystem properties and processes to simulated mountain pine beetle attack in a novel region

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Abstract. Natural forest disturbance regimes are changing, as evidenced by expansion of the mountain pine beetle (MPB) north and east from British Columbia into pine forests east of the Canadian Rockies. Thus, research that examines potential impacts of shifting disturbance regimes on ecosystem properties and processes in these forests is needed. We examined short-term effects (up to one year after treatment) of three treatments that emulated MPB attack and associated forest management disturbance (i.e., moderate and high intensity simulated MPB attack, salvage harvest) on above- and below-ground properties and processes of mature lodgepole pine forests in MPB's recently expanded range east of the Rockies. While the salvage logging treatment showed dramatic effects on the understory plant community and downed woody material with several less dramatic below-ground responses, there were no effects of the moderate MPB attack, and only limited below-ground responses to the high intensity attack. The salvage logged stands showed decreases in species richness and understory plant cover, increases in small downed wood, litter cover, forest floor pH, and plant available Ca, Mg, and P, and differences in multiple microbial properties compared with the other treatments. The high intensity simulated MPB attack showed increased respiration rates of several carbon substrates compared with the salvage treatment. There was considerable variation among years for many below-ground variables (e.g., multiple soil nutrients, microbial respiration rates and phospholipid fatty acids), and these were unrelated to treatments. For the majority of below-ground response variables, differences among study years rather than differences due to the MPB treatments suggest that inter-annual variability exerts a stronger influence than does disturbance effects of MPB red attack. The lack of potential response to MPB attack in the short-term suggests these forests are resistant to change early after attack, and/or have high ecological inertia. In contrast, salvage logging had immediate and dramatic effects. We don't yet know how these pine forests will develop under this modified disturbance regime of partial canopy disturbance, but it appears likely that salvage logging will push these stands in a potentially very different direction than the modified natural disturbance regime due to MPB will.

Key words: above-ground interactions; below-ground interactions; climate change; *Dendroctonus ponderosae;* disturbance regime; ecosystem change; lodgepole pine; *Pinus contorta;* range expansion; red attack; salvage logging.

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Introduction

Disturbance, both natural and anthropogenic, is an important ecological driver of successional change in forests. It influences the composition, abundance, and distribution of vegetation by altering the physical environment and the temporal and spatial distribution of resources (White and Pickett 1985). When disturbance reduces live plant biomass, surviving individuals can use the released resources (i.e., light, space, soil moisture, nutrients) and this will potentially alter the species composition of the remaining forest (Canham and Marks 1985). Depending on the intensity and frequency of disturbance, the structure of the forest, including the distribution of snags and downed woody material, will be altered to varying degrees (e.g., Tinker and Knight 2000, Page and Jenkins 2007). Following disturbance, changes in the below-ground soil nutrient availability (e.g., Thiffault et al. 2007) and microbial communities (e.g., Siira-Pietikäinen et al. 2001, Lindo and Visser 2003, Chatterjee et al. 2009), as well as losses of nutrients from the forests (Vitousek and Melillo 1979) can occur. However, studies have also shown resilience of microbial community structure and function to disturbance (e.g., Hannam et al. 2006), or that topographic position and elevation exert stronger influences than species- or disturbance-related effects on below-ground properties and processes (e.g., Swallow et al. 2009).

Natural disturbance regimes are rapidly changing, and there is a need for ecologists to better understand and anticipate the potential impacts of changing disturbance regimes on ecosystems and associated properties and processes (Turner 2010). While large lightning-caused wildfires have been the predominant natural disturbance throughout much of the boreal and near-boreal forest (e.g., Weber and Flannigan 1997), fire suppression and climate change are leading to increasing importance of other disturbance agents, including insects, disease, and drought (e.g., Ayres and Lombardero 2000, Logan et al. 2003, Soja et al. 2007). For example, the native mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae)) is a dominant disturbance agent over large areas of lodgepole pine (*Pinus contorta* Douglas ex Loud. var *latifolia* Engelm.) forests in British Columbia (BC) (Nealis and Peter 2008), and with recent range expansion east across the Rockies MPB is becoming an increasingly important disturbance agent in pine forests which were previously rarely or never exposed to it. MPB is considered the most destructive forest insect in western North America, with a recent epidemic in BC resulting in mortality of 710 million cubic meters of wood over a cumulative affected area of ~18.1 million hectares; the area and impacts of MPB continue to grow (Furniss and Carolin 1977, Safranyik and Carroll 2006, BC Ministry of Forests, Lands and Natural Resource Operations 2012). The current MPB infestation in BC is an order of magnitude larger in area and severity than all previously recorded outbreaks (Taylor et al. 2006, Safranyik et al. 2010). As a result of this unprecedented MPB outbreak, western Canadian pine forests formerly functioning as carbon sinks are now functioning as large net carbon sources, and this trend is expected to continue into the foreseeable future (Kurz et al. 2008).

Climate has historically limited the potential for MPB to expand north and east into suitable pine habitat in western Canada (Safranyik 1978, Carroll et al. 2004) but in the last few years, formerly climatically harsh environments have become more favorable, allowing significant expansion of MPB's historical range (Carroll et al. 2004, Nealis and Peter 2008). The availability and connectivity of suitable pine habitat has also contributed to MPB range expansion (Taylor and Carroll 2003). In 2005 MPB moved north and east across the Rocky Mountains and quickly spread through extensive stands of lodgepole pine in Alberta; attack in the novel host jack pine (*Pinus banksiana* Lamb.) has now also been confirmed (Cullingham et al. 2011). While the future course of the MPB attack east of the Canadian Rockies across the boreal is not yet known, MPB is likely to remain east of the Canadian Rockies (Safranyik et al. 2010), thus modifying the historic disturbance regimes for lodgepole pine and potentially other boreal pine forests (Nealis and Peter 2008, Coops et al. 2012).

The range expansion of MPB into novel habitats is expected to have large impacts on forest structure, plant community composition, forest floor and below-ground properties and processes, forest regeneration and the future

successional trajectory of stands. MPB differs from other types of disturbance including wildfire, windthrow, and timber harvest because it directly affects the overstory, but with no direct impacts on the understory or soil (Burton 2008). Edburg et al. (2012) suggested that, because of the legacy of living plant material, MPB attacked forests may recover net ecosystem productivity more quickly than after wildfire disturbance. Attacked trees are expected to lose their needles beginning in the second year post-attack, and lose most of their foliage between the second and third years post-attack when the stands transition from the red attack to grey attack stage (Chojnacky et al. 2000); minimal change in the quantity of light transmitted to the forest floor prior to this needle loss is expected. Instead, in the early red attack phase the major abiotic change in MPB-attacked stands is the stand hydrology, with an overall increase in water availability after attack (Knight et al. 1991, Schnorbus 2011). This hydrological change may, in turn, modify other abiotic and biotic components of the ecosystem, including the understory vegetation and below-ground properties and processes. A conceptual model of ecosystem biogeophysical and biogeochemical responses to MPB attack proposed that in the red attack stage increases in soil moisture would result in increased availability of soil nutrients, in turn influencing growth of surviving trees and the understory in the grey attack stage (Edburg et al. 2012). With the expansion of MPB range, Alberta has implemented a MPB management strategy that includes salvage harvest after MPB attack (ASRD 2007), but the potential impacts of this management practice on forest ecosystem properties and processes in the long run are also unknown.

To our knowledge, no previous studies have addressed the potential effects of MPB on both above- and below-ground ecosystem properties and processes in MPB's expanded range. We need to better understand the potential impacts of the shift in disturbance regime from a fire-dominated regime that dramatically reorganizes the ecosystem structure, to a regime that also includes MPB disturbance that kills trees without immediate direct impacts to downed woody material, understory vegetation, or below-ground ecosystem components. The main objectives of this study were to examine the effects of three different treatments that emulated MPB attack and associated forest management disturbance (i.e., moderate intensity MPB attack, high intensity MPB attack, and salvage harvest) on above- and below-ground properties and processes of mature lodgepole pine forests in western Alberta. Given the direct disturbance to the forest floor, we expected immediate significant changes in both above- and below-ground properties to occur in the salvage logged stands. However, we hypothesized that below-ground properties and processes would respond prior to above-ground properties in MPB-attacked stands that experienced canopy mortality without concurrent ground disturbance.

Methods

Study area

The study area was located in the Upper Foothills natural sub-region of Alberta (Natural Regions Committee 2006) in lodgepole pine forests near Robb, AB. This area is characterized by even-aged serotinous lodgepole pine forests, along with mixed conifer stands of white spruce (*Picea glauca* (Moench) Voss) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Stand ages in this region are generally younger than 100–120 years old reflecting the regional disturbance regime of relatively frequent stand-initiating wildfire (Beckingham et al. 1996). The climate is temperate continental with mean daily maximum air temperatures during the growing season ranging from a daily maximum of 16.2°C in May, to 20.6°C in August. Mean monthly precipitation during the growing season is as follows: 57.9 mm (May), 106.7 mm (June), 106.2 mm (July), and 82.2 mm (August), with a mean annual precipitation of 562.4 mm (30 year climate normal 1971–2000). The study stands were approximately 110–120 years old and were located on brunisolic gray luvisol soils. The study area was classified as ecosite UF e1.1-Pl/green alder/feather moss (Beckingham et al. 1996). The overstory included only lodgepole pine; there were very few white and black (*Picea mariana* (Mill.)) spruce, trembling aspen (*Populus tremuloides* Michx.), and balsam fir (*Abies balsamea* (L.) Mill) in the lower canopy. Notably, advance regeneration was absent or present in very low numbers (i.e., <10 seedlings or saplings ha^{-1}; see

McIntosh and Macdonald 2013). The understory was dominated by feather mosses, including *Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not., and *Hylocomium splendens* (Hedw.) Schimp., and the hair cap moss *Polytrichum commune* Hedw. Common forbs included *Cornus canadensis* L. and *Linnaea borealis* L., common small shrubs included *Rosa acicularis* Lindl. and *Vaccinium myrtilloides* Michx.; *Alnus crispa* (Aiton) Pursh was the dominant tall shrub, and the most common graminoid was *Calamagrostis montanensis* (Michx) Beauv. Because of the salvage harvested treatments, we selected stands reasonably close to general operating areas already scheduled for harvest in late winter or spring of 2009 in West Fraser Timber Company's forest management area spatial harvest sequence.

Experimental design

This study used a repeated measures before-after control-impact (Green 1979, Stewart-Oaten et al. 1992) randomized block design that was carried out over three years. There were three blocks in the study, which ranged in size from 4.8–8.8 ha (Table 1). Each block contained four experimental units (60 m $\times$ 80 m = 0.48 ha each), to which the treatments were applied in year two of the study. The four treatments were: (1) untreated control (hereafter "Control"), (2) simulated moderate intensity MPB attack (hereafter "50% kill"), (3) simulated high intensity MPB attack (hereafter "100% kill"), and (4) simulated salvage harvested, which were clear-cut harvested to simulate a typical management treatment post MPB attack (hereafter "Salvage"). While MPB selectively kills old and stressed trees during endemic phases of attack, our research was focused on epidemic levels of MPB, which are currently occurring at unprecedented levels on the landscape. Therefore, we selected targets of 50% kill and 100% kill to capture a gradient of mortality. Experimental units were relatively flat and covered by fairly homogenous mature lodgepole pine forest representative of the dominant forest cover type in this region that is susceptible to MPB attack. Treatments were randomly assigned to the experimental units within blocks, with the restriction that the salvage harvest unit had to be nearest the road to decrease impacts of forest harvest practices on remaining experimental units. All experimental units were surrounded by a 20-m (approximately one tree height) treated buffer to ensure hydroclimatic uniformity within them. Within each experimental unit we established nine systematically-located nested points that were used as the sampling points for measuring the overstory, downed wood, understory, and below-ground (n = 3 blocks $\times$ 4 experimental units $\times$ 9 sample points = 108 sampling points). Sample points were located a minimum of 10-m from the edge of the experimental unit and 20–30 m apart from one another to minimize spatial auto-correlation and were treated as sub-samples in statistical analyses. Because the sample points were systematically located, the distance of the nearest overstory tree (live or dead) varied from being directly adjacent to a sampling point to being several meters away from a sampling point.

