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REGULAR ARTICLE

Impact of postfire logging on soil bacterial and fungal communities and soil biogeochemistry in a mixed-conifer forest in central Oregon

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Abstract
Aims Postfire logging recoups the economic value of timber killed by wildfire, but whether such forest management activity supports or impedes forest recovery in stands differing in structure from historic conditions remains unclear. The aim of this study was to determine the impact of mechanical logging after wildfire on soil bacterial and fungal communities and other measures influencing soil productivity.
Methods We compared soil bacterial and fungal communities and biogeochemical responses of 1) soils compacted, and 2) soils compacted and then subsoiled, to 3) soils receiving no mechanical disturbance, across seven stands, 1–3 years after postfire logging.
Results Compaction decreased plant-available N on average by 27% compared to no mechanical disturbance, while subsoiling decreased plant-available P (Bray) on average by 26% compared to the compacted and non-mechanically disturbed treatments. Neither bacterial nor fungal richness significantly differed among treatments, yet distinct separation by year in both bacterial and fungal community composition corresponded with significant increases in available N and available P between the first and second postharvest year.
Conclusions Results suggest that nutrients critical to soil productivity were reduced by mechanical applications used in timber harvesting, yet soil bacteria and fungi, essential to mediating decomposition and nutrient cycling, appeared resilient to mechanical disturbance. Results of this study contribute to the understanding about impacts of harvesting fire-killed trees and bear consideration along with the recovery potential of a site and the impending risk of future fire in stands with high densities of fire-killed trees.

Keywords Postfire salvage logging · Wildfire · T-RFLP · Soil bacterial and fungal communities · Soil chemical and physical properties · Community level physiological profiles

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Introduction

The effects of mechanical disturbance that occur with logging operations, such as compaction and subsoiling, on soil productivity and forest recovery are of concern worldwide, and depend upon severity, time since disturbance, and site factors (Grigal 2000; Marshall 2000; Rab 2004; Bassett et al. 2005; Yildiz et al. 2007, 2010; Hartmann et al. 2009). Successful forest regeneration following logging operations may rely upon natural forest regeneration or upon successful reforestation from nursery stock (Bassett et al. 2005; Yildiz et al. 2007, 2010; Lindenmayer et al. 2008; Perry et al. 2008). Similarly, disturbance from fire, whether prescribed or natural, varies within forest ecosystems, depending on intensity and length of time since fire (Bárcenas-Moreno and Bååth 2009; Keeley 2009; Yildiz et al. 2010). Re-establishment of understory plant diversity and ecosystem functions of natural forest communities with herbs, shrubs, and tree species mixtures may be important in sustaining long-term productivity (Fisher and Binkley 2000; Fox 2000; Rothe and Binkley 2001; Rothe et al. 2002; Talkner et al. 2009).

Fire effects upon forest ecosystems have long been of interest in understanding forest recovery and subsequent management and sustainability of forests worldwide (Kauffman and Uhl 1990; Attiwill and Adams 1993; Fox 2000; Fisher and Binkley 2000; Cochrane and Laurance 2002; Boerner et al. 2008, 2009; Perry et al. 2008). Forest wildfires have been a universal concern, including in the western United States. This has prompted the need to evaluate the effect of postfire treatments on forest ecosystem recovery (Cochrane et al. 1999; McIver and Starr 2000; Beschta et al. 2004; Sessions et al. 2004; Lindenmayer et al. 2008; Perry et al. 2008). It is well established that severe wildfire negatively impacts soil nutrient pools (Neary et al. 1999; Knicker 2007; Bormann et al. 2008; Hebel et al. 2009); however, the effect of postfire timber removal on soil productivity is not well understood and its application remains highly controversial among land managers, scientists, and the interested public (Lindenmayer et al. 2008). Postfire logging, currently underway in forests to salvage the economic value of timber killed by wildfire, may reduce burn severity to soils in the event of reburning by removing large, dead wood (Poff 1989); may increase the risk of fire (Donato et al. 2006) or fire severity (Thompson et al. 2007); or may decrease the amount of carbon (C) for long-term storage (DeLuca and Aplet 2008; Mitchell et al. 2009).

Forest harvesting equipment, including that used in postfire logging, frequently results in soil compaction, reducing soil pore size and decreasing oxygen availability and water and nutrient movement to tree roots (Dick et al. 1988; Page-Dumroese et al. 2006; Craigg and Howes 2007; Hartmann et al. 2009). To alleviate compaction, the practice of subsoiling or deep tillage is used to fracture the lower soil strata. Based on results from agricultural soils, tillage may degrade soil structure, adversely affecting microbial biomass and diversity by loss of macro-aggregates (Lupwayi et al. 2001). In forest soils, as a remedial treatment for soil compaction, subsoiling may actually ameliorate the more severe soil structure degradation from compaction. Disruption of the belowground component has immediate and potentially long-lasting effects on the below- and aboveground ecosystem (Froehlich et al. 1985; Perry et al. 1989; Neary et al. 1999; Beschta et al. 2004). However, in the case of soil compaction, subsoiling as a remedial treatment has been found to increase rooting volume, decrease bulk density, and increase aeration porosity, potentially having a positive effect on soil productivity (Otrosina et al. 1996; Carlson et al. 2006).

Soil microbes can indirectly influence soil productivity by enhancing nutrient availability for plant uptake, or reducing plant productivity through competition for nutrients with plant roots by promoting nutrient loss via leaching (Wardle et al. 2004; van der Heijden et al. 2008). For example, beneficial rhizosphere microorganisms, including mycorrhizal fungi and plant growth-promoting rhizobacteria (PGPR), such as *Rhizobium* and certain *Pseudomonas* species, can increase the availability of nutrients or plant growth substances to plants or suppress parasitic and nonparasitic pathogens (Schippers et al. 1987; Smith and Read 2008; Courty et al. 2010). Disturbances such as fire and harvesting can impact the abundance, activity, and composition of soil microbial communities (Smith et al. 2005; Smith et al. 2008; Kennedy and Egger 2010), thereby contributing to changes in nutrient cycling, organic matter decomposition rates, and ecosystem C accrual (Pietikäinen and Fritze 1995; Neary et al. 1999). While some studies in pine and mixed-conifer forests have reported minimal or

no modification of the mineral soil microbial community size or activity (Dick et al. 1988; Chow et al. 2002; Shestak and Busse 2005; Busse et al. 2006), another has shown deep and long-lasting effects of organic matter removal and soil compaction on microbial community structures (Hartmann et al. 2009). Understanding soil microbial tolerance to levels and thresholds of disturbance severity is critical to long-term forest productivity (Marshall 2000).

