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Do biological legacies moderate the effects of forest harvesting on soil microbial community composition and soil respiration

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ABSTRACT

Ecological forestry is a management approach that uses natural disturbance processes as models for designing silvicultural prescriptions that restore or sustain ecosystem biodiversity and function in actively managed forests. We evaluated how a novel ecologically-based multi-cohort silvicultural treatment affects the soil microbial community (SMC) and tested whether supplemental dead wood in the form of girdled trees alters these effects. We also tested SMC function by measuring soil CO_2 flux over multiple growing seasons, and examined if these patterns were related to soil microbial groups. Our experimental harvests were conducted in second-growth northern hardwood forests in northern Wisconsin, USA. Treatments included a modified shelterwood harvest (SH), a shelterwood harvest plus dead wood supplementation (SH + CWD), and an unharvested control; here we report responses three to five years post-treatment. The SMC composition (determined using PLFA) in both harvests was significantly different from the control, a difference driven by greater bacterial abundance in the harvested areas, and particularly by gram negative bacteria in SH. Microbial community composition was not significantly different between the two harvests (SH and SH + CWD). Total soil respiration was significantly lower in SH than in the control and SH + CWD treatments, a difference most likely driven by a reduction of the autotrophic respiration component in SH treatments due to harvesting, while in the SH + CWD treatment roots from living girdled trees contributed to autotrophic soil respiration. The relationship between the SMC and soil respiration varied with treatment and season. In general, soil respiration in the unharvested controls was most significantly correlated with microbes that relate to autotrophic respiration sources, while respiration in SH + CWD was most significantly correlated with heterotrophic microbes. These results indicate that, although the SMC composition was affected by forest harvesting practices incorporating live and dead biological legacies, supplementing the number of standing dead trees through girdling and felling maintained SMC function, as measured through total soil respiration, an indicator of some important aspects of ecosystem function.

1. Introduction

Ecological forestry is a forest management approach that attempts to model silvicultural practices on patterns of natural disturbance for the purpose of increasing ecosystem complexity and biodiversity (Franklin et al., 2007). In the Great Lakes region, USA, wind-related treefalls of varying extent and severity are the primary natural disturbance structuring northern hardwood forests (Frelich and Lorimer, 1991; Schulte and Mladenoff, 2005). Simulating elements of this disturbance regime involves incorporating biological legacies that include standing live trees, standing dead trees (snags), and downed tree boles within the post-harvest stand. These residual structures have been referred to as "lifeboats" because they provide habitats for affected organisms post-disturbance (Franklin et al., 2007). Studies have addressed the effects of ecological forestry harvesting practices on the diversity of ectomycorrhizal (Luoma and Eberhart, 2008; Luoma et al., 2006) and saprotrophic fungi (Brazee et al., 2014; Junninen et al., 2007), but there has been little research of the effects on the overall

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structure of the soil microbial community (SMC). Understanding these effects is important due to the functional relationship of the SMC to ecosystem productivity through decomposition and the production of plant-available nutrients (McGuire and Treseder, 2010).

Forest harvesting, as traditionally applied, may alter soil microbial communities through its influence on the abundance of living and deadwood legacies following harvest. In particular, the removal of overstory trees directly affects the heterotrophic rhizosphere bacterial community that is dependent on labile carbon (C) inputs (Farrar et al., 2003; Myers et al., 2001; Outerbridge and Trofymow, 2009; Paterson et al., 2007), and can change the abundance of complex C decomposers, such as saprotrophic fungi (Wolf and Wagner, 2005) and actinomycete bacteria (Deslippe et al., 2012; Nakatsu, 2005) by altering the quantity and quality of litter inputs. Furthermore, both the amount of overstory tree removal and woody debris retention influence soil moisture and temperature regimes (Brais et al., 2004; Lal, 2005), which can affect microbial metabolism (Davidson and Janssens, 2006; Mentzer et al., 2006; Wixon and Balser, 2013), leading to higher organic matter mineralization and decomposition rates (Covington, 1981). Therefore, retaining live tree legacies in the form of overstory trees within a harvested stand may help to maintain belowground SMC structure, sustain ecosystem productivity, and enhance connectivity across the forested landscape (Franklin et al., 1997; Gustafsson et al., 2010; Lewandowski et al., 2016; Rosenvald and Lõhmus, 2008). At the same time, retaining greater amounts of dead wood following harvest increases substrate availability for the microbial decomposer community, which can positively affect microbial biodiversity (Bouget et al., 2012; Brazee et al., 2014).

An important indicator of the physiological activities of the SMC is respired soil CO_2. Total soil respiration is composed of autotrophic CO_2 flux due to root respiration of higher plants, and heterotrophic CO_2 flux originating primarily from soil microorganisms (Kuzyakov, 2006). Forest harvesting alters soil respiration rates by affecting both autotrophic and heterotrophic respiration sources (Jandl et al., 2007; Johnson and Curtis, 2001; Lal, 2005), contributing to an estimated 8% reduction of C stored in forest soils on average (Nave et al., 2010). Autotrophically derived CO_2 from plant roots and associated mycorrhizal fungi make up 50% or more of soil respiration (Högberg et al., 2001), and removal of overstory trees initially leads to a reduction in autotrophic soil respiration (Kurth et al., 2014; Mattson and Swank, 1989; Nakane et al., 1986; Noormets et al., 2012; Striegl and Wickland, 1998).