Application of treatments

Chemical girdling (glyphosate) was used to simulate MPB attack for the 50% and 100% kill treatments. Glyphosate is a systemic herbicide that kills vegetation by inhibiting the enzyme 5-enolpyruvylshikimate 3-phosphate synthase involved in the synthesis of aromatic amino acids, it rapidly reacts with and is inactivated by most soils (Baylis 2000). When applied at the recommended rate, glyphosate has benign effects on microbial community structure (Ratcliff et al. 2006). EZ-Ject selective injection herbicide capsules (Glyphosate 0.15 grams per capsule, ArborSystems, Omaha, NE; http://www.ezject.com/) were injected at a rate of 1 capsule per 5 cm tree diameter at breast height (dbh) per tree for trees 10–20 cm dbh, or 1 capsule per 3 cm dbh per tree for trees $>$ 20 cm, with capsules equally spaced around the circumference of the tree near the base of the bole. In the 100% kill experimental units, all trees $\geq$10 cm dbh (selected as minimum size of trees attacked by MPB; Safranyik and Carroll 2006) were injected. In 50% kill experimental units, because of possible root-to-root transfer of glyphosate among neighboring trees (M. Mihajlovich, *personal communication*), every third tree $\geq$ 10 cm dbh was injected with glyphosate to achieve the desired rate of 50% overstory mortality. Chemical girdling was completed in the treatment year from June 15–19, 2009.

Clear-cut 'salvage' harvest operations used a

Table 1. Summary of site characteristics for lodgepole pine (*Pinus contorta*) in Upper Foothills of Alberta for the three study units before the treatments were applied (2008). Given are the means for all trees >5 cm dbh; the minimum and maximum values for subplots are in parentheses.

Block	Latitude/Longitude	Basal area (m^2 ha^{-1})	Density (trees ha^{-1})	Dbh (cm)	Canopy cover (%)
1	53.2248/116.8094	39.6 (26.7–56.2)	1420 (950–1900)	18.3 (5–34.7)	63.9 (56.2–86.9)
2	53.24129/116.8288	37.3 (21.6–55.1)	978 (550–1350)	21.5 (6.6–43.3)	59.2 (51.4–70.7)
3	53.22647/116.8212	40.3 (27.1–54.0)	1182 (450–1850)	20.1 (8.0–38.3)	62.1 (54.9–77.4)

"stump-side processing system" in which a feller-processor unit de-limbed trees at the stump, leaving debris and cones distributed onsite to facilitate regeneration (trees were not herbicided to mimic the effects of MPB prior to being harvested). Harvest operations were completed by West Fraser Timber Company between late July and early August in the treatment year (2009). No site preparation, e.g., scarification or burning, was applied to any of the harvest areas and vegetation was allowed to regenerate naturally for the duration of the study.

Data collection

Data were collected for the growing seasons of three consecutive years in this study unless otherwise noted below: (1) pre-treatment year (summer 2008), (2) treatment year (summer 2009), and (3) post-treatment year (summer 2010) at each of the nine sampling points per experimental unit.

The overstory plant community was sampled in 8-m fixed-radius (0.02 ha) circular plots in the pre-treatment year. Standard forest mensuration data were collected for all trees (i.e., with dbh $\geq$ 5 cm and ht $>$ 1.3 m) within each plot (i.e., dbh, height (for a subset of n = 2 trees/canopy layer: lower canopy, mid canopy, and upper canopy), live/dead status, crown vigor (healthy = minimal red needles, moderate = intermediate levels of red needles, poor = mostly/all needles red)), and all stems were tagged (except in the stands assigned to be clearcut) to allow for repeated measures at the individual tree level. For a subset of stems (~10) within each circular plot (except for the salvage logged stands) the openness of serotinous cones visible within the canopy was classified (1 = all cones open, 2 = some cones open, 3 = all cones closed, 4 = no cones present). Basal area, stem density, and diameter distribution of the stems by live/dead status were calculated. In the post-treatment year tree live/dead status, crown vigor (healthy = no red needles present, moderate = intermediate levels of red needles, and poor = all needles red) and openness of cones were re-assessed. Crown vigor data were used to assess post-treatment survival and mortality rates among the experimental units, quantifying basal area by crown vigor class.

To estimate canopy cover, hemispherical photographs (digital Nikon Coolpix 4500 with FC-E8 fisheye lens) were taken in the middle of each growing season (mid July), with the camera leveled on a tripod ~1.4 m above the forest floor and the bottom of the camera oriented towards North. We analyzed canopy photographs using SLIM (Spot Light Intercept Model v. 3.01), using batch processing to analyze photos with manual color threshold adjustments by experimental unit and year to optimize differences between canopy and sky. The program calculates gap fraction, which measures the area of overhead view (in percent) which constitutes canopy gaps, and we subtracted gap fraction from 100 to provide an estimate of canopy cover at each sample point.

Downed woody material (DWM) was measured using the line intersect method (Van Wagner 1968, Brown 1974, Brown et al. 1982, Van Wagner 1982). Line transects ran from each sampling point out 8 m in a randomly selected direction and the same transects were sampled for three years. The diameter of each DWM piece at the point of intersection with the line transect was measured using calipers and categorized into diameter size classes as follows: 0–0.5 cm, 0.5–1.0 cm, 1–3 cm, 3–5 cm, 5–7 cm, and >7 cm (as adopted by the Canadian Forest Service; McRae et al. 1979, Van Wagner 1982). Pieces in diameter size classes 0–0.5, 0.5–1, and 1–3 cm were counted along the first 2 m length of each transect, size classes 3–5 and 5–7 cm along the first 4 m length of each transect, and for all pieces $\geq$7 cm we recorded diameter, length, and decay

class (i.e., 1–5, based on Table 8.1 in VRI 2007) along the full 8 m. Biomass of DWM (Mg ha^{-1}) for each of the size classes was calculated using the equation and coefficients for Central Alberta foothills lodgepole pine stands (Delisle and Woodard 1988, Nalder et al. 1997). For the large pieces (≥7 cm diameter) we also calculated the biomass of sound (i.e., decay classes 1 and 2) and rotten (i.e., decay classes 3–5) wood separately. We calculated the total biomass of DWM by summing the biomass for all size classes. Percent cover of DWM was estimated during assessment of understory communities (see below).

Visual estimates of percent cover to species were made within 1-m x 1-m quadrats for forest floor mosses, forest floor lichens, forbs, graminoids, and small shrubs (see Appendix for detailed list). Nomenclature follows the USDA Plants database (http://plants.usda.gov). Cover estimates were also recorded for litter, tree/snag boles, downed woody material (diameter > 3 cm), exposed mineral soil, and rock. The thickness of the forest floor (Fibric/Humic layers; i.e., F/H, mm) was measured in each of the four corners of each understory vegetation quadrat. We calculated understory species richness and diversity (i.e., Shannon Index, Magurran 1988) per quadrat. We measured tall shrubs/saplings (i.e., taller than 1.3 m ht but with dbh < 5 cm, e.g., *Alnus crispa*) in 4-m radius circular plots; to estimate their abundance we measured stem basal diameters for shrubs and saplings rooted within the plot and for shrubs that had canopy overhanging the plot. With interest in quantifying the total biodiversity of the experimental units, we also conducted a census at the peak of the growing season during which two people surveyed each experimental unit for the presence of understory species that had not been found in any of the quadrats within that unit. For understory multivariate analysis, we used data for 34 understory species/taxa that occurred in ≥5% of the experimental units (see Appendix for detailed species/taxa list). The uncommon/infrequent species were excluded from multivariate analysis because their sample sizes were too small to analyze patterns in their relative abundance among the experimental units over time.

Distributed soil moisture measurements using time-domain reflectometry (TDR) were collected at three sampling depths (0–20, 0–40, and 0–60 cm below the mineral soil surface) at two randomly selected sampling points in each experimental unit (this was the only component that we measured with lower sampling intensity than the nine systematic points per experimental unit), with measurements recorded approximately one to two times a month throughout the growing season when the ground was not frozen (mid-June to mid-September). Volumetric soil water content (VWC) using the empirical relationship for mineral soils proposed by Topp et al. (1980) was calculated and then converted to moisture depth (mm) for each of the three sampling depths. VWC was calibrated against actual soil moisture content in a paired hydrology study adjacent to our research sites. That study monitored soil moisture continuously throughout the duration of our study at the same three depths, and also measured growing season patterns in soil moisture at 5 cm depth in the mineral soil among the stand treatment types in the post-treatment year only (Piña 2012). Gross precipitation (mm) was measured in a nearby clear-cut throughout the year using a universal precipitation gauge and a Hobo datalogger (Hobo Event loggers and U12–008, Onset Computer Corporation, MA, USA).

We installed Plant Root Simulator (PRS) probe ion exchange membranes (Western Ag Innovations, Inc., Saskatoon, SK, Canada) to measure soil nutrient availability. The anion exchange PRS probes simultaneously adsorbed all nutrient anions, including NO_3^-, PO_4^{3-}, and SO_4^{2-}. Cation exchange PRS probes simultaneously adsorbed nutrient cations such as B^+, NH_4^+, K^+, Ca^{2+}, Mg^{2+}, Cu^{2+}, Fe^{2+}, Mn^{2+}, and Zn^{2+}. We installed four pairs (pair = 1 cation and 1 anion exchange membrane) of PRS probes vertically at the four corners of each understory quadrat at the interface between the forest floor and mineral soil. Probes were installed for the duration of the growing season each year (mid-June to mid-September), and at the end of the season they were cleaned and shipped to Western Ag for analysis of nutrient supply rates (μg 10 cm^2 burial $length^{-1}$); the four probe pairs from individual quadrats were pooled prior to elution and analysis. The few samples for which measured values were below the minimum detection limits were still included in analysis because

censoring data below MDL can bias your dataset (Western Ag, *personal communication*). We did not analyze the data for several elements because their calculated nutrient supply rates were predominately below the minimum detection limits [Cd (n = 227/324<MDL), Cu (n = 260/325 <MDL), NO_3^- (n = 175/324 <MDL), and Pb (n = 142/324 <MDL)].

To measure rates of decomposition, nylon mesh bags (1.5 mm × 1.5 mm mesh size) with four 90-mm diameter Whatman cellulose filter papers were buried at the forest floor - mineral soil interface for the growing season each year (same time span as PRS probes listed above). Filter papers were oven dried for 1 day (pre-burial) and 3 days (post-burial) at 70°C and weighed before and after being buried. Decomposition rate was calculated as 100 minus the percentage of original filter paper biomass remaining at removal.

Forest floor samples were collected to measure pH, microbial multiple carbon source substrate-induced respiration (MSIR), and phospholipid fatty acid analysis (PLFA) of the below-ground microbial community, as described below. We collected forest floor samples (i.e., the entire depth of litter, F and H layers) from each of the four corners of the understory 1-m^2 quadrats using aseptic techniques (sampling equipment was washed with 70% ethanol between samples) and combined them to form a single homogenous sample (~50 g) per quadrat. These were then divided into a portion to be used for pH and MSIR and another for PLFA analysis. Samples were kept cool on ice until transferred back to the lab. Upon arrival at the lab, samples for MSIR and pH were sieved (4 mm) and kept refrigerated (4°C) in bags prior to analysis. PLFA samples were stored at −86°C and then freeze-dried prior to PLFA extraction.

Forest floor pH was measured potentiometrically in a saturated paste in equilibrium with a soil suspension of a 1:4 soil:liquid mixture. We used 0.01 M $CaCl_2$ in place of water following the instructions for measuring pH of field-moist organic samples described in Kalra and Maynard (1991).

MSIR was used to examine the functional composition of microbial communities related to the activity of the soil microflora, particularly in the carbon cycle using the MicroResp method (Campbell et al. 2003, Chapman et al. 2007). Within the soil microbial community individual species have different abilities to respire different substrates, so by adding different substrates we obtained a community-level physiological profile for the soil sample that extended beyond the respiration data that could be obtained using in situ soil respiration chambers. We prepared detection agar plates containing a gel-based bicarbonate buffer with indicator dye that responded to the pH change within the gel resulting from CO_2 evolved from the soil. The plates were stored in a closed desiccation chamber in the dark when not being used for analysis.