Our objective was to compare microbial communities in soils compacted and decompacted (subsoiled) by mechanical equipment to soils receiving no mechanical disturbance after a wildfire in a mixed conifer forest in central Oregon. In this forest, we investigated the structure, metabolism, and function of soil bacterial and fungal communities in relation to physicochemical properties. Studies incorporating approaches for assessing both structural and functional diversity in examining microbial response to wildfire (Yeager et al. 2005), soil compaction (Axelrood et al. 2002a, b; Shestak and Busse 2005; Busse et al. 2006; Hartmann et al. 2009), or both (Kennedy and Egger 2010) are varied in their approaches and responses. We hypothesized that post-fire mechanized salvage logging would compact surface soils resulting in restricted microbial- and invertebrate-habitable pore space. This would reduce organic matter turnover and nutrient (N,P) mineralization. Restricted microbial grazing by soil invertebrates would stabilize microbial populations and increase diversity in compacted soils. Subsoiling would ameliorate these effects by increasing microbial access to nutrients, but result in a loss of microbial diversity due to an increase in predation from microbivores.

Materials and methods

Study area

This study was conducted within the Booth and Bear Butte (B&B) Fire Complex, located on the east side of the Cascade Mountains of Oregon in the Deschutes National Forest. The B&B Fire burned 36,733 ha in the summer of 2003. Timber sales approved prior to the B&B Fire and subsequently harvested 1 year after the fire provided a unique and timely opportunity to study the impacts of postfire logging without the uncertainty surrounding the approval of proposed postfire-logged stands. Timber harvest and subsoiling of portions of the compacted areas occurred in summer 2004. Subsoiling (on approximately 17% of a stand) was completed on all stands within a 3-day period. Compacted areas occupied approximately 2% to 5% of a stand. Stands, ranging in size from 5 to 12 ha (Table 1), were thinned from below with a feller buncher operation that consists of a shear machine used to cut and place trees into a trail, and a rubber tire skidder machine that pulls the trees to a landing.

Stands within the study are characterized by a dominant overstory of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) and Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco) with white fir (*Abies concolor* Gord. & Glend., Lindl. ex Hildebr.) or grand fir (*Abies grandis* Dougl. ex D. Don, Lindl.) occurring as co-dominants (Simpson 2007). Before logging, stands were comprised mainly of second-growth trees. Nearly all stands contain a few large, 100 to 200-year-old trees, and dense shrubs typifying early successional stages after fire and subsequent logging. Stands contain an understory of snowbrush ceanothus *(Ceanothus velutinus* Dougl.), dwarf rose *(Rosa gymnocarpa* Nutt.), common snowberry *(Symphoricarpos albus* [L.] Blake), dwarf Oregon-grape (*Mahonia nervosa* [Pursh] Nutt.), trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and red huckleberry (*Vaccinium parvifolium* Sm.). Soils are Vitricryands and Vitrixerands with sandy loam texture (Table 1). Elevations of all stands are about 1,000 m (Table 1). Average air temperatures range from −1°C in the winter months to 20°C in the summer months. Average annual precipitation ranges from 50 to 150 cm. About 70% of the precipitation falls during November through April. During the driest months (July, August, and September), the average monthly precipitation is less than 2.5 cm.

Study design

The study was a randomized genuine replicate block design (GRBD) (Hinkelmann and Kempthorne 2008) consisting of seven stands representing a mix of burn severities, including one stand that occurred within the perimeter of the B&B Fire, but was spared from fire. Since most fires are spatially heterogeneous, leaving unburned or low severity burned areas as well as more severely burned areas, all seven stands were included in the study. The study was designed to

Table 1 Stand locations and characteristics

Stand	Unit #	Unit size (ha)	Elevation (m)	Slope %	Aspect	Soil family	Location
TD	37	10.1	1030	4	SSE	Ashy-skeletal, frigid Typic Vitricryands	N 44°31′46, W 21°42′29
UN	54	6.9	955	6	NNE	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°29′25, W 21°42′15
MS	83	6.7	1000	6	E	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°29′46, W 21°43′48
Big	85	11.7	970	21	NNE	Ashy, frigid Typic Vitricryands	N 44°29′26, W 21°42′38
SP	118	7.3	970	3	E	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°00′00, W 21°42′45
AKA	140	7.1	955	4	SE	Ashy over medial-skeletal, frigid Alfic Vitrixerands	N 44°32′05, W 21°40′56
FT	143	5.3	1030	12	SE	Ashy-skeletal, frigid Typic Vitricryands	N 44°31′35, W 21°42′39

compare the effects on soil of mechanical harvesting to non-mechanically disturbed areas. Within each replicate stand, several areas representing each of the three treatments were identified: 1) compacted (compaction from heavy ground-based equipment), 2) subsoiled (compaction followed by subsoiling), and 3) no mechanical disturbance (Fig. 1).

A sampling grid with grid points every 4–6 m was established within each stand (Fig. 1). Grid points were marked with a wooden stake and all stake locations were recorded with the Global Positioning System (GPS). A 10 m buffer zone within the perimeter of each stand was not sampled to avoid potential edge effects. Compacted and subsoiled treatments were based on visual indications of soil disturbance with heavy equipment using a classification system similar to those of Craigg and Howes (2007) and Frey et al. (2009) in which the compacted treatment was identified by topsoil displaced in lateral berms, and the subsoiled treatment as areas where fracturing of the compacted soil was evident. Visual classification systems of soil disturbance have been successfully used by the British Columbia Ministry of Forests and are currently under developmental use in the U.S. Forest Service Region 6 (Pacific Northwest) (Curran et al. 2005). Treatment designations were further assessed by the ease or difficulty of pounding stakes into the ground and validated with a combination of soil strength and bulk density measurements (described below). Within each stand, plots were established at 3 grid points randomly selected from each treatment type for sampling soil physical, chemical, and biological properties (Table 2). Grid point plots were treated as genuine replicates because of their random placement on multiple discontinuous treatment areas within a stand (Hinkelmann and Kempthorne 2008) (Fig. 1). When measurements were made through time (more than one season and year), these data were treated as repeated measures and analyzed using the appropriate split-plot design. For the responses for which we did not composite the replicates we fit a mixed linear model that included fixed effects for treatment (df=2) and season (df=5). We included random effects for site (df=6) and for replicates within treatment areas within sites (df=54) and the residual error (df=300). For responses for which we composited the material from the 3 replicates for each treatment within each site we also fit a mixed linear model with fixed effects for treatment and season. The random effects included site (df=6), variation among site by treatment combinations (df=12) and the residual error (df=90). All models were fit using SAS's PROC MIXED (SAS Institute 2003). There were seven stands with

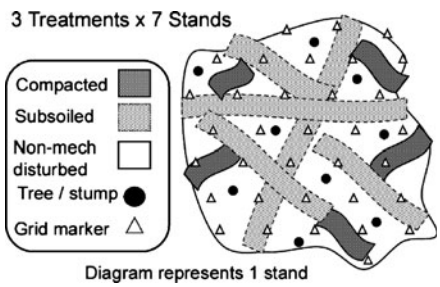

Fig. 1 Genuine replicate block study design with three discontinuous treatments within a stand 1) compacted (compaction from heavy ground-based equipment), 2) subsoiled (compaction followed by subsoiling), and 3) no mechanical disturbance. Three plots from each treatment were randomly selected for soil analyses (7 stands × 3 treatments × 3 plots = 63 plots)