The SMC composition and physiological activity contributing to soil respiration are affected by seasonal variability. The abundance of different groups within the microbial community changes due to seasonal variation; single-celled bacteria proliferate in the cooler, wet spring season, while fungi, because they are filamentous, better tolerate the warm, dry summer (Schimel et al., 2007). Total respiration generally increases throughout the growing season, peaking in mid-to-late summer, and individual respiration components also shift from primarily autotrophic to heterotrophic throughout the growing season (Czimczik et al., 2006). Autotrophic respiration potentially peaks earlier in the season due to greater aboveground plant growth (Högberg et al., 2001), while heterotrophic respiration peaks during mid to late summer when soil temperature is at its greatest (Czimczik et al., 2006).

In this research, we evaluate how the retention of live trees in an ecologically based timber harvest affects characteristics of the SMC, and test whether the increased complexity created by supplementing dead wood moderates this effect. In addition, we test how these establishment harvests affect soil surface CO_2 flux throughout the growing season, and examine the relationship of microbial groups to soil C dynamics. We used an operational scale field trial that compares the ability of active silvicultural treatments to accelerate the development of late successional characteristics in second-growth northern hardwoods while still allowing sustainable timber harvests (The Managed Old-growth Silvicultural Study or MOSS project; Fassnacht et al., 2013). The experiment crosses canopy treatments with dead wood additions. While a number of studies have focused on group selection openings or gaps, this trial includes a novel irregular multi-cohort treatment akin to a modified shelterwood. The modified shelterwood treatment is based on the work of Hanson and Lorimer (2007) and was designed to simulate a moderate-intensity wind disturbance that would remove 30–60% of the basal area using two entries 6–10 years apart. The treatment has four modified shelterwoods of two different sizes (two 0.40 ha and two 1.2 ha), and lightly-thinned and heavily-thinned "reserve" zones (Fassnacht et al., 2013). Here we are focused on the 1.2 ha shelterwoods only.

Our first objective in this research is to contrast the effects of ecological harvesting treatments on the SMC, soil moisture and soil temperature during the spring versus summer, five years following harvest. We expect that the SMC in the shelterwood harvests will differ from the unharvested control due to altered microclimatic conditions and resource availability, but that there will be a greater abundance of wood-decomposing microbes, such as fungi and actinomycetes, in the combined shelterwood and dead wood addition treatment due to greater abundance and diversity of resources. Microbial responses will be moderated by seasonal variation, with more single celled bacteria in the spring season and greater abundances of filamentous microbes during the summer. Our second objective is to evaluate the effects of experimental harvests on soil CO_2 flux 3–5 years following harvest. We expect a reduction in total soil respiration in the shelterwood due to the reduced autotrophic contribution. However, we expect that in the shelterwood with dead wood additions total soil respiration rates will remain more similar to the unharvested controls due to a potential increase in the heterotrophic contribution with the greater availability of substrate for heterotrophic bacteria and fungi. Finally, we evaluate the relationship between soil respiration and the SMC, soil moisture, and soil temperature during the spring and summer of year 5. We expect that heterotrophic activity will be a more important component of total respiration during the summer relative to spring, particularly in the combined canopy and dead wood addition treatment.

2. Methods

2.1. Site description

This study focused on a subset of treatments and sites within the MOSS project. Our research was conducted in the Northern Highland American Legion (NHAL) State Forest in Vilas County, and the Argonne Experimental Forest located within the Chequamegon-Nicolet National Forest in Forest County, Wisconsin (Fassnacht et al., 2013; Fassnacht and Steele 2016). Prior to treatment implementation, stands were even-aged, second-growth 70–90-year-old northern hardwood forests with no recent management activities. Stands are composed of two of the most common, mesic northern hardwood habitat types in the region; *Acer-Osmorhiza-Caulophyllum* and *Acer-Tsuga-Dryopteris*, (Kotar et al., 2002). The overstory is dominated by sugar maple (*Acer saccharum* Marsh.), with white ash (*Fraxinus americana* L.), basswood (*Tilia americana* L.), yellow birch (*Betula alleghaniensis* Britt.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) present as well. Soils are primarily sandy and coarse-loamy Haplorthods in NHAL (Natzke and Hvizdak, 1988), and coarse-loamy Fragiorthods and Haplorthods in Argonne (Boelter et al., 1995). However, soils at both sites are highly variable because they are derived from recent glacial origins (Fassnacht et al., 2013). The regional climate is continental, with an average temperature of 5 °C that ranges from a summer maximum of 32 °C to a winter minimum of −40 °C. Average precipitation is 813 mm, which occurs mostly during the growing season (USFS Argonne Experimental Forest; www.nrs.fs.fed.us/ef/locations/wi/argonne/).

2.2. Experimental design and treatment description

This study focused on one canopy treatment – the modified shelterwood combined with two coarse woody treatments nested within the canopy treatment. A passive, unharvested control was included for reference conditions. The canopy treatment and control are approximately 48.6 ha in area and replicated at two sites. Coarse woody debris treatments were applied to half of each canopy treatment. The establishment cut in each modified shelterwood harvest was designed to maintain 60–65% residual canopy cover and reduce mean stand basal area to 22.5 m^2 per ha. Treatments were implemented by professional loggers using cut-to-length harvesting systems between December 2007 and March 2008.

The 'harvest only' treatment (hereafter SH) included no special consideration for the addition of snags or downed woody material. The 'harvest-plus-CWD' (hereafter SH + CWD) treatment was designed to add dead wood over time, so some trees originally marked to harvest were instead girdled and left standing to increase snag density, or they were felled at the stump and left on site to increase the downed woody debris pool. The target for supplementation was to increase snag and CWD volumes to 65% of the amount found in old-growth forests based on amounts measured in Sylvania Wilderness Area, MI (Howe and Mossman, unpublished data; Fassnacht et al., 2013). Approximately five snags per hectare were added (Fassnacht and Steele, 2016).