Each MSIR substrate was prepared as 30 mg of substrate per gram of water (Cameron 2008); a separate set of substrates was prepared for each of the three study units (2008) or treatments (2009, 2010) because of differences in forest floor moisture content among them. To estimate mean forest floor moisture content within each study unit (in 2008) and within treatments (in 2009 and 2010), we sub-sampled ~1 g of each field-moist sieved forest floor MSIR sample and then combined all 36 samples (9 sampling points × 4 experimental units) within each block (2008) or all 27 samples (9 sampling points × 3 blocks) within each treatment (2009, 2010) into a single sample. Each of the pooled samples were weighed (fresh) and then dried for 48 hours at 65°C and reweighed (dry). Percent dry weight was calculated ((dry/fresh) × 100), and soil moisture content was calculated as 100 − percent dry weight; this moisture content was then used for calculating substrate concentrations. Fifteen substrates commonly used in MSIR analysis and thought to be associated with plant root exudates (e.g., Garland and Mills 1991, Stevenson et al. 2004) were used: five aminos acids (L-alanine, L-arginine, glutamine, L-lysine, γ aminobutyric acid), six carbohydrates (n-acetyl glucosamine, L-(+)-arabinose, D-(+)-galactose, glucose, mannose, trehalose), four carboxylic acids (citric acid, L-malic acid, oxalic acid, 3,4-dihydroxybenzoic acid), and water as a control to measure basal respiration. Substrates at desired concentrations were stored at 4°C for the duration of the respiration analysis.

Field-moist forest floor samples were incubated in a dark chamber at 25°C for ~24 hours prior

to MSIR analysis. Forest floor samples were added to the 96-well microtiter deep well plates after 30 μl of each substrate was dispensed (three replicate substrate wells per sample, two samples per deep well plate). The deep-well plate was then hermetically sealed with a gasket, face-to-face, with the detection plate, such that each well of the deep-well plate interacted with the opposite well of the detection plate. The two plates were incubated in the dark at 25°C for six hours. The color change in the detection plate was then read on a standard laboratory microplate reader (detection plate read before and after 6 hrs of incubation, absorbance = 570 nm). A maximum of 16 samples could be analyzed in a day, so samples were randomly selected each day to reduce bias associated with differences in time since collection and all analyses were completed within two weeks of sample collection. Respiration rates (μg CO_2-C/g/hr) for individual substrates were compared among treatments and time. Respiration rates for the 15 substrates were normalized to basal respiration (respiration rates were divided by basal respiration) and compared among treatments and time using multivariate analyses. Six samples had five or more carbon substrate respiration rates below basal respiration and were excluded from analysis. Catabolic evenness of respiration rates was calculated using the Simpson-Yule index ($1/\sum p_i^2$, Magurran 1988), where p_i was the respiration response for individual substrates as a proportion of total respiration rates from all substrates for a forest floor sample (Degens et al. 2000).

Microbial PLFA analysis produces a lipid profile of microbial communities. We transferred 0.30 g of each freeze dried forest floor sample to muffled test tubes and then analyzed them for PLFAs following the detailed methods described in Hannam et al. (2006). To summarize, we analyzed forest floor samples by extraction with a single-phase chloroform mixture, lipid fractionation on a solid-phase-extraction Si column and then subjected them to a mild methanolysis. The resulting fatty acid methyl esters were then analyzed using an Agilent 6890 Series capillary gas chromatograph (GC; Agilent Technologies, Wilmington, DE) equipped with a 25 m Ultra 2 (5%-phenyl)-methylpolysiloxane column. The MIDI peak identification software (MIDI, Newark, DE) was used to identify individual fatty acids. Fatty acids were designated X:YωZ, where X represents the number of carbon atoms, Y represents the number of double bonds, and Z indicates the position of the first double bond from the aliphatic (ω) end of the molecule. The suffixes c and t indicate cis and trans geometric isomers. The prefixes 'a' and 'i' refer to anteiso and iso branching and Me and OH specify methyl groups and hydroxyl groups, respectively. PLFAs that were present in 5% or less of the samples were excluded from analysis. PLFAs for 16:1ω9c and 16:1ω11c were combined and 18:2ω6,9c and a18:0 were combined for analysis as they could not be distinguished by the GC. We excluded seven samples with <85% peak matching from analysis. There were a total of 59 PLFAs included in the final analysis. PLFAs used as biomarkers for functional groups (i.e., fungi, bacteria, actinomycetes, and arbuscular mycorrhizae) were quantified on a mol % basis to standardize for differences in the amounts of forest floor PLFAs among samples. The fungal PLFAs 18:1ω9c, 20:1ω9c, and 18:3ω6c were used to estimate the contribution of fungi (Myers et al. 2001, Hamman et al. 2007), and 16:1ω5c was used to estimate arbuscular mycorrhizae (Frostegård and Bååth 1996, Olsson 1999). Bacterial PLFAs included 10:0 3OH, 12:0, 12:0 2OH, 12:0 3OH, 14:0, i14:0, 15:0, a15:0, i15:0, i16:0, i17:0, a17:0, 17:0, cy17:0, 18:1 ω5c, 18:1ω7c (Bååth et al. 1992, Frostegård and Bååth 1996, Olsson and Alstrom 2000, Myers et al. 2001, Hassett and Zak 2005). The ratio of fungal to bacterial PLFAs was used to estimate the relative contributions of fungi and bacteria. The 10-methyl branched fatty acids (10me16:0, 10me17:0 and 10me18:0) were used to measure actinomycetes (Kroppenstedt 1985, Brennan 1988). Total PLFAs were compared among treatments and time as nmol g^{-1} forest floor. Mol percent of 56 PLFAs present in >5% of samples were used in multivariate analyses.

We calculated the microbial metabolic quotient for each forest floor sample as the ratio of soil basal respiration to microbial biomass (qCO_2; Anderson and Domsch 1985).

Statistical analyses

For univariate analyses, we first determined whether each variable met the assumptions for analysis of variance (ANOVA) and transformed response variables when necessary. Repeated

measures ANOVAs were used to test for significant ($\alpha = 0.05$) differences in the response of individual variables (e.g., DWM, total Nitrogen, mean total cover, Shannon Diversity, pH) to the treatments and to differences in treatments within years, as well as for significant interactions ($\alpha = 0.10$) between treatment and year (Proc Mixed, SAS Institute, Version 9.2 (32-bit), Cary, NC, USA; SAS Institute 2008). For overstory data, we compared among years and treatments, excluding the salvage harvested stands from our analyses because they did not have stems present for assessment post-treatment. To calculate species richness we looked at both species richness per 1 m^2 quadrat, as well as species richness per experimental unit, based on the total species list from sampling of the understory quadrats combined with the species census. When the treatment effect was significant we used post-hoc linear contrasts to compare among treatments within each year separately to assess whether there were differences among the experimental units prior to the treatments being applied, in the treatment year, and the post-treatment year. When treatment was not significant but time was significant and there was no significant interaction, we compared among years, combining data for all treatments within each year. When there was a significant treatment by time interaction we compared among treatments for each year separately and among years for each treatment separately. For all of these post-hoc comparisons we used Bonferroni-adjusted α-values (family-wise $\alpha = 0.05$) as follows: comparisons among treatments $\alpha = 0.008$ (i.e., 0.05/6); comparisons among years $\alpha = 0.0167$ (i.e., 0.05/3) (Proc Mixed, SAS Institute, Version 9.2 (32-bit), Cary, NC, USA; SAS Institute 2008).

Multivariate patterns among treatments and years were examined using nonmetric multidimensional scaling (NMS) ordination (McCune and Grace 2002) for the understory plant community, soil nutrient availability, and forest floor microbial communities (MSIR and PLFA). Ordinations used PC-ORD (Version 5; MjM Software Design, Gleneden Beach, OR), with Sørenson as the distance measure, 100 runs with real data and 100 Monte Carlo randomized runs, starting with a six-dimensional solution and stepping down to a one-dimensional solution. We determined the number of dimensions of our final solution by evaluating the scree plot and the reduction in stress with step-down in dimensionality of the preliminary runs (McCune and Grace 2002). Stability of the solution (stability criterion = 0.00005) was assessed by plotting stress versus iteration. After the preliminary runs we ran a final NMS with the optimal number of dimensions, using the starting configuration that worked best in our preliminary runs, and omitting the Monte Carlo test. We then calculated the Pearson correlation coefficients of the vegetation and forest floor descriptive variables (e.g., pH, soil moisture at each of the three sampling depths, downed wood biomass, understory cover by growth form) with the NMS ordination axes and overlaid variables with correlation ($R^2 > 0.25$) on the ordination plots.

We used permutation-based MANOVAs (perMANOVA, PC-ORD version 5, MJM Software Design, Gleneden Beach, OR, USA) to test for statistically significant differences in understory plant community composition, below-ground nutrient supply rates, and microbial (MSIR and PLFA) community composition among the treatments over time. For the perMANOVA, 4999 randomizations were used and significance was based on the proportion of randomized trials with a response value greater than or equal to the observed response value. The initial perMANOVA comparing the treatments over time was followed up by pairwise comparisons among treatments and years following the same procedure as for the ANOVAs and similarly using alpha-values that were Bonferroni-adjusted so the family-wise $\alpha = 0.05$.

Results

Above-ground

There was a decrease in healthy basal area in both the 50% kill and 100% kill stands in the post-treatment year, but not in the control, and the three treatments differed from one another only in the post-treatment year (Table 2, Fig. 1). There were no significant differences among treatments or years for canopy cover or the openness of cones (Table 2).

Biomass of the three smallest downed wood size classes increased over time in salvage stands, which had increased biomass in the treatment and post-treatment years compared with the pre-

Table 2. Results (P values) for repeated measures ANOVAs testing for the effects of treatment, year (pre- to post-treatment) and the interaction between treatment and year for overstory, downed woody material (DWM), understory, and below-ground variables for lodgepole pine study units. Significant P-values highlighted in bold.

Variable	Treatment	Year	Treatment × Year
Overstory†			
Healthy basal area	**0.002**	**<0.0001**	**<0.0001**
Canopy cover	0.37	0.44	0.98
Openness of cones	0.26	0.88	0.52
DWM biomass			
Class 1: <0.5cm‡	**<0.0001**	**<0.0001**	**0.02**
Class 2: 0.5–1 cm‡	**0.0005**	**<0.0001**	**0.014**
Class 3: 1–3 cm	**<0.0001**	**0.03**	**0.03**
Class 4: 3–5 cm§	**0.03**	0.45	0.67
Class 5: 5–7 cm§	0.10	0.37	0.99
Class 6: >7 cm‡	0.17	0.05	0.97
Total biomass‡	0.49	**0.03**	1.0
Understory			
Understory vegetation richness per quadrat	**0.04**	0.28	**0.03**
Understory vegetation richness per experimental unit	**<0.0001**	0.43	0.14
Total cover	**<0.0001**	0.78	**0.0004**
Forb cover‡	**0.0007**	0.86	**0.01**
Shrub cover‡	**0.0023**	0.26	**0.01**
Graminoid cover	0.16	0.96	0.33
Bryophyte cover	**<0.0001**	0.91	**0.06**
Shannon diversity per quadrat	0.10	0.23	0.26
Litter cover	**<0.0001**	**<0.0001**	0.07
Large shrub basal area	0.17	0.81	0.52
Below-ground			
Forest floor depth§	**0.02**	**<0.0001**	0.51
Soil moisture: 0–20 cm depth	0.42	**0.0011**	0.99
Soil moisture: 0–40 cm depth‡	0.55	**0.0004**	0.99
Soil moisture: 0–60 cm depth	0.39	**<0.0001**	0.95
Forest floor pH	**<0.0001**	**0.02**	0.97
Nutrient supply: Al§	0.32	**0.001**	0.99
Nutrient supply: B§	0.96	**<0.0001**	0.94
Nutrient supply: Ca	0.12	**<0.0001**	**0.03**
Nutrient supply: Fe§	0.78	**<0.0001**	0.69
Nutrient supply: K‡	0.27	0.34	0.99
Nutrient supply: Mg	**0.005**	**<0.0001**	0.31
Nutrient supply: Mn‡	0.81	**0.02**	0.31
Nutrient supply: NH_4-N‡	0.74	**0.03**	0.74
Nutrient supply: P	**0.04**	**0.0008**	**0.03**
Nutrient supply: S§	0.20	**0.0018**	0.79
Nutrient supply: Zn	0.10	**<0.0001**	0.63
Decomposition	0.25	0.85	0.90
MSIR: N-acetyl glucosamine§	0.82	**<0.0001**	0.31
MSIR: L-alanine	0.29	**<0.0001**	0.20
MSIR: Aminobutyric acid	0.19	**<0.0001**	**0.01**
MSIR: Arabinose	0.55	**<0.0001**	0.18
MSIR: L-arginine	0.33	**<0.0001**	0.27
MSIR: Citric acid§	0.59	**<0.0001**	0.15
MSIR: 3,4-Dihydroxybenzoic acid§	0.59	**<0.0001**	0.08
MSIR: Galactose§	0.36	**<0.0001**	0.19
MSIR: Glucose§	0.49	**<0.0001**	0.73
MSIR: Glutamic acid§	0.32	**<0.0001**	0.22
MSIR: L-lysine§	0.30	**<0.0001**	0.07
MSIR: Malic acid§	0.51	**<0.0001**	0.13
MSIR: Mannose	0.54	**<0.0001**	0.26
MSIR: Oxalic acid	0.11	**<0.0001**	**0.03**
MSIR: Trehalose	0.95	**<0.0001**	0.75
MSIR: Basal (water)§	0.49	**<0.0001**	0.22
Catabolic evenness	0.73	**<0.0001**	0.97
PLFA Total biomass	0.63	**0.002**	0.97
Bacterial PLFA mol%	**0.02**	**<0.0001**	0.62
Fungal (excl. myco) PLFA mol%	0.14	**0.02**	0.82
Arbuscular mycorrhizae PLFA mol%	0.57	**0.005**	0.30
Actinomycetes PLFA mol%	**0.045**	**0.002**	0.93