Table 2 Soil physical, chemical, biochemical, biological, and biodiversity response variables measured for each stand

Soil response variable	2005		2006			2007	
	Summer	Fall	Spring	Summer	Fall	Spring	Summer
Texture	1[a]						
Soil resistance (MPa)	1[b]						
Bulk density (g cm^{-3})		1[b]	1[b]			1[b]	
Moisture (%)	3[c]	3[c]	3[c]	3[c]	3[c]	3[c]	
CEC (c mol_c kg^{-1})	3[c]			3[c]			3[c]
C:N	3[c]			3[c]			3[c]
pH	3[c]			3[c]			3[c]
Total C (g kg^{-1})	3[c]			3[c]			3[c]
Total P (mg kg^{-1})							3[c]
Available P (P-Bray) (mg kg^{-1})	3[c]			3[c]			3[c]
Total N (g kg^{-1})	3[c]			3[c]			3[c]
Anaerobic net N mineralization NH_4–N (mg kg^{-1})							3[c]
Anaerobic incubation NH_4–N (mg kg^{-1})							3[c]
Bacterial richness	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Fungal richness	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Bacterial functional diversity						3[c]	
Respiration (μmol m^{-2} s^{-1})	3[a]	3[a]	3[a]	3[a]	3[a]	3[a]	
Phosphatase activity (μmol g^{-1} h^{-1})						3[c]	

Numerals indicate the number of times a variable was measured per treatment per stand for season(s) indicated

[a] Treatments × $stand^{-1}$

[b] Selected stake × $treatment^{-1}$ × $stand^{-1}$

[c] Combined samples within treatment × $stand^{-1}$

three treatments each and three plots of each treatment, for a total of 63 plots; each plot was sampled over seven seasons: summer and fall 2005; spring, summer, and fall 2006; and spring and summer 2007. The response variables were selected based on their ability to influence and measure soil microbes and their processes.

Soil physical properties

Soil physical properties were measured at various times and replications, as shown in Table 2. Differences in soil strength were measured at each stand in one plot per treatment in the fall of 2005 (Table 2) using the Rimik 4011 recording soil penetrometer (Rimik International Pty Ltd, Queensland, Australia) at 2.5 cm increments. Five measurements at each sampling point were taken to a maximum depth of 60 cm. Bulk density was assessed in the fall of 2005 (0–5 cm) and the springs of 2006 (5–10 cm) and 2007 (0–5 cm, 5–10 cm). Gravimetric water content (% moisture) was measured in each plot during each sampling period to calculate water-filled pore space, an attribute critical to mass flow of nutrients, as well as to limits to biological activity.

Soil chemistry, N mineralization, and incubation N

Mineral soils for chemical analysis, N mineralization, and incubation N were collected to a 10 cm depth, using a garden trowel on each plot during each summer sampling period (Table 2). Soil samples were combined by treatment per stand and then sieved (2.0 mm) and air-dried before being analyzed. Total C and N were analyzed by the dry combustion technique (Bremner 1996; Nelson and Sommers 1996) using a Flash EA112 NC soil analyzer (Thermo Electron Corporation, Milan, Italy). Cation exchange capacity (CEC) was estimated using the sum of exchangeable cations (Robertson et al. 1999) for the

summer 2005 and 2006 samplings, and the ammonium acetate method (Rhoades 1982) for the summer 2007 soils. Soil pH was measured employing the 1:2 (soil:water) dilution method using deionized water (Robertson et al. 1999). Plant available P was analyzed using the dilute acid-fluoride method (P-Bray) (Kuo 1996) at the Oregon State University Central Analytical Lab (OSU CAL). Total P was measured at the OSU CAL using a Kjeldahl digestion (Bremner 1996; Taylor 2000), followed by P determination on an ALPKEM autoanalyzer (Technicon Instruments, Saskatoon, Canada).

Nitrogen mineralization potential, the conversion of organic N in microbial biomass to inorganic N under laboratory conditions, is considered a potential estimate of biologically available N (Myrold 1987; Perry et al. 2008). Anaerobic incubation N and net minerlizable N were measured in summer 2007 at the OSU CAL using the procedure of Bundy and Meisinger (1994). After incubation at 40°C for 7 days, 50 ml of 2 M KCl was added to extract NH_4–N for 1 h. The extracted NH_4 was determined on an ALPKEM autoanalyzer (Technicon Instruments, Saskatoon, Canada).

Genetic analysis of samples

Bacterial and fungal richness was measured at each plot within each stand for the first 6 sampling periods (Table 2). At each plot, a sparse litter layer of pine needles was removed and the mineral soil sampled to a depth of 10 cm and put in a 50 ml tube. Samples were placed in a cooler, transported to the lab and stored in a −80°C freezer until further processing. Small pebbles and vegetation (not including roots) were removed from the sample prior to DNA extraction. A MoBio Power Soil™ DNA isolation kit was used to extract total genomic DNA from approximately 0.5 g of each soil sample (MoBio Laboratories, Carlsbad, CA, USA).

Soil bacteria DNA was amplified using 16S rDNA gene primers 8F (FAM) and 907R (Edwards et al. 1989; Muyzer et al. 1995) in a 50 μl reaction mix containing: 1x PCR buffer, 2 mM $MgCl_2$, 0.2 mM dNTPs, 0.2 μM Primer, 0.064% BSA. Each soil DNA extract was run twice under the following conditions: 95°C for 3 min, followed by 30 cycles at 95°C for 30 s, 55°C for 1 min, 72°C for 45 s, and ending with an extension step of 72°C for 7 min. Once amplified, the two products were pooled to capture the diversity more fully. These pooled products were then purified using a MoBio Ultra Clean DNA Clean Up kit (MoBio Laboratories, Carlsbad, CA). Restriction enzyme *Msp*I was selected over *Alu*I for terminal restriction fragment length polymorphism (T-RFLP) community analysis after comparison trials on replicate samples revealed its ability to identify the greatest amount of variation. *Msp*I consistently is considered a top performing restriction enzyme for T-RFLP of bacterial samples (Liu et al. 1997; Engebretson and Moyer 2003). Digests were run according to the manufacturer's specifications by incubating the restriction digest for 3 h at 37°C. Restricted samples were submitted to Oregon State University Center for Gene Research and Biotechnology for analysis using an ABI Prism 3100 Genetic Analyzer (Applied Biosystems Inc., Foster City, CA, USA) to run capillary gel electrophoresis. Approximately 1 ng of amplified DNA was submitted for analysis for each sample. The analysis produced one community profile for each sample, where a profile consists of peaks of varying height and base pair length. The peaks (operational taxonomic units or OTUs) can be used to determine the richness of a given sample (Liu et al. 1997). Length and fluorescence of the terminal restriction fragments (TRF) were determined using GeneScan version 2.5 and Genotyper version 3.7 software (Applied Biosystems Inc., Foster City, CA). OTUs were binned to 1 bp in width.