2.3. Field methods

Measurements were focused within four 1.2 ha shelterwood openings - two openings within the SH treatment and two openings within the SH + CWD treatment at each sites. Two plot centers within each shelterwood opening were established using randomly generated coordinates. Four random locations were designated as permanent plots within the control stand at each site. At each plot, four soil respiration collars (PVC pipe 20 cm diameter × 10 cm height) were inserted into the soil to a depth of 7.5 cm during the spring of 2010; collars were oriented at fixed locations for repeated measurements on a north-south transect with 2 m spacing. We waited approximately one month after installing collars to begin flux measurements. Soil respiration was measured approximately every 4 weeks from late April to early November of the third through fifth post-treatment growing seasons (2010, 2011, and 2012). The order of measurements was randomized per round. A 90 sec measurement was recorded at each respiration collar using a LI-8100 infrared gas analyzer with 20 cm survey chamber (Li-Cor, Inc., Lincoln, NE). Collar depths were re-measured each sampling round and used to offset respiration calculations. Vegetation within each collar was periodically removed, although the forest floor and litter were not disturbed. All soil respiration measurements were completed within 1–2 days during each sampling round, and care was taken not to sample within 24 h of a rain event. Soil moisture and soil temperature were recorded at the time of soil respiration measurement. Moisture was measured at a depth of 6 cm with a portable, calibrated TDR moisture probe and HH2 Moisture Meter (Delta-T Devices, Cambridge, England). Soil temperature was measured at a depth of 7.5 cm using a portable probe long stem thermometer (model no. 15-078k, Fisher Scientific).

Soil samples for microbial lipid analysis were collected during the spring (May; 142 Julian Days) and summer (August; 219 Julian Days) of 2012; five growing seasons post-harvest. A soil core was taken to a depth of 15 cm using a 2.36 cm push probe (Hoffer sampler, JBK, Beavercreek, OH) at each of the four soil respiration collars and composited into one sample per plot. Prior to core collection, forest floor litter was cleared from the sampling location. Composite microbial soil cores were stored at 5 °C the day of collection, then transported to the University of Wisconsin-Madison within four days, where they were frozen at −20 °C prior to being dried by lyophilization (Freezemobil 12, Virtis of Gardiner, NY). Dried samples were cleared of roots and stones, and then ground in preparation for microbial lipid extraction.

2.4. Lipid extraction and analysis

Phospholipids are found in the cell membrane of all living organisms and, because different microbial groups have different phospholipid compositions (Tunlid and White, 1992), can be used to differentiate microbial groups in the soil (Frostegård and Bååth, 1996; Zelles, 1999). We used a modified phospholipid fatty acid (PLFA) and fatty acid methyl ester (FAME) method to assess the response of the SMC composition to experimental treatments (Balser and Firestone, 2005); complete details can be found in Lewandowski et al. (2015). Briefly, PLFAs were extracted from 3.5 g of lyophilized soil (Bligh and Dyer, 1959), analyzed using a Hewlett-Packard 6890 Gas Chromatograph (San Fernando, CA) with a flame ionization detector, and chromatogram peaks were identified by comparing retention times with calibration standards using the MIDI Sherlock microbial identification system (MIS) software (MIDI Inc., Newark DE). To determine the absolute amount of individual lipids, chromatogram peaks were multiplied by a response factor (Rfact) that normalized the peak area to lipid mass relationship (Personal communication, MIDI Inc., Newark, DE; Christie, 1989) then quantified by comparison with two external standards, methyl nonanoate (9:0) and methyl nonadecanoate (19:0).

We evaluate the response of the SMC to treatment effects by assessing both absolute and relative abundance PLFAs. To obtain the absolute (μmol lipid/ g soil) biomass of lipids, we used an open source licensed Microsoft Access® Database (Devin Wixon, 2013, Lipid GC Process) to process raw lipid data. Total microbial biomass was calculated as the sum of absolute abundances for all lipids present in the dataset (Balser and Firestone, 2005; Hill et al., 1993; White et al., 1979; Zelles et al., 1992). The relative abundance of lipids was calculated as the moles of a lipid/total moles of lipids in the sample, and is expressed as a %. Prior to analyses, lipids with an average relative abundance of less than 0.5% were removed from the dataset, leaving a total of 31 PLFAs. Fatty acid nomenclature is as described elsewhere (Frostegård, et al., 1996; Zelles, 1997; Aanderud et al., 2008).

Chemically similar fatty acids were classified into indicator groups, or guilds, including: arbuscular mycorrhizal fungi (AMF) (16:1ω5); Ectomycorrhizal/Saprotrophic Fungi (18:2ω6,9); Gram Positive bacteria (GmP) (15:0anteiso, 15:0iso, 16:0iso, 17:0anteiso, 17:0iso); Gram Negative bacteria (GmN) (16:1ω7, 18:1ω7, 19:0 cyclo, 17:0 cyclo); Actinomycetes (Act.) (16:0 10 methyl, 18:0 10 methyl). Although other lipids may also be potentially classified into these groups, we feel most confident in these classifications based on the literature (Bossio et al., 1998; Frostegård et al., 1996, 1993; Kieft et al., 1997; Olsson, 1999; Vestal and White, 1989; Wilkinson, 1988; Zelles, 1999; Zelles et al., 1992). To assess bacterial stress, we analyzed the ratio of monoenoic fatty acids to cyclopropyl fatty acids (17:0 cyclo, 19:0 cyclo/16:1ω7c, 18:1ω7c) as the CYC bacterial stress ratio. When GmN bacteria experience nutritional or anaerobic stress, they alter their monenoic fatty acids to cyclopropyl, resulting in an increase in the CYC ratio (Guckert et al., 1986; Kieft et al., 1997). This physiological stress ratio can indicate change due to nutritional fluctuations, environmental conditions or shifts in species composition (Willers et al. 2015).