Table 2. Continued.

Variable	Treatment	Year	Treatment × Year
Fungi:bacteria ratio	**0.02**	**0.0005**	0.81
Metabolic quotient‡	0.55	**<0.0001**	0.30

† Only comparing among the three treatments of control, 50% kill, and 100% kill because overstory stems were all removed in the salvage logged treatment.
‡ Square-root transformed for analysis.
§ Log transformed for analysis.

treatment year (Tables 2 and 3). Further, in both the treatment and post-treatment years, salvaged stands had greater biomass of the three smallest size classes of DWM than the other treatments did (Tables 2 and 3). There was a significant effect of treatment on biomass of DWM in the 3–5 cm size class (Table 2); post-hoc comparisons showed no differences among treatments in individual years (Table 3). With all years combined, biomass of this size class was significantly higher in the salvage stands compared with the 50% kill stands (Table 3). Biomass of DWM in the 5–7 and >7 cm size classes showed no effects of treatment or year (Table 2). Total DWM biomass was significantly greater in the post-treatment year compared with the pre-treatment year, with intermediate levels in the treatment year, independent of treatment (all treatments combined; Tables 2 and 4).

There was an increase in litter in each year in the salvage stands, and between the pre-treatment year compared with the treatment and post-treatment years for the 50% kill stands (Tables 2 and 3). There was higher litter cover in the salvage stands compared with the control and 50% kill stands in the pre-treatment year, compared with the control in the treatment year, and compared with all three treatments in the post-treatment year (Tables 2 and 3).

There was a decrease in understory species richness per quadrat for the salvage stands in the treatment and post-treatment years compared

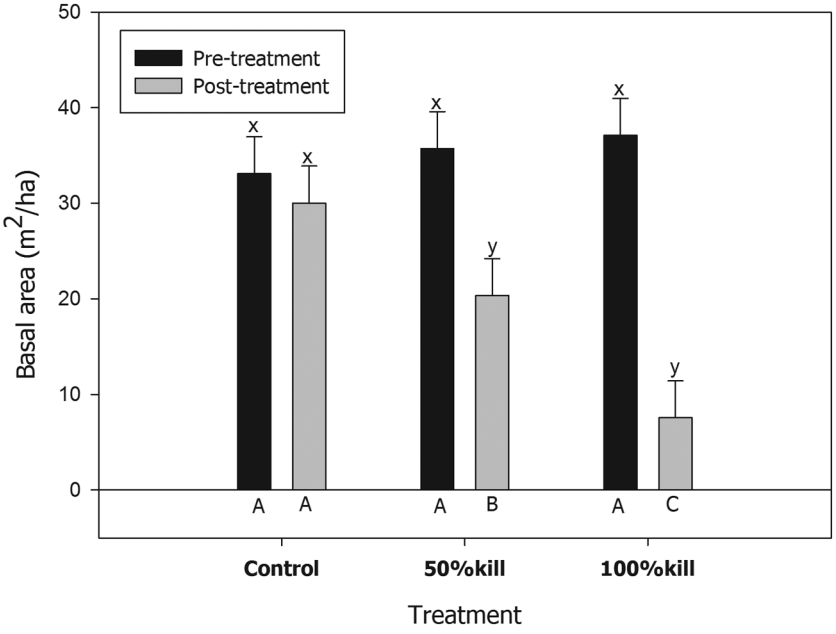

Fig. 1. Mean basal area for trees with healthy crown vigor by treatment and year (±95% CI). Years with different letters (x, y) within a treatment and treatments with different letters (A, B, C) within a year were significantly different.

Table 3. Mean and 95% confidence intervals for measured variables broken out by treatment within each year (Pre = pre-treatment year, Trtmt = treatment year, and Post = post-treatment year). Years with a different lower case letter (x, y, z) within a given treatment and treatments with different capital letters (A, B, C, D) within a year were significantly different for that variable. These were based on post-hoc lsmeans comparisons for variables that showed significant treatment, treatment and year, and/or treatment-year interaction effects in the ANOVA (see Table 2).

Variable and Year	Treatment			
	Control	50% kill	100% kill	Salvage
DWM				
0–0.5 cm				
Pre	0.16 (0.07–0.26)	0.16 (0.07–0.26)	0.19 (0.09–0.28)	0.17 (0.07–0.26)x
Trtmt	0.26 (0.17–0.35)A	0.27 (0.18–0.36)A	0.27 (0.18–0.37)A	0.56 (0.47–0.65)By
Post	0.24 (0.14–0.33)A	0.20 (0.10–0.29)A	0.21 (0.11–0.30)A	0.57 (0.48–0.66)By
0.5–1 cm				
Pre	0.25 (0.09–0.42)	0.30 (0.14–0.46)	0.37 (0.21–0.54)	0.32 (0.16–0.48)x
Trtmt	0.45 (0.29–0.61)A	0.35 (0.19–0.52)A	0.45 (0.29–0.62)A	0.99 (0.83–1.16)By
Post	0.48 (0.32–0.65)A	0.45 (0.29–0.61)A	0.38 (0.22–0.55)A	0.89 (0.73–1.06)By
1–3 cm				
Pre	1.03 (−0.22–2.28)	0.99 (−0.26–2.24)	1.43 (0.18–2.68)	1.21 (−0.04–2.46)x
Trtmt	1.06 (−0.19–2.31)A	1.06 (−0.19–2.31)A	1.32 (0.07–2.60)A	4.47 (3.22–5.72)By
Post	1.58 (0.33–2.83)A	1.32 (0.07–2.57)A	1.36 (0.11–2.61)A	4.51 (3.26–5.76)By
3–5 cm				
Pre	1.93 (0.66–3.20)	1.05 (−0.22–2.32)	2.28 (1.01–3.55)	2.02 (0.75–3.29)
Trtmt	1.84 (0.57–3.11)	1.14 (−0.13–2.41)	2.11 (0.84–3.36)	4.04 (2.77–5.31)
Post	2.11 (0.84–3.38)	1.23 (−0.04–2.50)	2.63 (1.36–3.90)	4.39 (3.12–5.66)
All†	1.96 (1.16–2.76)AB	1.14 (0.34–1.94)A	2.34 (1.54–3.14)AB	3.48 (2.68–4.28)B
Understory				
Litter cover				
Pre	42.3 (34.9–49.7)A	43.7 (36.4–51.0)Ax	50.2 (42.7–57.6)AB	59.5 (52.0–66.9)Bx
Trtmt	51.7 (44.3–59.1)A	59.8 (52.5–67.1)ABy	61.9 (54.5–69.4)AB	69.8 (62.4–77.3)By
Post	55.4 (48.0–62.9)A	57.0 (49.7–64.4)Ay	62.5 (55.1–70.0)A	89.1 (81.7–96.6)Bz
Below-ground				
Forest floor depth				
Pre	0.90 (0.76–1.04)ABy	1.05 (0.91–1.18)By	0.89 (0.75–1.03)AB	0.82 (0.68–0.95)A
Trtmt	0.63 (0.49–0.77)x	0.71 (0.57–0.85)x	0.74 (0.60–0.88)	0.66 (0.53–0.80)
Post	0.76 (0.62–0.90)xy	0.79 (0.65–0.92)x	0.82 (0.69–0.96)	0.64 (0.50–0.78)
pH				
Pre	3.52 (3.33–3.71)	3.56 (3.37–3.75)	3.64 (3.45–3.82)	3.68 (3.49–3.87)
Trtmt	3.51 (3.33–3.70)A	3.53 (3.34–3.72)A	3.66 (3.47–3.85)AB	3.74 (3.55–3.92)B
Post	3.56 (3.38–3.75)A	3.63 (3.45–3.82)AB	3.76 (3.57–3.95)AB	3.82 (3.63–4.01)B
Nutrient supply rates				
Ca				
Pre	1192 (1070–1314)x	1362 (1241–1484)	1394 (1272–1516)x	1302 (1174–1430)x
Trtmt	1275(1154–1397)Ax	1357(1235–1478)AB	1281(1160–1403)Ax	1529 (1401–1657)By
Post	1522 (1400–1643)y	1493 (1371–1615)	1648 (1526.–1770)y	1554 (1426–1682)y
Mg				
Pre	234 (200–269)x	269 (234–304)	246 (212–281)x	279 (243–315)x
Trtmt	272 (238–307)Axy	292 (257–327)AB	256 (221–291)Ax	338 (302–373)By
Post	316 (281–350)y	313 (278–348)	320 (285–354)y	333 (297–369)y
P				
Pre	13.2 (8.1–18.3)	16.6 (11.5–21.7)	19.2 (14.1–24.4)xy	13.4 (8.1–18.6)x
Trtmt	16.9 (11.8–22.0)	17.4 (12.3–22.5)	15.2 (10.1–20.3)x	17.8 (12.6–23.1)x
Post	15.4 (10.3–20.5)A	20.1 (15.0–25.3)AB	23.1 (18.0–28.2)ABy	27.9 (22.6–33.1)By
MSIR respiration rates				
Aminobutyric acid				
Pre	21.5 (18.8–24.1)y	19.7 (17.1–22.4)x	19.4 (16.8–22.1)y	21.1 (18.5–23.8)y
Trtmt	16.8 (14.2–19.5)x	16.9 (14.3–19.6)x	14.9 (12.3–17.5)x	14.8 (12.1–17.4)x
Post	23.9 (21.3–26.6)Ay	25.4 (22.7–28.0)ABy	29.4 (26.8–32.1)Bz	21.5 (18.9–24.2)Ay
3,4-Dihydroxybenzoic acid				
Pre	20.3 (17.7–22.8)y	19.3 (16.7–21.8)xy	19.1 (16.5–21.6)y	20.4 (17.8–23.0)y
Trtmt	16.4 (13.9–19.0)x	16.6 (14.0–19.1)x	14.7 (12.1–17.2)x	14.7 (12.2–17.3)x
Post	21.7 (19.2–24.3)yAB	24.3 (21.7–26.8)ABy	28.8 (26.3–31.4)Bz	21.8 (19.2–24.4)Ay
L-lysine				
Pre	15.8 (13.6–18.0)xy	14.8 (12.7–17.0)x	14.0 (11.9–16.2)x	14.9(12.8–17.1)y
Trtmt	13.2 (11.0–15.3)x	12.8 (10.6–15.0)x	11.4 (9.2–13.6)x	11.2 (9.0–13.4)x
Post	17.3 (15.1–19.5)ABy	19.2 (17.1–21.4)ABy	22.4 (20.2–24.5)By	16.0 (13.8–18.1)Ay

Table 3. Continued.