Methods for identifying soil fungi were followed as stated above with the following exceptions. The fungal ITS spacer region was amplified using ITS-1f (Gardes and Bruns 1993) and ITS-4 (FAM) (White et al. 1990) and the reaction mixture and thermocycling program of Dickie et al. (2002). Restriction enzyme *Hinf*I was selected over *Hae*III for T-RFLP community analysis after comparison trials on replicate samples revealed its ability to identify the greatest amount of variation. Both *Hinf*I and *Hae*III are widely used in fungal T-RFLP profiling (Avis et al. 2006; Dickie and FitzJohn 2007; Alvarado and Manjon 2009). GeneMapper software 4.0 (Applied Biosystems Inc., Foster City, CA) was used to determine fragment fluorescence, OTUs were binned to 1 bp in width, and a binary analysis of presence or absence was performed following the methods of Rinehart (2004).

Community level physiological profiles

Soils for CLPPs were collected and processed in spring 2006 to a 10 cm depth at each plot. Soil samples were combined by treatment per stand, sieved (2.0 mm) and approximately 10 g was placed in small envelopes, and stored at 4°C until processing. The physiological potential, an estimate of functional diversity of the bacterial community, can be determined through the utilization patterns of various C sources (Garland 1996; Garland et al. 1997) but obviously is biased towards culturable, aerobic and fast-growing bacteria. The CLPPs were qualitatively assessed using Biolog EcoPlates™ (Biolog Inc., Hayward, CA, USA) following the method described in Sinsabaugh et al. (1999). Plates were incubated at room temperature and color development was determined using a BioTek PowerWave X 340 spectrophotometer (BioTek Instruments, Winoski, VT, USA) at a wavelength of 596 nm. Absorbance values were recorded at 24 h intervals for 5 consecutive days (Sinsabaugh et al. 1999). The data used in this analysis are from the day 3 readings and have been standardized to the water control. The water column values (all zeros) were removed and all resulting negative values were changed to zero.

Soil respiration

Soil respiration was measured at 3 plots per treatment in each stand for the first six sampling periods (Table 2). Soil respiration data were obtained following the methods in Law et al. (2001) using a LI6200 infrared gas analyzer (LiCor, Lincoln, NE, USA). Soil respiration rates were expressed as μmol m^{-2} s^{-1} of CO_2, using the same convention and quantification as Sulzman et al. (2005).

Phosphatase enzyme activity

Phosphatase enzyme activity was assayed from soil samples collected in spring 2007 using the *p*-nitrophenyl-phosphate (*p*-NPP) assay of Tabatabai (1994) as modified by Caldwell et al. (1999). After soils were sieved (<2 mm), slurries were prepared with deionized water, and 1 ml of slurry was incubated with 1 ml of 50 mM *p*-NPP at 30°C. These assays were run without conventional buffers to measure enzyme activity under actual soil matrix conditions (pH, cation concentrations), rather than to estimate potential enzyme activities present at optimum pH with increased ionic strength. After 1 h, 0.5 ml of 0.5 M $CaCl_2$ was added and reactions were terminated by adding 2 ml of 0.5 M NaOH to the assay. Controls consisted of slurry without substrate and substrate without slurry. After centrifugation, supernatant *p*-nitrophenol (*p*-NP) concentrations were measured at 410 nm, and enzyme activities were calculated on a dry weight basis (Caldwell et al. 1999).

Statistical analyses

The mean responses for soil properties (Table 3) were compared among treatments, and when appropriate, among seasons and years. No significant treatment by season interactions were detected for any of the measured response variables; therefore, only main effects are presented. Results were considered significant at $P=0.05$ and were considered a statistical trend at $P=0.1$. The variability inherent in field studies with smaller sample numbers, such as when soil samples were composited in this study, affords practical value for using statistical trends at $P=0.1$ (Steel et al. 1997). The F statistic and α level of significance are presented in the text when not included in a table.

Multivariate statistical analyses were performed using PC-ORD version 5.0 (McCune and Grace 2002). Sample community profiles were examined using nonmetric multidimensional scaling (NMS) with the Sørensen distance measure. The medium NMS autopilot mode was selected, with 200 maximum iterations, 0.0001 instability criterion, 15 real runs, and 30 randomized runs. The final model dimensions were chosen by comparing the NMS runs with real data to Monte Carlo simulations with random numbers. The proportion of variation represented by each axis was assessed by calculating the coefficient of determination (R^2) between distances in the ordination space and Sørensen distances in the original distance matrix. The relationships between plots in ordination space and their corresponding environmental variables were assessed by over laying the variables as a joint plot. Preliminary ordinations were examined and the data set further modified, first by excluding peaks occurring in fewer than five samples and then by an arcsine square root transformation of each response in order to normalize the data

Table 3 Effects of management treatments on soil physical, biochemical, chemical, biological and biodiversity response variables, with means and ANOVA results

Soil response variable	Treatment				
	Compacted	Subsoiled	Non-mechanically Disturbed	$F_{[df,df]}$	P
Bulk density at 5 cm depth (g cm^{-3})	0.98 (0.04)	0.95 (0.04)	0.90 (0.04)	$2.71_{[2,12]}$	0.08
Bulk density at 10 cm depth (g cm^{-3})	1.02 (0.04) a	0.85 (0.04) b	1.00 (0.04) a	$5.17_{[2,12]}$	**0.02**
Moisture (%)	17.61 (1.37)	18.44 (1.37)	20.60 (1.37)	$2.02_{[2,12]}$	0.18
CEC (c mol_c kg^{-1})	18.61 (1.01)	19.06 (1.01)	19.64 (1.01)	$0.62_{[2,12]}$	0.56
C:N	20.61 (0.55)	19.82 (0.55)	20.53 (0.55)	$0.87_{[2,12]}$	0.44
pH	6.76 (0.08)	6.69 (0.08)	6.86 (0.08)	$2.13_{[2,12]}$	0.16
Total C (g kg^{-1})	31.4 (2.8)	30.2 (2.8)	31.5 (2.8)	$0.14_{[2,12]}$	0.87
Total P (mg kg^{-1})	1189.54 (73.89) a,b	1152.09 (73.89) a	1296.24 (73.89) b	$2.86_{[2,12]}$	0.10
Available P (P-Bray) (mg kg^{-1})	9.57 (0.66) a	7.29 (0.66) b	9.80 (0.66) a	$13.69_{[2,12]}$	**<0.01**
Total N (g kg^{-1})	1.6 (0.1)	1.6 (0.1)	1.6 (0.1)	$0.10_{[2,12]}$	0.90
Anaerobic net N mineralization NH_4–N (mg kg^{-1})	28.11 (4.22) a	32.73 (4.22) a,b	38.03 (4.22) b	$6.53_{[2,12]}$	**0.01**
Anaerobic incubation NH_4–N (mg kg^{-1})	29.51 (4.41) a	35.19 (4.41) a,b	40.47 (4.41) b	$6.65_{[2,12]}$	**0.01**
Mean # bacterial OTUs (*Msp*I)	24.43 (0.99) a	21.00 (0.99) b	22.36 (0.99) b	$3.00_{[2,12]}$	0.09
Mean # fungal OTUs (*Hinf*I)	20.29 (1.38)	17.67 (1.38)	18.38 (1.38)	$1.38_{[2,12]}$	0.29
Cumulative # bacterial OTUs (*Msp*I)	52.17 (3.98)	43.83 (3.98)	47.31 (3.98)	$1.11_{[2,12]}$	0.36
Cumulative # fungal OTUs (*Hinf*I)	38.17 (2.61)	32.40 (2.61)	36.12 (2.61)	$1.25_{[2,12]}$	0.32
Respiration (μmol m^{-2} s^{-1})	2.45 (0.19) a	2.36 (0.19) a	2.93 (0.19) b	$2.55_{[2,54]}$	0.09
Phosphatase (μmol g^{-1} h^{-1})	28.08 (3.32) a,b	22.74 (3.32) a	32.63 (3.32) b	$2.77_{[2,54]}$	0.07