2.5. Analysis

Prior to statistical analyses, all data (including soil respiration, microbial community, soil moisture and temperature) collected at the soil respiration collar level was averaged to the plot level. To avoid pseudoreplication in the linear mixed models, data from the canopy treatments were further averaged to the shelterwood level, resulting in two measurements for each shelterwood treatment and four measurements per control. Sites were treated as replicates, so sample sizes are four per harvest treatment and eight per control unless otherwise noted.

Datasets were transformed as needed to achieve normality. We used

mixed linear models to evaluate the effects of experimental treatments on repeated measurements of soil CO_2 flux, temperature, and moisture from three growing seasons. The repeated measures mixed effects models included the fixed effects of treatment, sampling time, and site as a block factor. A spatial power covariance structure was used to account for unequal spacing among sampling dates. A similar mixed model approach was used to characterize the response of the absolute and relative abundances of microbial guilds, microbial biomass and the bacterial stress ratio to the fixed effects of treatment and season. Site was included as fixed effects in these models. Analyses were conducted using the multiple mixed effects procedure (PROC MIXED) in SAS version 9.3 (SAS, 2008; System for Windows, SAS Institute Inc., Cary, NC, USA)).

To determine the effect of treatments and sampling season on the SMC guilds, we performed a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), in PRIMER version 7 (2015 PRIMER-E Ltd.) with the PERMANOVA+ add-on package (Anderson et al., 2008; Clarke and Gorley, 2015) using a Bray-Curtis resemblance measure on untransformed absolute and relative abundance PLFA data. PERMANOVAs were run using the default options of 9999 random permutations, Type III sum of squares, and permutation of residuals under a reduced model. To aid in visualization of variability in the lipid dataset, we use an unconstrained principal coordinates analysis (PCO) (Gower, 1966). PCO plots were produced using the plot function in R (R Core Team, 2012). Pearson correlation vectors for microbial guilds and the bacterial stress ratio, along with soil temperature and soil moisture at the time of microbial sampling are displayed, and the most highly correlated coefficients are given to evaluate the relationship with treatment and season effects.

Finally, we performed a series of regressions to explore the relationships of soil respiration with potential drivers including the absolute abundance of microbial guilds, soil moisture, and soil temperature. These soil variables were measured on the same day the cores were collected for microbial analysis (Julian day 142 and 219, year 5). Multiple regressions were used to compare the influence of environmental and biotic predictors on soil respiration in spring and summer separately. Data were pooled at the plot level (n = 8 per treatment) and a stepwise procedure was used to find the best model. Simple linear regression analyses were used to correlate soil respiration individually with each variable. The lm function in R (R Core Team, 2012) was used for model creation, and regressions were visualized using the ggplot2 (Wickham, 2009), grid, and gridextra packages within R (R Core Team, 2012).

3. Results

3.1. Soil microbial community biomass and composition

Multivariate PERMANOVA analysis of relative abundance data indicates significant seasonal variability in the SMC composition ($p = 0.0001$), and significant treatment effects ($p = 0.01$), which were driven by differences between unharvested controls versus SH + CWD ($p = 0.03$) and SH ($p = 0.06$) treatments. A seasonal separation in the SMC composition was also indicated in the PCO along axis 1 (Fig. 1), which was highly positively correlated with the relative abundances of AMF ($r = 0.77$) and soil fungi ($r = 0.62$), soil temperature ($r = 0.72$), and soil respiration ($r = 0.48$), and negatively correlated with the relative abundances of actinomycete ($r = -0.86$) and GmN bacteria ($r = -0.58$), and soil moisture ($r = -0.43$). Control treatments marginally separate from both SH + CWD and SH treatments along axis 1 (see previous correlations) and axis 2, which is positively correlated with the relative abundance of soil fungi ($r = 0.15$) and bacterial stress ($r = 0.3$), and negatively correlated with actinomycete ($r = -0.24$), GmP ($r = -0.69$), and GmN ($r = -0.25$) relative abundances (Fig. 1). The absolute abundances of the SMC exhibited significant seasonal variability ($p = 0.03$), but did not differ due to treatment effects (data not shown).

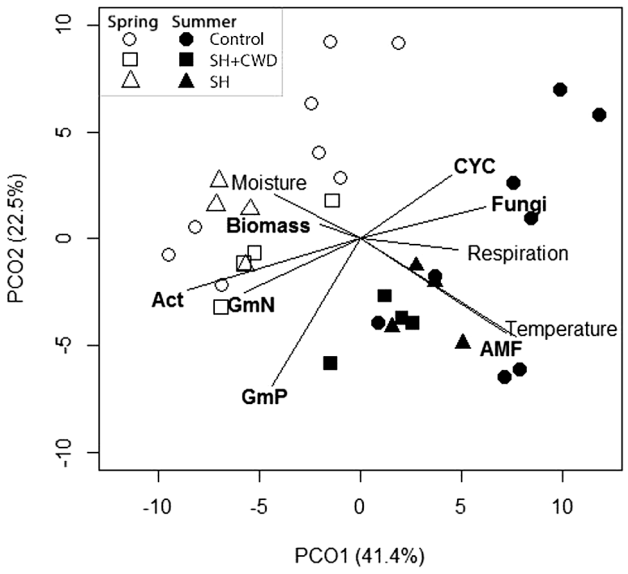

Fig. 1. Unconstrained principal coordinates analysis (PCO) of SMC among experimental treatments based on Bray-Curtis dissimilarities. We display the multivariate pattern among treatments (unharvested control, shelterwood harvests (SH), and shelterwood harvests plus CWD supplementation (SH + CWD)) during spring and summer sampling periods five years post-treatment to allow general position and dispersion patterns to be visualized. Pearson correlation vectors for microbial groups, soil respiration, temperature and moisture are displayed, and significant correlations are given in the text. A majority of the variation can be explained by seasonal differences in microbial community structure, which correlate with soil moisture, temperature, and respiration. Harvested treatments (n = 4 per treatment) have much lower variability in microbial community composition than controls (n = 8).