Variable and Year	Treatment			
	Control	50% kill	100% kill	Salvage
Oxalic acid				
Pre	25.4 (22.4–28.5)y	25.4 (22.4–28.5)xy	24.9 (21.9–28.0)y	26.7 (23.6–29.7)y
Trtmt	19.8 (16.8–22.9)x	20.8 (17.8–23.9)x	18.2 (15.2–21.3)x	17.6 (14.5–20.6)x
Post	28.9 (25.8–31.9)ABy	29.5 (26.5–32.6)ABy	34.0 (31.0–37.1)Bz	24.6 (21.5–27.7)Ay
Bacteria PLFA				
Pre	27.6 (25.6–29.5)	27.9 (26.0–29.9)xy	27.6 (25.6–29.5)x	29.7 (27.7–31.7)xy
Trtmt	26.9 (24.9–28.8)	26.5 (24.5–28.4)x	27.0 (25.1–29.0)x	27.5 (25.6–29.5)x
Post	28.6 (26.6–30.5)	28.9 (27.0–30.9)y	30.0 (28.0–31.9)y	30.6 (28.6–32.5)y
All†	27.7 (26.0–29.3)A	27.8 (26.1–29.4)A	28.2 (26.5–29.9)AB	29.3 (27.6–30.9)B
Actinomycete PLFA				
Pre	4.69 (4.08–5.30)	4.79 (4.19–5.40)xy	4.54 (3.93–5.14)	5.06 (4.44–5.67)
Trtmt	4.44 (3.83–5.05)	4.30 (3.69–4.91)x	4.49 (3.88–5.10)	4.80 (4.19–5.41)
Post	5.07 (4.46–5.68)	5.13 (4.52–5.74)y	4.87 (4.27–5.48)	5.64 (5.03–6.25)
All†	4.73 (4.27–5.20)AB	4.74 (4.27–5.21)AB	4.63 (4.16–5.10)A	5.17 (4.70–5.64)B
PLFA fungi:bacteria				
Pre	0.78 (0.72–0.83)	0.78 (0.72–0.83)	0.77 (0.72–0.83)	0.72 (0.67–0.78)x
Trtmt	0.74 (0.69–0.79)	0.74 (0.69–0.80)	0.76 (0.70–0.81)	0.73 (0.67–0.78)x
Post	0.71 (0.65–0.76)	0.71 (0.67–0.77)	0.72 (0.66–0.77)	0.64 (0.58–0.69)y
All†	0.74 (0.70–0.78)AB	0.74 (0.71–0.78)AB	0.75 (0.71–0.79)B	0.70 (0.66–0.73)A

Notes: Units are: DWM, Mg ha^{-1}; nutrient supply rates, μg /10 cm^2/burial length; MSIR respiration rates, μg CO_2-C/g/hr; bacteria and actinomycete PLFA, mol %.

† All years combined is also reported because pairwise comparisons of treatments within each of the three years did not show any significant differences.

with the pre-treatment year (Table 2, Fig. 2a). In the post-treatment year, the salvage stands had lower quadrat-level species richness than the 100% kill stands with intermediate levels in the control and 50% kill stands (Table 2, Fig. 2a). For experimental unit-level species richness, the salvage stands had lower species richness compared with the 50% kill stands in the treatment year, and with the 50% and 100% kills stands in the post-treatment year, but no differences with the control stands in any of the years (Table 2, Fig. 2b).

There were decreases in total, forb, and shrub cover for the salvage stands in the treatment and post-treatment years compared with the pre-treatment year, but no difference for the other three treatments among years (Table 2, Fig. 3a, b, c). Bryophyte cover decreased for the salvage stands in the post-treatment year compared with the pre-treatment year, with intermediate levels in the treatment year (Table 2, Fig. 3d). Total understory cover was lower in both the treatment and post-treatment years for the salvage stands compared with the other treatments (Fig. 3a). Shrub cover was lower in the salvage stands compared with the 50% kill and 100% kill stands in the treatment year, and compared with all the other treatments in the post-treatment year (Table 2, Fig. 3b). The salvage stands had lower forb cover compared with the control and 100% kill stands in the treatment year, and compared with all three other treatments in the post-treatment year (Table 2, Fig. 3c). In the salvage stands there was also lower bryophyte cover compared with the control and 50% kill stands in the treatment year, and compared with all three other treatments in the post-treatment year (Table 2, Fig. 3d).

The NMS two-dimensional solution (final stress = 11.9 after 29 iterations) explained 91.9% of the variation in the understory vegetation community and visualized the separation between the salvage stands post-treatment and the other treatments; the separation of the salvage stands was associated with decreased vegetation cover and increased litter cover and pH, with the greatest separation occurring one year post-treatment (Fig. 4). There were significant differences in community composition among the treatments ($P = 0.0002$); salvage logged stands differed from all three other treatments (salvage vs control $P = 0.003$; salvage vs 50% kill $P = 0.0004$, salvage vs 100% kill $P = 0.0004$). PerMANOVA of the understory vegetation community showed no significant differences among

Table 4. Mean and 95% confidence intervals in each year of the study; years with a different lower case letter (x, y, z) were significantly different for that variable. These were based on post-hoc lsmeans comparisons for variables that showed significant year effects, but for which there was no significant interaction between treatment and time in the ANOVA (see Table 2).

Variable	Pre-Treatment Year	Treatment Year	Post-treatment Year
Total DWM	37.0 (23.0–50.9)x	43.4 (29.4–57.3)xy	50.7 (36.7–64.6)y
Soil moisture			
0–20 cm depth	48.2 (42.5–54.0)x	57.8 (52.1–63.6)y	59.5 (53.7–65.2)y
0–40 cm depth	112.6 (104.6–120.7)x	123.3 (115.2–131.4)y	132.4 (124.4–140.5)y
0–60 cm depth	163.6 (154.1–173.2)x	178.5 (168.8–188.1)y	208.4 (198.8–217.9)z
Nutrient supply rates			
Al	69.1 (60.3–77.9)x	88.2 (79.3–97.0)y	83.0 (74.2–91.9)y
B	0.90 (0.78–1.02)x	1.00 (0.88–1.12)x	0.49 (0.38–0.61)y
Fe	69.1 (60.3–78.0)x	88.2 (79.3–97.0)y	83.1 (74.2–91.9)z
Mn	53.1 (40.3–65.8)x	59.8 (47.1–72.6)xy	67.9 (55.2–80.7)y
NH_4-N	3.90 (2.58–5.22)x	6.20 (4.89–7.52)y	5.58 (4.26–6.89)xy
S	73.8 (26.7–120.9)x	96.3 (49.2–143.4)y	87.6 (40.5–134.7)y
Zn	3.57 (2.57–4.56)x	4.22 (3.22–5.22)x	5.28 (4.29–6.28)y
pH	3.60 (3.43–3.76)x	3.61 (3.45–3.77)xy	3.70 (3.53–3.86)y
Multiple carbon source SIR			
Basal (water)	13.1 (12.1–14.1)x	10.8 (9.8–11.7)y	16.5 (15.5–17.5)z
N-acetyl glucosamine	17.7 (16.3–19.1)x	14.4 (13.0–15.8)y	22.7 (21.3–24.1)z
L-alanine	19.6 (18.4–20.9)x	14.9 (13.6–16.1)y	23.7 (22.5–24.9)z
Arabinose	22.0 (20.7–23.4)x	16.8 (15.4–18.2)y	26.0 (24.6–27.3)z
L-arginine	15.3 (14.1–16.5)x	12.1 (10.9–13.3)y	19.6 (18.3–20.8)z
Citric acid	22.0 (20.5–23.5)x	17.9 (16.4–19.3)y	26.4 (24.9–27.9)z
Galactose	21.2 (19.8–22.6)x	16.5 (15.1–18.0)y	26.5 (25.0–27.9)z
Glucose	24.9 (23.1–26.7)x	18.7 (17.0–20.5)y	28.7 (26.9–30.5)z
Glutamic acid	23.6 (22.0–25.2)x	17.4 (15.8–19.0)y	26.2 (24.6–27.8)z
Malic acid	29.2 (27.1–31.3)x	23.3 (21.1–25.4)y	32.4 (30.2–34.5)z
Mannose	23.3 (21.5–25.1)x	17.8 (16.1–19.6)y	27.7 (26.0–29.5)z
Trehalose	21.9 (20.2–23.7)x	16.6 (14.8–18.4)y	26.2 (24.5–28.0)z
Catabolic evenness	15.6 (15.5–15.6)x	15.8 (15.7–15.9)y	15.8 (15.7–15.9)y
Total PLFA biomass	1198 (1121–1275)x	1414 (1338–1491)y	1305 (1229–1382)xy
Fungal (excl. myco)	15.9 (15.3–16.4)x	15.3 (14.7–15.8)xy	15.0 (14.5–15.6)y
Arbuscular mycorrhizae	2.70 (2.34–3.05)x	2.27 (1.92–2.63)y	2.63 (2.28–2.99)x
Metabolic quotient	0.011 (0.011–0.012)y	0.008 (0.007–0.009)x	0.013 (0.012–0.014)y

Notes: Units are: DWM, Mg ha^{-1}; soil moisture, mm; nutrient supply rates, μg/10 cm^2/burial length; MSIR respiration rates, μg CO_2-C/g/hr; PLFA biomass, nmol g^{-1}; Fungal and arbuscular mycorrhizae, mol, %.

years ($P = 0.15$) and no interaction between treatment and year ($P = 0.49$). For Shannon diversity of the understory plant community, graminoid cover, and basal area of tall shrubs, no significant differences among treatments or years were detected (Table 2).

Below-ground

The forest floor was deeper in the pre-treatment year compared with the treatment and post-treatment years for the 50% kill stands, and compared with the treatment year in the control stands, with no inter-annual differences for the other two treatments (Tables 2 and 3). There were only differences in forest floor thickness among treatments in the pre-treatment year (Tables 2 and 3).

Soil moisture increased over time for all three soil depth increments, independent of treatment (Tables 2 and 4). Soil moisture at both 0–20 cm and 0–40 cm was significantly lower in the pre-treatment year compared with both the treatment and post-treatment years, while at 0–60 cm depth it increased in each year (Table 4).

The pre-treatment year pH was lower than the post-treatment year, independent of treatment (Tables 2 and 4). The control and 50% kill stands had lower forest floor pH than the salvage stands, with intermediate pH in the 100% kill stands in the treatment year, with the same pattern in the post-treatment year except that 50% kill had pH intermediate between the control and salvage stands (Tables 2 and 3).