Means are listed with standard errors in parentheses. The F statistic is testing the null hypothesis of no difference among treatment means. Within a column, means with a common lowercase letter are not different at α=0.1. Means differing at α=0.05 are shown in bold

set. Using the blocked multiresponse permutation (MRBP, Euclidean distance, treatments or year/season as groups) and unblocked multiresponse permutation (MRPP, Sørenson distance, treatments or year/season as groups) procedures, the strength and statistical significance of group membership was tested. If data contained repeated measures, MRBP was used, otherwise MRPP was used. The *P*-value and *A* statistic (*A*) describing within-group heterogeneity compared to the random expectation, were recorded for each MRBP and MRPP analysis. Similarities of each of the bacterial and fungal communities among treatments were assessed using a nested PerMANOVA with Sørenson distance where samples were nested within site. Soil biogeochemical properties were correlated with community compositional ordinations to investigate links between community composition and functional capability for the six seasons.

NMS, where samples were ordinated in C-substrate space, was used to analyze the Biolog™ spectrophotometer data for bacteria. The data needed no further transformation after looking at initial ordinations for normalization. For outlier analysis, MRPP and PerMANOVA Sørensen distance was used.

Diversity was estimated using the Shannon-Wiener index (*H*): $H = -\sum p_i (\ln p_i)$, where p_i is the ratio of the number of OTUs for bacteria or fungi found in each sample to the total number of peaks for bacteria or fungi found in all samples for the OTU data (Magurran 1988). Biolog™ substrate diversity was similarly calculated, except that p_i was the ratio of average well color development (AWCD) on each substrate to the sum of all AWCD on all substrates. Evenness was calculated for the OTU data using: $E = H'/H_{max} = H'/\ln S$, where H is the Shannon-Wiener diversity index, S is the total number of peaks found

in all samples, and E is a number between 0 and 1 (Magurran 1988).

Results

Soil physical properties

Overall, soil strength was greatest in the compacted treatment and least in the subsoiled treatment (Fig. 2). Soil strength measurements revealed distinct differences among all treatments at most 2.5 cm increments between 7.5 and 17.5 cm and distinct differences between compacted and other treatments at all increments to a depth of 17.5 cm (Fig. 2). At levels deeper than 17.5 cm, compacted and non-mechanically treated soils did not differ in soil strength; however, the subsoiled treatment showed distinctly less resistance compared to those treatments at depths of 25–35 cm (Fig. 2). Bulk density at 10 cm taken more than 1 year after harvesting was 15% lower, on average, in the subsoiled treatment (95% (Confidence Interval (CI)=6–24%)) (Table 3).

Percent moisture was up to 85% lower in summer compared with fall and spring (95% CI=70–93%, 95% CI=74–94%, respectively) ($F_{[2,\ 111]}$=119.69, P<0.0001), but differences among treatments were not observed (P=0.18) (Table 3).

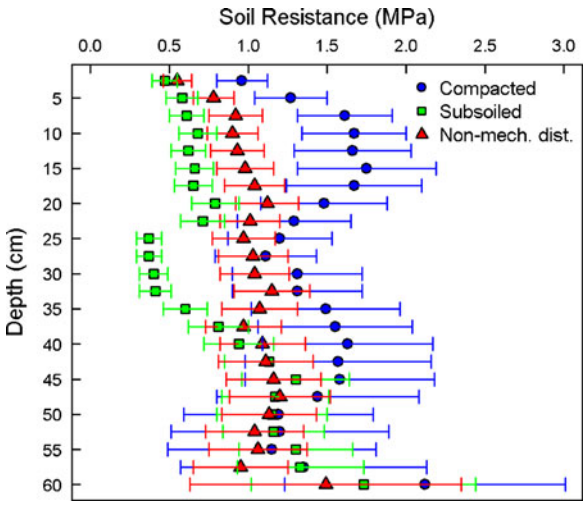

Fig. 2 Soil strength measurements by treatment. Measurements were taken at 2.5 cm increments to a maximum depth of 60 cm. Differences in soil strength were seen to a depth of 17.5 cm for most measurements. *Error bars* represent 1 SE

Soil chemistry, N mineralization, and incubation N

Differences were not observed among treatments for soil CEC, C:N, pH, total C, total N (P>0.1) (Table 3). Soil CEC was higher in summer 2005 compared to summers 2006 or 2007 ($F_{[2,\ 36]}$=16.63, P<0.0001). Plant-available P (Bray) was up to 26% lower in the subsoiled treatment compared to the compacted or non-mechanically disturbed treatments (95% CI=9–39%, 95% CI=11–41%), respectively (P<0.001) with a similar tendency for total P (P=0.1, 95% CI=−1.2–24%) (Table 3). Plant-available P (Bray) was higher in summer 2006 than in summers 2005 or 2007 ($F_{[2,\ 36]}$=18.76, P<0.0001). Compaction decreased anaerobic incubation NH_4-N by 26% (95% CI=3.5–51%) and net mineralizable (anaerobic) NH_4 by 27% (95% CI=2–50%) compared to the non-mechanically disturbed treatment (P=0.01 for both) (Table 3). Total N ($F_{[2,\ 36]}$=27.58, P<0.001) was higher in summer 2006 than in summer 2005. Increased N in the second summer led to lower C:N ($F_{[2,\ 36]}$=47.78, P<0.0001) in summer 2006 compared to summers 2005 and 2007.

Soil microbial communities

A total of 275 OTUs for soil bacteria were detected. Compaction tended to increase the mean number of bacteria OTUs, on average, by 9% and 14% when compared to both the non-mechanically disturbed and subsoiled treatments (95% CI=−0.5–19%, 95% CI=5–25%), respectively (P=0.09, Table 3). Shannon-Wiener indices for bacteria OTUs among treatments (4.0 to 4.1) suggest that bacteria OTUs in our samples were equally distributed and showed high community complexity, and evenness values of 0.70 to 0.73 suggest that OTUs were equally abundant. The average number of soil bacteria OTUs differed with respect to sampling period ($F_{[5,\ 90]}$=11.53, P<0.0001) (Fig. 3). Similarly, Shannon-Wiener indices were higher in year 1 (summer 2005, fall 2005, spring 2006) (4.0 to 4.1, with evenness values of 0.71 to 0.73) compared to year 2 (summer 2006, fall 2006, spring 2007) (3.6, with evenness values of 0.63 to 0.65).