Total microbial biomass, actinomycete, GmN, and GmP biomass were 10–33% greater during the spring relative to summer, while AMF biomass was 63% greater in summer relative to spring measurement period (Table 1). Significant differences in seasonal fungal biomass were not detected (Table 1). Neither total biomass nor the biomass of individual microbial guilds differed among treatments ($p \geq 0.4$), or among treatments within seasons ($p \geq 0.14$). The relative abundance of microbial groups exhibited significant variability due to season; actinomycetes were 21% more abundant during the spring, while AMF and fungal relative abundances were 100% and 15% greater, respectively, and the CYC bacterial stress ratio was 9% greater during the summer (Table 1). Only the relative abundance of GmN bacteria ($p = 0.06$) responded to treatment effects; pairwise comparisons indicate that GmN relative abundance increased in the SH relative to the controls

Table 1
Absolute and relative abundance of microbial groups during the spring (n = 24) and summer (n = 24). Symbols following numbers denote statistical significance ($^{\Psi}p \leq 0.1$; $^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$) and indicate the season with greater absolute/relative abundance. ($^{\#}$CYC ratio units are %/%).

	Absolute (μmol lipid/g soil)		Relative (%)	
	Spring	Summer	Spring	Summer
Total biomass	0.220^{Ψ}	0.200	–	–
Fungi	0.007	0.007	3.30	3.80^{Ψ}
AMF	0.008	0.013^{***}	3.50	7.00^{***}
Actinomycete	0.012^{***}	0.009	5.10^{***}	4.20
Gram Positive	0.029^{*}	0.025	13.30	13.10
Gram Negative	0.039^{**}	0.032	17.90	17.00
CYC$^{\#}$	–	–	0.35	0.38^{*}

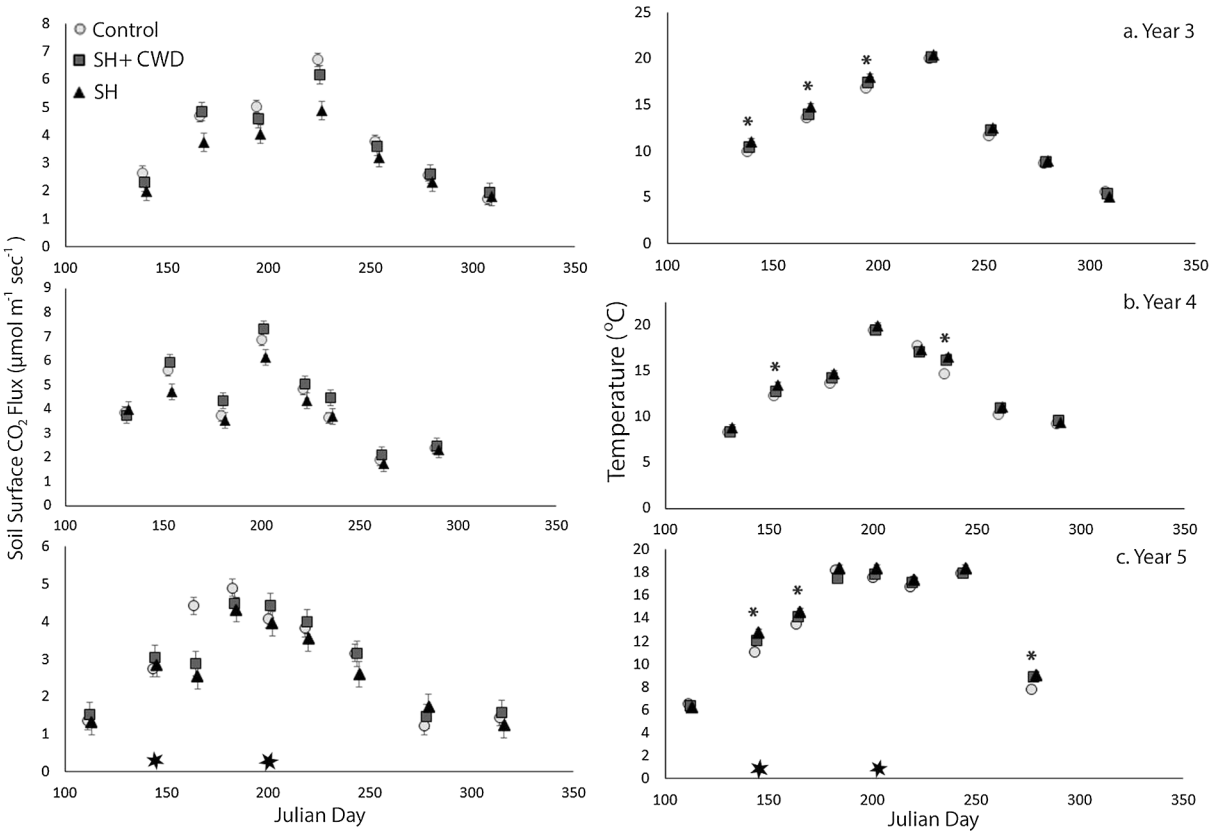

Fig. 2. Total soil respiration 3, 4, and 5 years after treatment implementation in control (n = 8), shelterwood harvests (SH; n = 4), and shelterwood harvests plus CWD supplementation (SH + CWD; n = 4). Significant differences among treatments ($p < 0.10$) are indicated by asterisks above treatment means. The two black stars in year 5 indicate sampling of the soil microbial community. Error bars indicate standard error of the mean.

(18.3% vs 16.6%, p = 0.02).