There was no consistent pattern in supply rates of the nutrients (Tables 2–4). Calcium and Mg supply rates differed among treatments only in the treatment year; the control and 100% kill stand rates were lower than the salvage, with

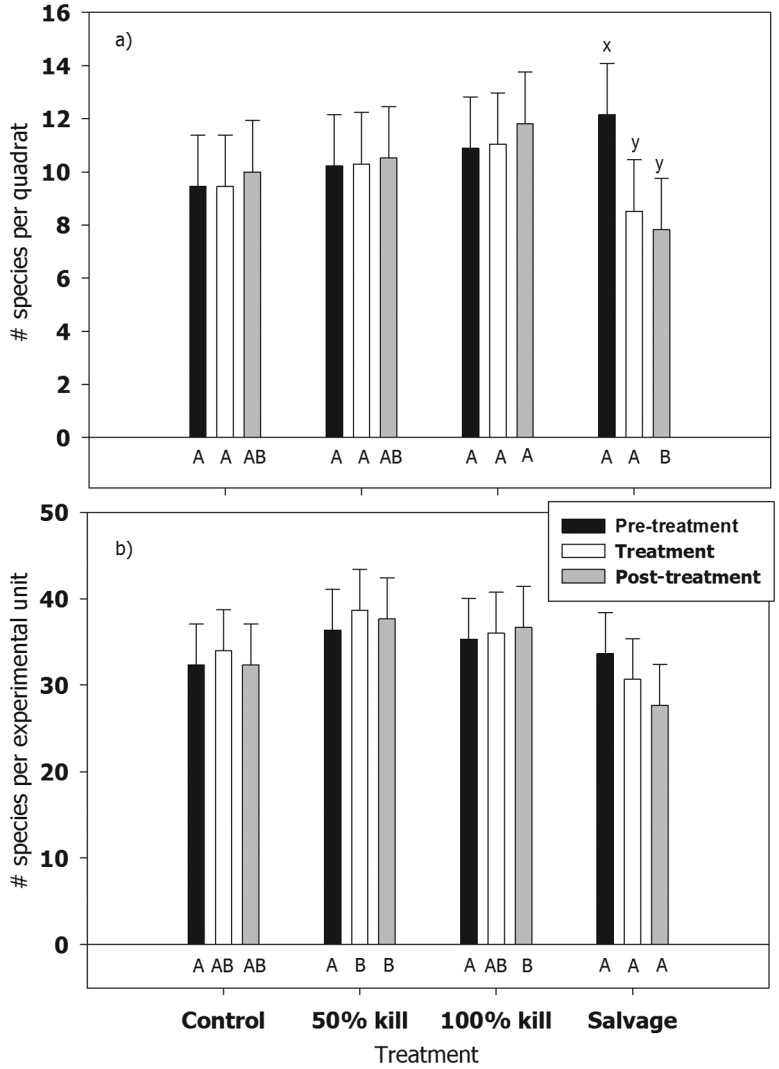

Fig. 2. Mean understory vegetation species richness at the scale of (a) 1-m^2 quadrat, and (b) 0.48 ha experimental unit, by treatment and year (±95% CI). Years with different letters (x, y) within a treatment and treatments with different letters (A, B, C) within a year were significantly different.

intermediate rates in the 50% kill stands (Tables 2 and 3). Phosphorus rates differed among treatments only in the post-treatment year; salvage stand rates were higher than for the control, with intermediate rates in the MPB treatments (Tables 2 and 3). In the control stands, Ca rates significantly increased in the post-treatment year compared with the previous two years, whereas Mg rates increased in the post-treatment year compared with the pre-treatment year, with intermediate levels in the treatment year (Table 3). There were no differences in Ca, Mg, and P rates among years for the 50% kill stands (Table 3). In the 100% kill stands, Ca and Mg increased in the post-treatment year compared with the previous two years, whereas P increased in the post-treatment year compared with the treatment year, but with intermediate levels in the pre-treatment year (Table 3). For the salvage stands, both Ca and Mg significantly increased in the treatment and post-treatment years compared with the pre-treatment year, whereas P increased only in the post-treatment year compared with the previous two years (Table 3). For the nutrient

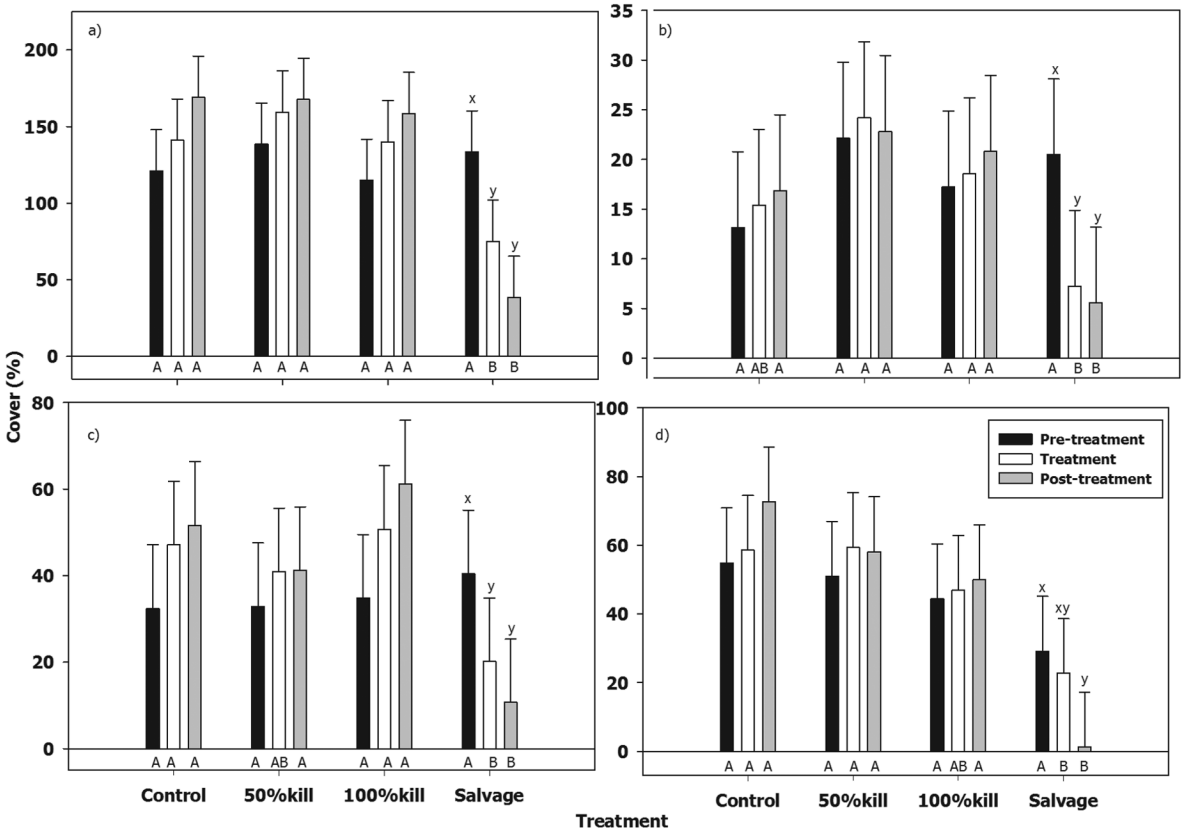

Fig. 3. Mean percent cover for (a) total understory, (b) bryophytes, (c) forbs, and (d) shrubs by treatment and year (±95% CI). Years with different letters (x, y) within a treatment and treatments with different letters (A, B, C) within a year were significantly different.

supply rates of Al, B, Fe, Mn, NH_4-N, S, and Zn there were only differences among years independent of treatment and there was no consistent pattern in rates among years for these nutrients (Tables 2 and 4). The NMS two-dimensional solution (final stress = 10.0 after 35 iterations) explained 95.0% of the variation in the nutrient supply rate profiles and showed separation among the years; the annual increases in soil moisture at 0–60 cm depth and catabolic evenness and decrease in the ratio of PLFA fungi:bacteria ratio appeared to be consistent among treatments (Fig. 5). Consistent with findings for individual nutrients, there were differences in nutrient supply rate profiles among years (PerMANOVA $P = 0.0002$); post-treatment nutrient supply profiles differed from both pre- ($P = 0.0002$) and treatment year ($P = 0.00006$) profiles. There were no differences in nutrient supply rates among treatments (perMANOVA $P = 0.07$) and no interaction between treatment and year (perMANOVA $P = 0.42$).

The carbon respiration substrates aminobutyric acid, 3,4-dihydroxybenzoic acid, lysine, and oxalic acid only differed among treatments in the post-treatment year; aminobutyric acid respiration rates were higher in the 100% kill stands than in the control and salvage stands, whereas 3,4-dihydroxybenzoic acid, lysine, and oxalic acid respiration rates were also higher in the 100% kill stands, but only significantly higher than in the salvage stands (Tables 2 and 3). The differences among years within each treatment for aminobutyric acid, 3,4-dihydroxybenzoic acid, lysine, and oxalic acid generally showed a pattern of having the lowest respiration rates in the treatment year (Table 3). The only differences for basal respiration and MSIR of the remaining 12 carbon substrates were among years, independent of treatment; their respiration rates

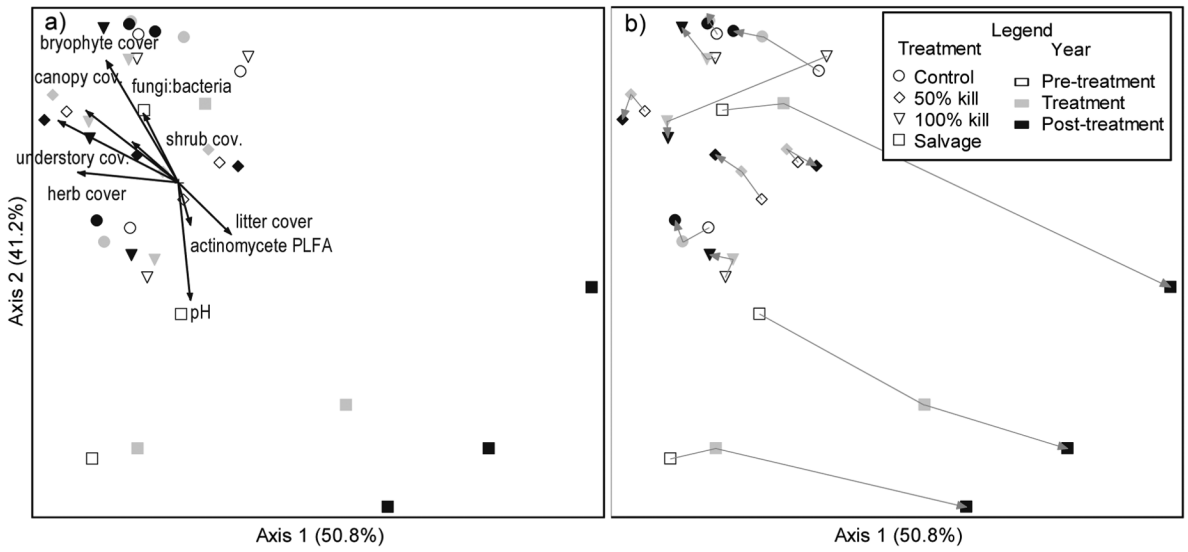

Fig. 4. Results of Nonmetric Multidimensional Scaling (NMS) ordination for the understory vegetation community delineated by treatment and year presented with: (a) the angles and lengths of the vectors which indicate direction and strength of relationships of the variables (see Table 2 for information on the variables) with the ordination axes (cut-off for displayed variables was $R^2 > 0.25$, and vector scaling was set to 65% so that vectors could be displayed without going beyond the ordination plot); and (b) vectors that connect each experimental unit among the pre-treatment, treatment, and post-treatment years. The amount of variation explained by each axis is included in parentheses.

decreased in the treatment year, and then subsequently increased in the post-treatment year, compared with the pre-treatment year (Tables 2 and 4). Pre-treatment year catabolic evenness was significantly lower than both the treatment and post-treatment years, independent of treatment (Tables 2 and 4). The NMS two-dimensional solution (final stress = 10.1 after 48 iterations) explained 94.8% of the variation in the MSIR profiles and illustrated separation among the years, independent of treatment (Fig. 6; vectors connecting experimental units among years were excluded because they showed similar patterns among all treatments). Pre-treatment year respiration profiles were associated with higher values for gross precipitation, treatment year respiration profiles were positively associated with Al and catabolic evenness, and post-treatment year profiles were negatively associated with B and Fe (Fig. 6). There were differences among years (perMANOVA P = 0.004); pre-treatment respiration profiles differed from treatment year profiles (P = 0.005), but there were no differences among treatments (P = 0.90) or interaction between treatment and year (perMANOVA P = 0.75).