A total of 160 OTUs for soil fungi were detected. There were no detected differences in the average number of fungi OTUs among treatments ($F_{[2,\ 12]}$=1.38, P=0.29) but differences were detected among sampling periods ($F_{[5,\ 90]}$=51.39, P<0.0001) (Fig. 3).

Fungal richness in all treatments declined after the first sampling season (summer 2005) and increased in the last sampling season (spring 2007) (Fig. 3). Similarly, Shannon-Wiener indices were higher in the first and last sampling seasons (4.0 and 4.2, evenness 0.81 and 0.83, respectively) compared to the other sampling seasons (3.4 to 3.6, evenness 0.67 to 0.72).

There were no observed differences in the cumulative number of bacteria and fungi OTUs among treatments (P=0.3 for both) (Table 3). All treatments showed a gradual increase in the cumulative mean number of bacteria and fungi OTUs over time (Fig. 4).

Variation in bacterial community composition was not detected among treatments (PerMANOVA $F_{[2,\ 105]}$= 0.61, P=0.76). NMS ordinations of the average number of OTUs showed differences in the bacterial community composition between year 1 (summer 2005, fall 2005, spring 2006) and year 2 (summer 2006, fall 2006, spring 2007) (MRPP P<0.0001, A= 0.13) and among seasons (PerMANOVA $F_{[2,123]}$=4.91, P=0.0002). Responses of CEC and percent moisture helped explain the variation in the soil sample community from summer 2005, spring 2006, and spring 2007 (Table 4). In addition to these variables, available P explained separation of the bacterial community in summer 2006 soil samples. No environmental measures explained variation in either of the fall measurement periods (Table 4).

Variation in fungal community composition was also not detected among treatments (PerMANOVA $F_{[2,105]}$=1.27, P=0.23). NMS ordinations showed differences in the fungal community composition between year 1 (summer 2005, fall 2005, spring 2006) and year 2 (summer 2006, fall 2006, spring 2007) (MRPP P<0.0001, A=0.12), and among seasons (PerMANOVA $F_{[2,123]}$=5.41, P=0.0002). Responses of CEC, total C, and percent moisture (Table 3) helped explain the variation in the soil sample community from fall 2005 and summer 2006 (Table 4). No environmental measures explained variation in summer 2005, fall 2006, or either spring measurement periods (Table 4).

Community level physiological profiles

Variation in functional diversity, as measured by absorbance values, was not detected among treatments (MRBP P=0.11, A=0.022) (Table 4). Differentiation in Shannon-Wiener indices for CLPPs for bacteria was not observed among treatments (3.0 in compacted, 2.9 in both the subsoiled and non-mechanically disturbed treatments). Ordinations of the CLPP data in species space showed that C substrate groups, amines/amides, amino acids, and carbohydrates significantly correlated with the variation in species composition in spring 2007 (Table 4); amines/amides were more correlated with axis 3 (R^2= 0.460), amino acids with axis 1 (R^2=0.634), which explains more variation than axis 3, and carbohydrates with axis 2 (R^2=−0.456). Proportion of variation (R^2) explained by each axis was 0.63, 0.16, and 0.21, respectively.

Soil respiration and phosphatase activity

Soil respiration rates tended to be higher in the non-mechanically disturbed treatment compared to both

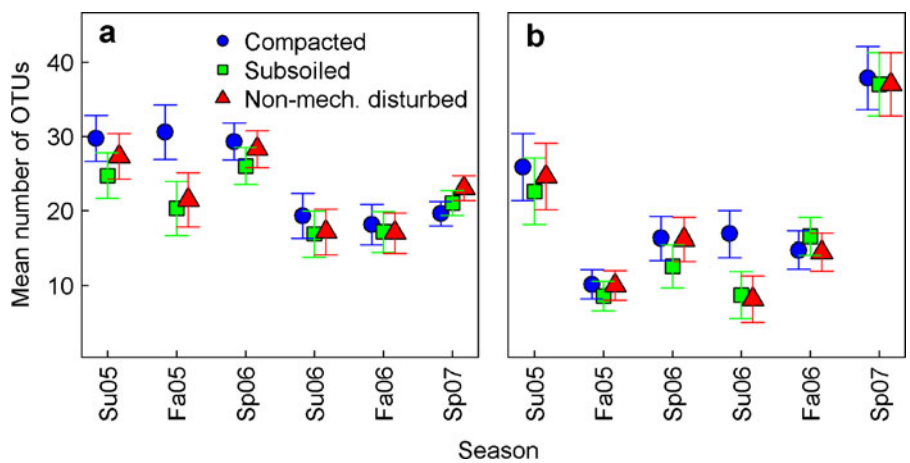

Fig. 3 Mean number of **a** bacterial (*Msp*I) and **b** fungal (*Hinf*I) OTUs differed among seasons. Bacterial OTUs tended to be higher in the compacted treatment; however there were no differences among treatments in the mean number of fungal OTUs

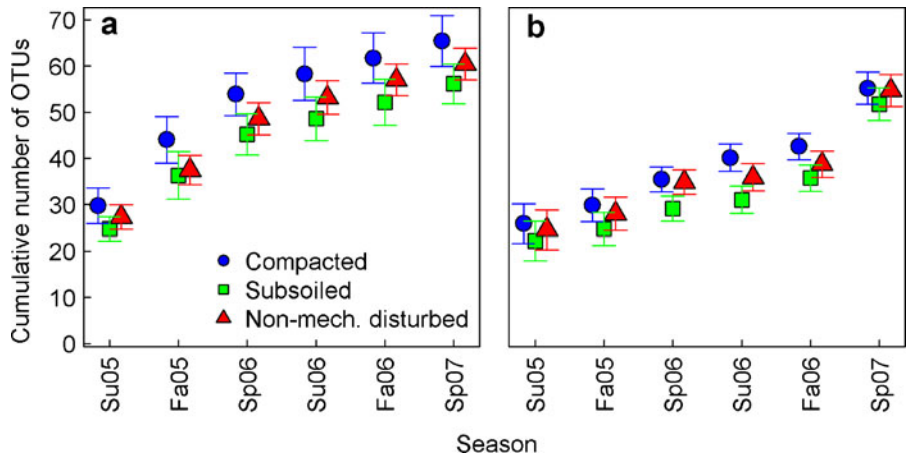

Fig. 4 Cumulative mean number of **a** bacterial (*Msp*I) and **b** fungal (*Hinf*I) OTUs by season and treatment. All treatments showed a gradual increase in the cumulative mean number of bacteria and fungi OTUs over time

the compacted and subsoiled treatments (P=0.09) (Table 3). Soil respiration rates were, on average, more than 20% lower in fall compared to summer or spring (95% CI=26–42%, 95% CI=14–33%, respectively, P<0.01 for both). Evidence suggested that phosphatase activity was, on average, 30% lower in the subsoiled treatment compared to the non-mechanically disturbed treatment (P=0.07, 95% CI= 10–51%) (Table 3).