3.2. Total soil respiration, temperature and moisture

The canopy treatment influenced patterns of soil respiration (F = 5.30, p = 0.02); average emissions in the SH treatment (3.2 μmol m^{-2} sec^{-1}) were significantly lower than average emissions in controls (3.6 μmol m^{-2} sec^{-1}; p = 0.01) and SH + CWD treatments (3.7 μmol m^{-2} sec^{-1}; p = 0.02) (Fig. 2). The effect of treatments did not differ significantly by sampling date (trt * date F = 1.2, p = 0.19), but sampling date (F = 41.24, p < 0.0001) strongly influenced the variation in soil respiration. In general, respiration ranged from 1 to 2 μmol m^{-2} sec^{-1} in early spring and late fall, and peaked between 5 and 7 μmol m^{-2} sec^{-1} during the summer. Soil respiration was significantly greater during the summer (Julian day 200) than the spring (Julian day 143) soil microbial collection dates in year 5 (p = 0.0001) (Fig. 2).

Soil temperature varied among the experimental treatments throughout the growing season (treatment * sampling date, p = 0.006) with significantly higher temperatures in SH treatments compared to the unharvested control early and late in the growing season. In one instance in mid-August (Julian day 234, year four) temperature in SH + CWD was also significantly higher than the control, but generally soil temperature in this treatment was intermediate between the harvest only and controls and not significantly different from either (Fig. 2). Soil moisture in both harvests was significantly lower relative to values in the unharvested controls (SH + CWD = 14.7%, p = 0.06; SH = 13.8%, p = 0.006; controls = 16.3%). Moisture differed among sampling dates (p = 0.0001) and, in general, was highest during year 3 and lowest in year 5 (data not shown).

3.3. Soil respiration and biotic/abiotic soil factors

Stepwise multiple regressions indicated AMF biomass was the only measured significant predictor of springtime soil respiration (R^2 = 0.30, p = 0.005). During the summer measurement period, fungal biomass (standardized β = 0.51, p = 0.003), soil temperature (standardized β = 0.43, p = 0.01), and harvest treatments (standardized β = 0.41, p = 0.01) were significant factors influencing soil respiration (R^2 = 0.60, p = 0.003). During both the spring and summer, we observed strong correlations in the SH + CWD areas and unharvested controls, but none in the SH treatment (Table 2). During the spring, soil respiration was significantly correlated with the relative biomass of actinomycete bacteria in SH + CWD (r^2 = 0.39; p = 0.06), and with the CYC bacterial stress ratio, AMF biomass, and soil moisture in controls (r^2 = 0.34–0.56; p ≤ 0.08) (Table 2; Figs. 3 and 5). During the summer, soil respiration was strongly correlated with soil fungal biomass, the CYC bacterial stress ratio, and soil temperature in SH + CWD (r^2 = 0.46–0.58; p ≤ 0.04), and with soil fungal biomass, CYC bacterial stress ratio and GmN bacterial biomass in controls (r^2 = 0.32–0.76; p ≤ 0.08) (Table 2; Figs. 4 and 5).

4. Discussion

4.1. The soil microbial community

We captured seasonal shifts of the SMC between our spring and summer microbial sampling dates, this seasonality explains the largest proportion of variation within the community. The microclimate metrics were highly correlated with these compositional patterns. Soil temperatures were 6° lower and soil moisture 4.4% greater in the spring versus summer (both p-values = 0.0001). We attribute the greater

Table 2
Results of linear regression models relating soil respiration individually with microbial guilds, stress ratio, soil temperature, and soil moisture in unharvested controls, shelterwood harvests (SH), and shelterwood harvests plus coarse woody debris supplementation (SH + CWD) treatments at eight plots per treatment. P-values ($p \leq 0.1$) indicate significant linear relationships (R^2) between variables. All significant regression relationships are positively correlated with the exception of a significant negative correlation between soil respiration and the CYC bacterial stress ratio in SH + CWD treatments during the summer.

		Control		SH		SH + CWD	
		Adj. R^2	p-value	Adj. R^2	p-value	Adj. R^2	p-value
Spring	Fungi	0.24	–	0.00	–	0.23	–
	AMF	0.41	0.050	0.10	–	0.00	–
	Actinomycetes	0.00	–	0.00	–	0.39	0.060
	Gram Positive	0.00	–	0.00	–	0.18	–
	Gram Negative	0.09	–	0.00	–	0.20	–
	CYC	0.56	0.020	0.00	–	0.00	–
	Temperature	0.01	–	0.24	–	0.00	–
	Moisture	0.34	0.080	0.00	–	0.00	–
Summer	Fungi	0.76	0.003	0.00	–	0.46	0.040
	AMF	0.16	–	0.00	–	0.00	–
	Actinomycetes	0.25	–	0.14	–	0.00	–
	Gram Positive	0.17	–	0.19	–	0.00	–
	Gram Negative	0.32	0.080	0.11	–	0.00	–
	CYC	0.40	0.050	0.00	–	0.58	0.017
	Temperature	0.17	–	0.00	–	0.53	0.020
	Moisture	0.00	–	0.10	–	0.00	–

biomass in the spring to a much larger bacterial population (GmP, GmN, Actinomycetes) that predominates during the cool, wet spring (Myers et al., 2001), a pattern similar to that reported by Moore-Kucera and Dick (2008). The other pattern of AMF biomass and the relative abundances of both AMF and fungi being greater during the warm, dry summer has also been observed in other studies (Lewandowski et al., 2015) and can be attributed to filamentous microbes, such as AMF and soil fungi, being better able to withstand low moisture conditions by translocating water throughout the soil matrix, while soil bacteria are less abundant in low moisture or nutrient conditions (Schimel et al.,