Examining patterns in PLFAs, for bacterial and actinomycete PLFAs in the 50% kill stands, PLFAs increased in the post-treatment year compared with the treatment year (Tables 2 and 3). For the bacterial PLFAs there were also increases in the 100% kill stands in the post-treatment year compared with the pre-treatment and treatment years, and increases in the salvage stands in the post-treatment year compared with the treatment year. Comparing treatments among individual years did not reveal any differences but combining data for all years for each treatment showed higher PLFA mol % in the salvage stands, compared with the control and 50% kill stands for bacterial PLFAs, and compared with the 100% kill stands for actinomycete PLFAs. The fungi:bacteria ratio was lower in the post-treatment year, compared with the pre-treatment and treatment years for the salvage stands (Tables 2 and 3). There were no differences among treatments within years, but combining data for all years, there was a lower ratio of

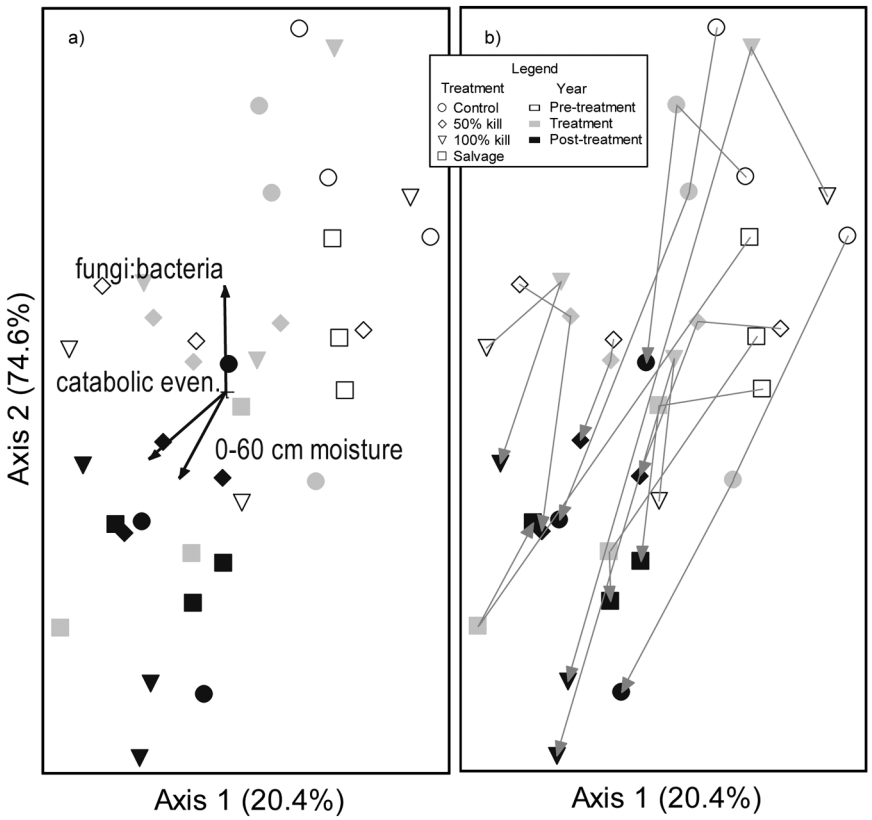

Fig. 5. Results of Nonmetric Multidimensional Scaling (NMS) ordination for the nutrient supply rates delineated by treatment and year presented with: (a) the angles and lengths of the vectors which indicate direction and strength of relationships of the variables (see Table 2 for information on the variables) with the ordination axes (cut-off for displayed variables was $R^2 > 0.25$); and (b) vectors that connect each experimental unit among the pre-treatment, treatment, and post-treatment years. The amount of variation explained by each axis is included in parentheses.

fungi:bacteria in the salvage stands compared with the 100% kill stands, with intermediate levels in the other treatments (Tables 2 and 3). There were only differences among years, independent of treatment, for total PLFA biomass, fungal PLFAs, arbuscular mycorrhizae PLFAs, and metabolic quotient, and there was no consistent pattern among years for these PLFA variables (Tables 2 and 4). The NMS two-dimensional solution (final stress = 9.88 after 37 iterations) explained 93.9% of the variation in the PLFA dataset, and illustrated the separation of the stands among years, independent of treatment (Fig. 7; vectors connecting experimental units among years were excluded because they showed similar patterns among all treatments). Pre-treatment year PLFA communities were most positively associated with gross precipitation, treatment year PLFA communities were positively associated with B, Fe, S, and the PLFA ratio of fungi:bacteria, and post-treatment year PLFA communities were positively associated with below-ground variables including Mg, soil moisture, basal respiration, actinomycete PLFAs, and litter cover. PLFA community structure in all three years differed (perMANOVA $P = 0.0002$; post-hoc comparisons all had $P = 0.0002$) but there were no differences among treatments (perMANOVA $P = 0.29$) or their interaction with year (perMANOVA $P = 0.99$). There were no differences in decomposition or plant available K among treatments or years (Table 2).

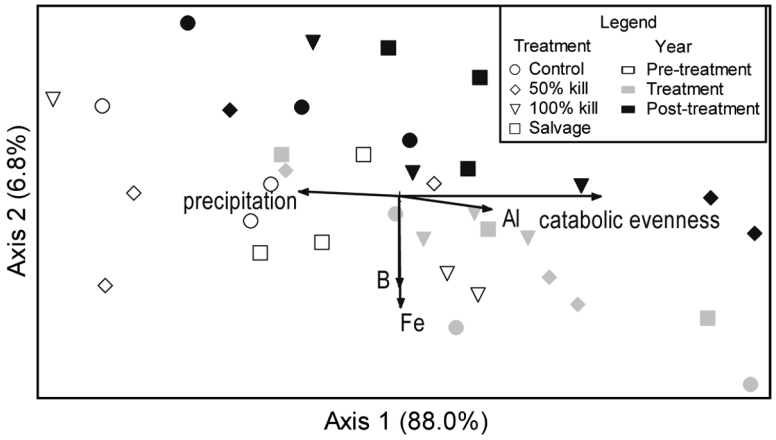

Fig. 6. Results of Nonmetric Multidimensional Scaling (NMS) ordination for the MSIR delineated by treatment and year. The amount of variation explained by each axis is included in parentheses. The angles and lengths of the vectors indicate direction and strength of relationships of the variables (see Table 2 for information on the variables) with the ordination axes (cut-off for displayed variables was $R^2 > 0.25$).

Discussion

To our knowledge, this is the first experimental study that provides an evaluation of the potential impacts of MPB early attack and associated forest management on downed woody material, vegetation composition, and below-ground responses to attack, rather than using a chronosequence to substitute space for time. The gradient of decreased basal area of healthy trees in the 50% and 100% kill stands supported that our treatments were effective in capturing a gradient of overstory tree mortality associated with simulated MPB attack, and these findings were also supported by evidence of decreased sapflow conductivity in killed trees in a paired hydrology study that was conducted on our study sites (Piña 2012). Despite the canopy mortality resulting from simulated MPB attack, we saw no effects of the MPB treatments on other above- and below-ground properties and processes in these forests, except for increased microbial respiration of four carbon substrates. Our results differ with Edburg et al.'s (2012) conceptual model of MPB ecosystem impacts, which proposes biogeochemical ecosystem responses will occur during the red attack stage (within months after attack). As we hypothesized, we saw more immediate changes in the above-ground plant community, DWM, and several below-ground properties for the salvage logged stands than in the MPB treatments. Our findings suggest

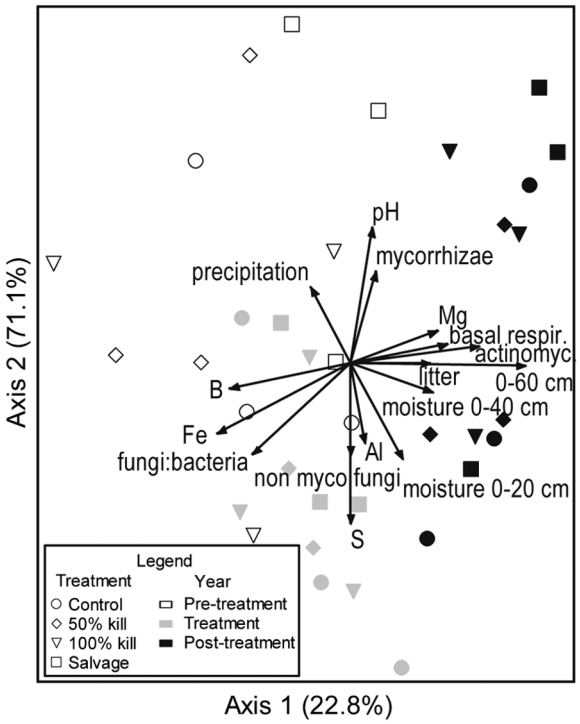

Fig. 7. Results of Nonmetric Multidimensional Scaling (NMS) ordination for the phospholipid fatty acid profiles delineated by treatment and year. The amount of variation explained by each axis is included in parentheses. The angles and lengths of the vectors indicate direction and strength of relationships of the variables with the ordination axes (cut-off for displayed variables was $R^2 > 0.25$).

ecological resistance in the early green and red attack stages of MPB, and that the ecological inertia (i.e., the lag in time before the plant community and associated ecosystem properties and processes respond to disturbance; Jentsch and Beierkuhnlein 2008) is higher for the MPB-disturbed stands compared with the salvage logged stands.

We saw increases in the three smallest DWM size classes (<0.5, 0.5–1, and 1–3 cm diameter) in the salvage treatment compared with the other treatments in the treatment and post-treatment years. The lack of response of DWM to the MPB treatments is likely a result of the lag between when the trees are attacked and the needles drop and the trees fall. Our findings are in agreement with previous studies which also showed minimal changes in DWM biomass associated with MPB red attack. Previous research in ponderosa pine forests showed that MPB-attacked trees lost most of their foliage between the second and third year post-attack (Chojnacky et al. 2000). In an Oregon lodgepole pine study, snags began falling three years after MPB attack, and 80% of trees fell within 10 years (Mitchell and Preisler 1998). Lewis and Thompson (2011) found that for pine trees killed by MPB in central BC, most dead trees did not start to fall until eight years after they died. Interestingly, a study in Colorado found there were no differences in fine or coarse DWM loads between unattacked stands and stands with current or recent (up to 7 years prior) MPB attack (Klutsch et al. 2009). Simard et al. (2011) compared surface fuel loads for multiple size categories for unattacked, red, and grey stages of MPB attack and also found no differences among them. Rather than changes in biomass of DWM in the red attack stage, Simard et al. (2011) concluded that there were changes in the moisture content of DWM, which we did not measure. In the harvested stands it was surprising that we did not detect increases in biomass across all size classes compared with the other treatments, as the stump-side processing system leaves debris on site. Instead we observed increases in total biomass of downed wood in the treatment and post-treatment years across all treatments. This overall increase is likely a function of both natural mortality associated with the mature successional stage of these stands, and blow-down resulting from windthrow. There were multiple extreme wind events recorded in the study area in both the treatment and post-treatment years that could have contributed to the DWM increases we observed.

Previous studies have shown significant effects of harvest on the understory vegetation of boreal forests after harvest, with a gradient of effects dependent on the intensity of harvest/thinning (e.g., Bergstedt and Milberg 2001). Thus, with mortality and loss of the overstory canopy as a result of disturbance, we expected associated changes in the understory plant community in the salvage logged stands. Changes in the salvage logged stands are likely a result of the direct impact of harvesting on the understory and forest floor, including trampling of the vegetation by the harvesting machinery and increased deposition of litter. The impact of mechanical disturbance to the forest floor is great, and is the primary difference between disturbance by MPB—and other insects—versus fire or any kind of harvesting, which translates to more immediate effects on the understory plant community. The increased litter that was associated with the salvage logged stands is likely a consequence of the slash and the mortality in the understory that occurred after harvest in these stands. While harvesting frequently increases overall understory species richness relative to unharvested forests by increasing the number of early-successional shrub and herb species while decreasing the number of late-successional lichens, mosses and herbs (e.g., Battles et al. 2001, Haeussler et al. 2002), it takes time post-disturbance for these changes to occur. One-year post treatment is likely too early to see these patterns and instead we likely saw decreases in plant cover and richness because of the machinery damage, and exposure of remaining plants to higher levels of solar radiation, compared with the other treatments that did not directly affect the forest floor.