Discussion

Following forest ecosystem disturbances, such as wildfires and logging, soil microorganisms, including fungi, bacteria, and protozoans, facilitate decomposition processes for both aboveground forest floor and wood residues, and for belowground components, such as fine and coarse roots (Stark 1972; Richards 1987; Perry et al. 2008). These important soil biota help to sustain forests by re-establishing nutrient cycling processes following forest disturbance, while also facilitating establishment of trees and understory vegetation components, which depend upon both free-living and symbiotic microbes for nutrient uptake (Paul and Clark 1996; Dighton 2003; Perry et al. 2008; Smith and Read 2008; Simard 2009; Courty et al. 2010).

The net mineralizable N mean values for all of our treatments (Table 3) shows that most of the available mineral soil N pool is being maintained in microbial tissues, based upon research used to develop the anaerobic N mineralization method employed in our study (Myrold 1987; Bundy and Meisinger 1994; Perry et al. 2008). The soil microbial biota, such as bacteria and fungi, also are important in taking up other key nutrient elements, including P and base cations from soil mineral and organic matter sources (Stark 1972; Cromack et al. 1975; Entry et al. 1992; Tiessen et al. 1994; Smith and Read 2008).

Soil organic matter is a primary source of soil N required for the decomposition of residual forest floor and woody components aboveground and fine and coarse roots belowground (Richards 1987; Tiessen et al. 1994; Dighton 2003). Fungi, due to their ability to create hyphal networks through long-lived fungal rhizomorphs and mycelial strands (Treseder et al. 2005), facilitate translocation of important nutrients such as N and P from soil sources into the residual forest floor aboveground woody components. Similar fungal networks are created by ectomycorrhizal fungi of trees, including Douglas-fir and ponderosa pine (Simard 2009; Courty et al. 2010), enabling N to be mobilized from a variety of soil organic matter sources (Lilleskov et al. 2010), soil P from organic and inorganic soil sources (Entry et al. 1992; Perry et al. 2008; Smith and Read 2008), and soil water from transport by ectomycorrhizal fungi to tree seedlings (Warren et al. 2008).

Soil N availability studies have provided a useful comparative basis in forest productivity studies (Fisher and Binkley 2000) and for evaluating forest management activities, such as thinning, fertilization or prescribed burning (Waring et al. 1992; Monleon et

Table 4 Statistical outcomes for NMS ordinations for each season, and MRBP and PerMANOVA results showing no community differences for bacteria (*Msp*I) and fungi (*Hae*III) by treatment (TRT)

Season	Microbe	NMS	MRBP-TRT	PerMANOVA-TRT	Vectors
Summer 2005	Bacteria	[a]Stress=10.80 Instability=0.000001	A=−0.004 P=0.60	P=0.46	CEC
	Fungi	[b]Stress=38.74 Instability=0.001070	A=−0.011 P=0.80	P=0.88	None
Fall 2005	Bacteria	[a]Stress=9.77 Instability=0.000001	A=−0.005 P=0.56	P=0.53	None
	Fungi	[c]Stress=9.54 Instability=0.000001	A=−0.005 P=0.58	P=0.15	% Moisture
Spring 2006	Bacteria	[c]Stress=10.75 Instability=0.000001	A=0.023 P=0.09	P=0.29	None
	Fungi	[c]Stress=9.08 Instability=0.000001	A=0.047 P=0.05	P=0.02	None
Summer 2006	Bacteria	[c]Stress=9.34 Instability=0.000001	A=0.005 P=0.36	P=0.29	P-Bray, CEC, % Moisture
	Fungi	[c]Stress=4.21 Instability=0.000001	A=0.005 P=0.39	P=0.31	CEC, Total C
Fall 2006	Bacteria	[c]Stress=10.07 Instability=0.000001	A=0.012 P=0.22	P=0.43	None
	Fungi	[a]Stress=13.56 Instability=0.000090	A=−0.033 P=0.93	P=0.52	None
Spring 2007	Bacteria	[c]Stress=8.304 Instability=0.000001	A=−0.0104 P=0.70	P=0.57	% Moisture
	Fungi	[b]Stress=32.24 Instability=0.000010	A=0.018 P=0.20	P=0.11	None
	CLPP	[c]Stress=8.30 Instability=0.000001	A=0.022 P=0.11	P=0.41	Amines/Amides, Amino Acids, Carbohydrates

The "Vectors" column contains variables that showed a significant correlation (R^2) with the bacterial, fungal, and functional community structure

[a] Denotes 2-D solution

[b] Denotes 1-D solution

[c] Denotes 3-D solution

al. 1997; Velazquez-Martinez and Perry 1997; Jones et al. 2010). In support of our hypothesis, compaction decreased plant-available N by 27%, on average, and NH_4–N and N mineralization by 26%, on average, compared to the non-mechanically disturbed treatment. Similarly, Lindo and Visser (2003) found decreased NH_4–N after clearcut harvesting, whereas DeLuca and Zouhar (2000) reported an increase in the levels of NH_4–N and potentially mineralizable N immediately following harvesting and prescribed fire. The anaerobic N availability index values in our study were similar to values reported by Myrold (1987) and Hebel et al. (2009) for other central Oregon forest sites (Table 3). Myrold (1987) also found a highly significant correlation (R^2=0.731) between anaerobic mineralizable N and microbial biomass N, using data from seven sites across Oregon. Based upon results of that research (Myrold 1987), the significantly higher net mineralizable anaerobic N on the non-mechanically disturbed treatment in our study (Table 3) may indicate that there was a greater microbial biomass N pool present under that treatment. Breland and Hansen (1996) postulated that N mineralization in compacted soil was reduced by increased physical protection of organic materials and microbial biomass against attack by microbivores. Busse et al. (2006) suggested that a decrease in pore size that benefits microbial community

stability may reduce plant nutrient availability. These observations are in agreement with several other studies on how soil structure affects habitable pore space for microorganisms and the turnover of soil organic matter and nutrients, such as N (Elliott et al. 1980; Battigelli et al. 2004; Li et al. 2004; Coleman 2008).

In support of our hypothesis, soils subjected to mechanical harvesting equipment after wildfire, and measured 1 year after harvesting, exhibited increased soil resistance compared to soils receiving no mechanical disturbance (Fig. 2). However, there were no observed differences in bulk density at 10 cm between the compacted and non-mechanically disturbed treatments 1 and 3 years after harvesting. Page-Dumroese et al. (2006) reported that in coarse-textured soils, bulk density measurements change relatively quickly with time and at the 10 cm depth may indicate recovery not reflected in soil strength measurements after 1 and 5 years. Frey et al. (2009) found no difference in bulk density at 10 cm between their lightly compacted and undisturbed treatments or between their moderately compacted and undisturbed treatments in two of three study sites, even though moderate compaction was characterized as topsoil displaced in lateral or side berms. Furthermore, Frey et al. (2009) reported that the physical effects of different levels of compaction from heavy logging machinery significantly changed the bacterial community structure in their severely compacted soil (approximately 32% increase in bulk density relative to undisturbed soil) and resulted in only minimal changes in bacterial OTU abundance in moderately (18% increase in bulk density) and lightly (3% increase in bulk density) compacted soils. In contrast, we did not observe variation in bacterial community composition among treatments.