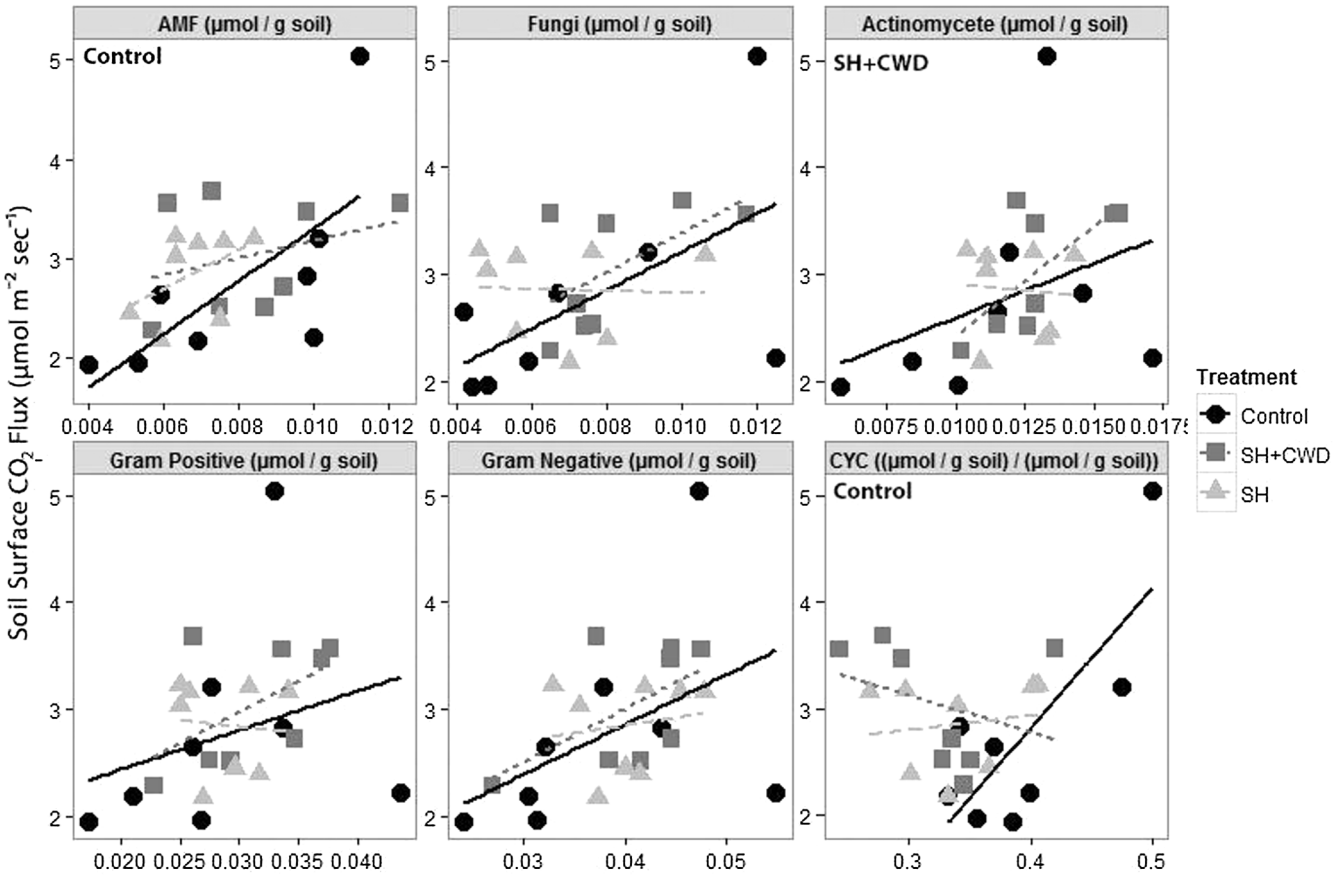

Fig. 3. Spring linear regressions among relative abundance of microbial groups and soil respiration in control, shelterwood harvests (SH), and shelterwood harvests plus CWD supplementation (SH + CWD). This analysis was performed at the plot-level with eight samples per treatment. Treatments that have significant regression relationships ($p < 0.1$) are indicated in the upper corner within each graph. X-axis labels and units are indicated in the bar above the graph.