Past research on the response of the understory community to MPB attack has primarily been focused on tree regeneration with little attention to the understory composition and biodiversity after MPB attack. Kovacic et al. (1985) studied ponderosa pine after MPB attack and found that understory biomass peaked five years post MPB attack. In the red stage of MPB attack, Griffin et al. (2011) found significantly higher total and

forb cover compared with undisturbed stands, but no differences in shrubs and graminoids. Stone and Wolfe (1996) found changes in understory biomass depended upon the mortality rate of lodgepole pine in the overstory of stands in Utah that were attacked within the previous 10 years, with exponentially increasing understory biomass with increasing overstory mortality, but species richness peaking at intermediate levels of MPB attack. A redistribution of biomass production from overstory trees to understory vegetation in lodgepole pine ecosystems was still seen in Waterton Lakes National Park 25 years after the disturbance (Dykstra and Braumandl 2006). Our findings suggest that while one year after simulated MPB treatment changes in the understory have not yet occurred, we expect changes to occur in the future. This is supported by Klutsch et al. (2009) who compared MPB-infested and uninfested lodgepole pine stands both 0–3 years and 4–7 years post-infestation in Colorado and also found no difference in percent cover among understory vegetation groups in the short term. Given that attacked trees do not lose most of their foliage until between the second and third year post-attack, perhaps changes in the forest understory plant community will not occur until the needles have dropped and in turn have altered other ecosystem properties and processes, such as nutrient cycling. Thus, we expect that as the stands transition from red attack to grey attack and drop their needles, increases in light transmission to the understory and increased litter inputs will alter forest floor nutrient cycling properties and processes, which are likely to modify plant growth in the understory. However, for the understory vegetation variables we studied, the lack of differences among the MPB treatments and control stands suggests that the understory plant community is resistant to changes in the forest associated with the early red-attack stage of MPB.

For most below-ground response variables we saw differences among years across treatments rather than differences among the treatments. Our findings of inter-annual differences in soil moisture—rather than differences among treatments—differ from those obtained in the paired hydrology study. That study found a gradient of moisture in the shallower regions of the soil (5 cm and 0–20 cm) from the driest conditions in the control stand treatment type, with a trend of increasing soil moisture in the 50% kill, and 100% kill stand treatment types, and the salvage logged stands being the wettest (Piña 2012). These findings suggest that there are differences in soil moisture associated with both salvage harvest and MPB attack. Our sampling resolution (only 2 sub-samples per site rather than the 9 used for other properties) and intervals at which we sampled in this study were likely too low to capture these differences; future studies should focus on sampling soil moisture shallower with more sample points and increased frequency of measurement. Our findings of no significant differences in microbial biomass between the control and clearcut stands are consistent with Entry et al. (1986), who also found no differences in microbial biomass between control stands and clearcut lodgepole pine stands in Montana that had both residue removed and residue left on-site. Instead, Entry et al. (1986) found that for soil temperatures above 5°C, microbial biomass was positively correlated with soil moisture. In a comparison of seven different forest types in BC, including lodgepole pine, Brockett et al. (2012) found the properties most closely related to microbial community characteristics were soil moisture and organic matter, which is consistent with our observations of the inter-annual patterns of soil moisture at 0–60 cm depth that were associated with the separation of microbial PLFA communities, although we would have expected soil moisture at shallower depths to also be important. The lack of difference in MSIR among stands post-salvage is supported by Siira-Pietikäinen et al. (2001), who also did not find differences in respiration one year post harvest for Norway spruce (*Picea abies* (L.) Karst.)–Scots Pine (*Pinus sylvestris* L.)–*Betula* spp. stands in central Finland. Siira-Pietikäinen et al. (2001) did find differences two years after clear-cut harvest, suggesting that changes are more likely to occur in these stands as time post-disturbance advances and nutrient cycling dynamics change in response to additions of litter and changes in soil moisture and light. The increased microbial respiration rates in the 100% kill stands for the three carboxylic acids and lysine in the post-treatment year compared with the salvage treatment suggest that below-ground changes

are beginning to occur in the MPB-attacked stands, with a shift to a microbial community that differs in its respiration patterns compared to the salvage microbial community, although this was not illustrated in the MSIR ordination.

Even though we did not observe short-term responses of PLFA biomass to harvesting, other studies have shown that these responses do eventually occur (e.g., Mummey et al. 2010), and can in fact be very long lasting (e.g., Chatterjee et al. 2008). We did see signs of differences in the relative composition of the PLFA microbial community among treatments suggesting that the structure of the PLFA community may be more sensitive to salvage than PLFA biomass, but this trend couldn't be separated out within individual years (although there seemed to be a trend in which the fungi:bacteria PLFA ratio was shifting towards an increasing proportion of bacterial PLFAs in the salvage logged stands). The microbial community is impacted by soil pH, and it is generally accepted that fungi are favored over bacteria at low pH (Alexander 1977). This pattern has been shown across large pH ranges (e.g., Högberg et al. 2003), but also within narrow ranges of soil pH (e.g., Pennanen et al. 1999) such as the increased pH we observed in the salvage logged stands in the treatment and post-treatment years compared with the control stands. This variation in pH and the microbial community composition, in turn, will influence biogeochemical cycles among the treatments, including potentially affecting the soil concentrations of plant root exudates and plant available nutrients. However, our findings suggest that in the immediate post-disturbance time period, patterns of increased availability of nutrients are not yet evident in the MPB-attacked stands or in the salvage, except for Ca, Mg, and P. Our findings correspond with Bock and Van Rees (2002) who also found an increase in exchangeable Ca in boreal mixed-wood forests after harvest compared with uncut forests. These findings contrast with marginally significant decreases of Ca found under newly MPB-killed trees compared with live trees in mature pine forests in Colorado (Xiong et al. 2011). Our findings also differ with Griffin et al. (2011) who found significantly higher Ca in Yellowstone red attacked lodgepole pine stands compared with unattacked stands, along with higher rates of N mineralization and nitrification compared with undisturbed forests. Hynes and Germida (2012) showed higher levels of ammonia and nitrate in lodgepole pine stands 2–19 years after clear-cutting in western Alberta, with ammonia peaking four years post clearcut. Our results suggest the assart effect is just beginning one year after disturbance in our stands, and should peak in the coming years as decomposition processes respond to the treatments. Overall, our dominant finding of differences among study years rather than differences among the treatments suggests that inter-annual variability at the landscape scale exerts a stronger influence on most forest floor properties and processes than treatment effects of MPB or associated forest management in the short term (i.e., one year post treatment) do.

In the salvage logged stands we saw immediate changes in the understory plant community, DWM, and in several below-ground properties. However, we found short-term resistance to simulated MPB at the early red-attack stage for DWM, understory, and the majority of below-ground properties and processes in these forests. Thus, it remains uncertain what successional trajectory lodgepole pine forests in Alberta will follow post-MPB attack in the longer term, but our research demonstrates that the successional trajectory of stands that are salvage logged will be very different from that of stands that are attacked by MPB and left unmanaged. Research on MPB in other regions that has been carried out over longer periods suggests that as these MPB-attacked stands transition from red to grey attack they will begin to show more significant responses compared with the undisturbed stands, however when and the magnitude of these delayed responses to this novel disturbance agent remain unknown. Longer-term research that continues to follow MPB-attacked stands temporally post-disturbance is needed to better understand how these stands will continue to respond to this novel disturbance agent and shifting disturbance regimes from stand-replacing disturbances such as fire and clear-cut harvesting, to the addition of partial canopy disturbances that result from MPB attack.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Plant species identified in the study, grouped by growth form.

Code	Genus	Species	Authority	Growth form
CLspp.	*Cladina*	spp.		lichen
PEAP	*Peltigera*	*aphthosa*	(L.) Willd.	lichen
BRST	*Brachythecium*	*starkei*	(Brid.) Schimp.	bryophyte
DIPO	*Dicranum*	*polysetum*	Sw.	bryophyte
HYSP	*Hylocomium*	*splendens*	(Hedw.) Schimp.	bryophyte
PLSC	*Pleurozium*	*schreberi*	(Brid.) Mitt.	bryophyte
POCO	*Polytrichum*	*commune*	Hedw.	bryophyte
PTCR	*Ptilium*	*crista-castrensis*	(Hedw.) De Not.	bryophyte
LYAN	*Lycopodium*	*annotinum*	L.	club-moss
LYCL	*Lycopodium*	*clavatum*	L.	club-moss
LYCO	*Lycopodium*	*complanatum*	L.	club-moss
DRAU	*Dryopteris*	*austriaca*	(Jacq.) Woynar ex Schinz & Thellung	fern
GYDR	*Gymnocarpium*	*dryopteris*	(L.) Newm.	fern
CACA	*Calamagrostis*	*canadensis*	(Michx.) Beauv.	grass
CAMO[†]	*Calamagrostis*	*montanensis*	Scribn. ex Vasey	grass
CILA	*Cinna*	*latifolia*	(Trevir. ex Göpp.) Griseb.	grass
ELIN	*Elymus*	*innovatus*	(Beal) Pilg.	grass
PHPR	*Phleum*	*pratense*	L.	grass
POPA	*Poa*	*palustris*	L.	grass
CAAE	*Carex*	*Aenea*	Fern.	sedge
ARNU	*Aralia*	*nudicaulis*	L.	herb
ARCO	*Arnica*	*cordifolia*	Hook.	herb
CHAN	*Chamerion*	*angustifolium*	L.	herb
COCA	*Cornus*	*canadensis*	L.	herb
EQSY	*Equisetum*	*sylvaticum*	L.	herb
FRVI	*Fragaria*	*virginiana*	Duchesne	herb
GABO	*Galium*	*boreale*	L.	herb
GOOB	*Goodyera*	*oblongifolia*	Raf.	herb
LIBO	*Linnaea*	*borealis*	L.	herb
LICO	*Listera*	*cordata*	(L.) R. Br.	herb
MACA	*Maianthemum*	*canadense*	Desf.	herb
MEPA	*Mertensia*	*paniculata*	(Ait.) G. Don	herb
MINU	*Mitella*	*nuda*	L.	herb
PEPA	*Petasites*	*palmatus*	(Aiton) A. Gray	herb
PYAS	*Pyrola*	*asarifolia*	Michx.	herb
PYSE	*Pyrola*	*secunda*	L.	herb
PYVI	*Pyrola*	*virens*	Schreb.	herb
SMTR	*Smilacina*	*trifolia*	(L.) Desf.	herb
STAM	*Streptopus*	*amplexifolius*	(L.) DC	herb
TRHY	*Trifolium*	*hybridum*	L.	herb
TRPR	*Trifolium*	*pratense*	L.	herb
VIRE	*Viola*	*renifolia*	A. Gray	herb
ALCR	*Alnus*	*crispa*	(Aiton) Pursh	shrub
LOIN	*Lonicera*	*involucrata*	(Richards.) Banks ex Spreng.	shrub
OPHO	*Oplopanax*	*horridus*	(Sm.) Miq.	shrub
RHGR	*Rhododendron*	*groenlandicum*	(Oeder) Kron & Judd	shrub
RILA	*Ribes*	*lacustre*	(Pers.) Poir.	shrub
ROAC	*Rosa*	*acicularis*	Lindl.	shrub
RUID	*Rubus*	*idaeus*	L.	shrub
RUPE	*Rubus*	*pedatus*	J. E. Smith	shrub
RUPU	*Rubus*	*pubescens*	Raf.	shrub
SOSC	*Sorbus*	*scopulina*	Greene	shrub
SPBE	*Spirea*	*betulifolia*	Pallas	shrub
VACA[‡]	*Vaccinimum*	*caespitosum*	Michx.	shrub
VAMY[‡]	*Vaccinium*	*myrtilloides*	Michx.	shrub
VAVI	*Vaccinium*	*vitis-idaea*	L.	shrub
VIED	*Viburnum*	*edule*	(Michx.) Raf.	shrub
ABBA	*Abies*	*balsamea*	(L.) Mill.	tree
PIGL	*Picea*	*glauca*	(Moench) Voss	tree
PIMA	*Picea*	*mariana*	(Mill.) Britton, Sterns & Poggenb.	tree

Table A1. Continued.

Code	Genus	Species	Authority	Growth form
PICO	*Pinus*	*contorta*	Douglas ex Loudon	tree
POTR	*Populus*	*tremuloides*	Michx.	tree

† *Calamagrostis montanensis* did not flower in our sites, so a small number of individuals may have been misidentified as *C. montanensis* that were in fact other graminoid species.

‡ *Vaccinium caespitosum* and *Vaccinium myrtilloides* were combined for analysis because they were only identified to genus in the field.