In contrast to our hypothesis that subsoiling may alleviate nutrient loss due to compaction, we observed that plant-available P (Bray) was up to 26% lower in the subsoiled treatment compared to the non-mechanically disturbed and compacted treatments. This decrease would be expected to lead to decreased plant growth; however, subsoiling improved tree seedling growth compared to the compacted and non-mechanically disturbed treatments (JE Smith, unpublished data). Subsoiling also tended to decrease total P by 11%, on average, compared to the non-mechanically disturbed treatment. The decrease in plant-available and total P in the subsoiled treatment in this study may be linked to fractions of the organic matter that were not measured. Some P stored in plant residues becomes associated with the active and passive fractions of soil organic matter, where it can be stored for future release and very slowly converted to soluble inorganic forms that plants can use (Brady and Weil 2002).

The decrease in plant-available P (Bray) could be related to the 30% reduction in phosphatase activity that we detected in the subsoiling treatment, which mineralizes this P from organic forms. Dick et al. (1988) found that compaction in skid trails lowered phosphatase by 41% (and all enzyme activities assayed by 41–75%) in the 10–20 cm depth. However, there was a consistent trend that enzyme activities in the top 10 cm were lower in the compacted treatment compared to the control, but differences were small and not significant. Dick et al. (1988) did not detect differences in phosphatase between subsoiled treatments and the control. Boerner et al. (2008) found that fire and the combination of fire and mechanical treatment from harvesting lowered phosphatase activity compared to the mechanical treatment alone in a dry mixed conifer forest in Oregon. They further noted that phosphatase activity was reduced by treatments that included fire in the majority of fire and fire surrogate sites in the western United States. In contrast, phosphatase activity in our study did not differ between the one stand that escaped fire and the others that burned.

Contrary to our hypothesis, salvage logging soil disturbance did not appear to have an effect on microbial diversity; however, compaction tended to increase the mean number of bacterial OTUs by 9% and 14% when compared to the non-mechanically disturbed and subsoiled treatments, respectively. Variation in fungal richness was not detected between mechanically disturbed treatments and the non-mechanically disturbed treatment. However, the ordination approach we used revealed distinct separation in both the bacterial and fungal community composition between the first and second postharvest year that corresponded with significant increases in total and available N and available P. Tree mortality from fire and the removal of trees in our study may have led to a shift from root and rhizosphere associated bacteria and fungi to saprotrophic dominated communities. Studies suggest that overstory harvesting and the presence of living trees more greatly

influences soil microbial communities than an intact forest floor (Busse et al. 2006; Kennedy and Egger 2010). Disruption of root C transport after tree girdling or root severing leads to changes in both fungal and bacterial communities (Högberg and Högberg 2002; Brant et al. 2006; Yarwood et al. 2009) and induces the rapid growth of opportunistic saprophytic fungi that utilize dying mycorrhizal mycelia (Lindahl et al. 2010).

A trend over six sampling seasons suggested that the compacted soil contained a slightly greater cumulative mean number of bacterial OTUs (Fig. 4). A decrease in pore size may have led to less predation on the bacterial community, as suggested for compacted conditions in similar forest types (Shestak and Busse 2005; Busse et al. 2006). Soil compaction alters pore size distribution and may benefit the bacterial community by increasing the volume of habitable pores and decreasing the pore space available to larger microbivores such as nematodes and protozoa (van der Linden et al. 1989; Hassink et al. 1993; Breland and Hansen 1996). Moldenke et al. (2000) found that compaction caused by skid trails in the Deschutes National Forest in central Oregon contributed to a shift in the food web to one that utilized primarily bacteria.

Soil respiration is a direct measure of both microbial and root activity. In our study, compaction tended to reduce respiration rates and this effect was not alleviated by subsoiling. Lindo and Visser (2003) found that clearcutting significantly reduced soil respiration in the forest floor. In contrast, Concilio et al. (2005) reported increased soil respiration with selective harvesting. Ma et al. (2004) found that thinning resulted in nominal impact on soil respiration, but that burning significantly reduced soil respiration. These varied responses may be attributed to the influence of understory vegetation on soil moisture and temperature. For example, Ma et al. (2004) reported that soil respiration was reduced significantly in burned ceanothus patches, but increased in unburned but thinned ceanothus patches. Law et al. (2001) showed that soil surface CO_2 effluxes were lowest for bare soil, and highest near shrubs, some of which were N_2 fixers with higher photosynthetic rates. The increased activities shown by respiration and by phosphatase in the non-mechanically disturbed treatment, for example, may indicate the effects of increased ceanothus and other understory plant recovery and colonization. Thus, there may be greater microbial activity with more plants, such as ceanothus, but not necessarily greater bacterial diversity than is being shown in the compacted treatment. The more compacted soil may have shown greater bacterial genetic diversity, yet less activity for respiration and phosphatase.

Varied responses of microbial communities and soil physicochemical properties to compaction and other soil disturbances may be explained by the complexity of soil disturbances that occur during mechanized harvesting and to levels of soil disturbance (Shestak and Busse 2005; Busse et al. 2006; Boerner et al. 2009; Frey et al. 2009). Busse et al. (2006) suggested that soil microbial response to compaction is typically more pronounced in studies with additional impacts of soil displacement and mixing such as that which occurs with the creation of skid trails. Recent studies in 100-year-old mixed-conifer forests (Shestak and Busse 2005) and in younger pine and mixed-conifer plantations (Li et al. 2003, 2004; Busse et al. 2006) reported little or no effect of compaction on microbial community size, activity, or function. Nevertheless, negative responses by microbial communities to compaction in forest ecosystems abound (Dick et al. 1988; van der Linden et al. 1989; Torbert and Wood 1992; Li et al. 2003; Tan et al. 2005, 2008) and can be long-lasting (Hartmann et al. 2009), emphasizing the need for scrutiny and thoughtful interpretation when investigating soil microorganism response to disturbance and its relation to soil processes.

Conclusions

Postfire logging in a dry, mixed conifer forest with sandy loam volcanic soils appeared to have minimal effects on soil microbial richness. However, this short-term study revealed decreased plant-available N and P in the soil after postfire logging disturbances that could have long-lasting effects in a system that already is nutrient limited. A shift in bacterial communities corresponding with an increase in plant available N and P suggests that soil microbes in these postfire landscapes are resilient to mechanical disturbance. Clearly, effects of postfire timber harvesting on soil microbes, nutrients, and processes warrant longer term investigation. Management decisions about whether or not to harvest fire-killed trees should be balanced with

the recovery potential of a site, and the potential for high densities of fire-killed trees to increase the area of severely burned soil in the event of future fire.

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