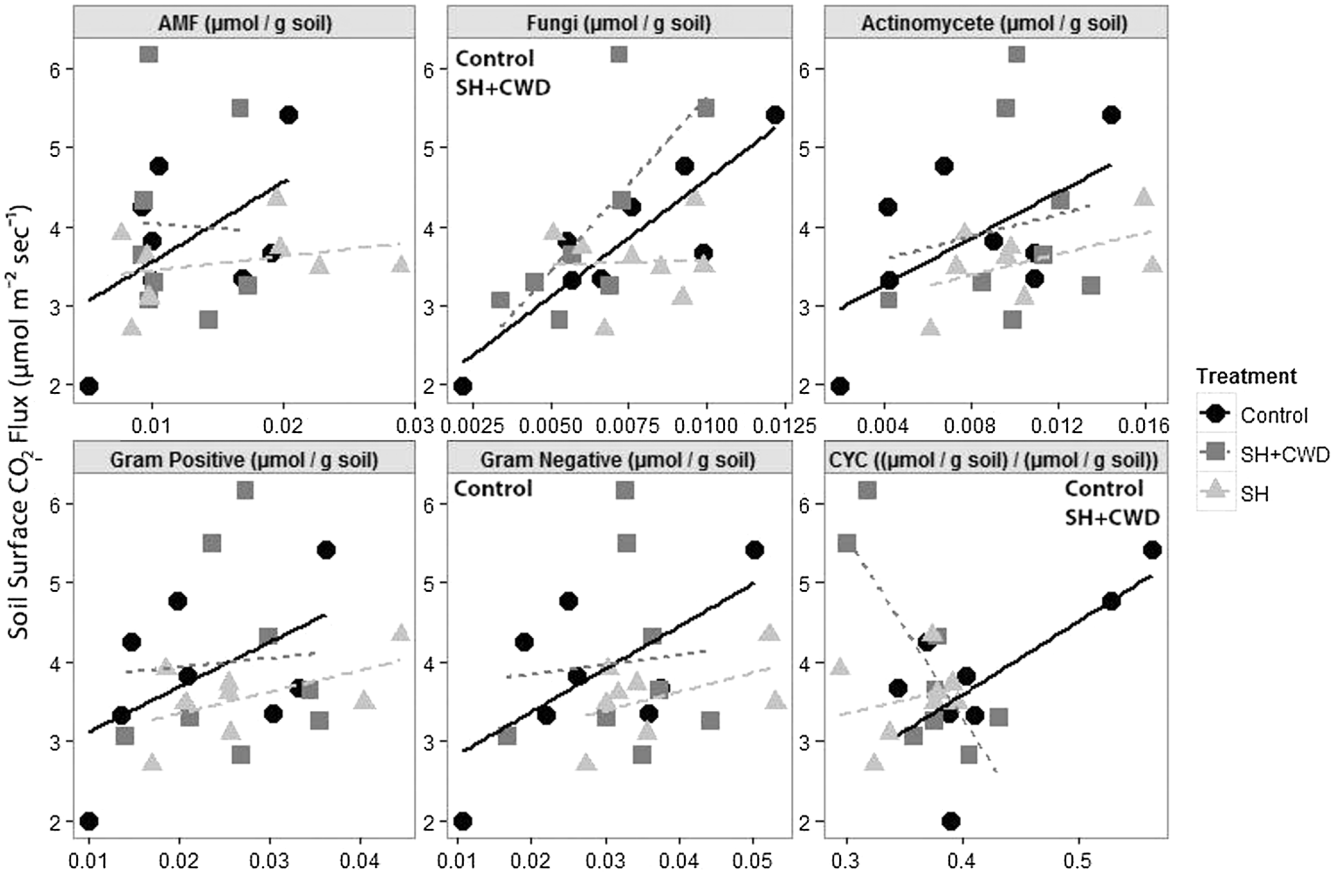

Fig. 4. Summer linear regressions among relative abundance of microbial groups and soil respiration in control, shelterwood harvests (SH), and shelterwood harvests plus CWD supplementation (SH + CWD). This analysis was performed at the plot-level with eight samples per treatment. Treatments that have significant regression relationships ($p < 0.1$) are indicated in the upper corner within each graph. X-axis labels and units are indicated in the bar above the graph.

2007).

The positive response by bacteria to both shelterwood treatments is similar to responses measured in other studies conducted in different forest types and at different response intervals. Notably, a measured increase in bacterial abundance was observed 1–2 years post-harvest in a Norway spruce stand (Siira-Pietikäinen et al. 2001), 4 years post-harvest in an oak/hickory stand (Ponder and Tadros, 2002), and 8 years post-harvest in a Douglas-fir stand (Moore-Kucera and Dick, 2008). In the case of GmN bacteria, the increase in abundance within the shelterwoods is likely caused by greater resource availability from rhizodeposition following the harvest treatment. GmN bacteria are common, single-celled soil bacteria that utilize recent plant C sources such as rhizodeposition (Kieft et al., 1997; Kramer and Gleixner, 2008; Nakatsu, 2005; Zelles, 1999). Previous research at these sites found that a significant percent of girdled trees in the SH + CWD treatment lived for multiple years post-treatment (Fassnacht and Steele, 2016) which may have moderated understory regrowth compared to the response in the harvest only treatment. This might account for the greater abundance of GmN bacteria in SH treatments, but not in SH + CWD. We expected to observe a greater relative abundance of wood-decomposing fungi and actinomycetes in the SH + CWD treatment compared to SH due to greater quantities and types of woody debris; however, no differences in microbial composition were observed between the snag treatments. Fassnacht and Steele (2016) report that nearly 85% of girdled trees had died within 4.5 years of girdling and 30–77% of girdled trees were still standing 5.5 years after treatment. This slow transition from standing dead to downed dead wood indicates that more time may be needed to fully assess the microbial response to the CWD inputs with further decomposition.

4.2. Total soil respiration, temperature and moisture

Total soil respiration is the sum of autotrophic root respiration and respiration of the heterotrophic soil community (Kuzyakov, 2006). Heterotrophic soil respiration is typically positively correlated with soil temperature and increases with soil moisture up to a certain point after which there is a negative correlation (Shao et al., 2013). Therefore, if we thought the heterotrophic community would cause the bulk of the response, we would expect that respiration would increase along with higher soil temperatures. Yet, we observed the lowest respiration rates in SH treatments which had the highest temperatures throughout the season and this likely reflects the negative relationship with soil moisture. Interestingly, the SH + CWD treatment, was cooler than SH with similar soil moisture but had soil respiration rates similar to the unharvested controls. An alternative, and more plausible, explanation for the reduced respiration in SH but not SH + CWD treatments compared with the control is that this observed trend is being primarily driven by the autotrophic component. Because a significant percentage of girdled trees in the SH + CWD treatment lived for multiple years post-treatment (Fassnacht and Steele, 2016), living, growing roots from these trees would have maintained autotrophic soil respiration at rates comparable to the unharvested control.

4.3. Relationships among soil respiration and biotic/abiotic soil factors

We sought to relate total soil respiration with individual biotic/abiotic soil factors within each treatment during the spring and summer to explore patterns that might improve our understanding of when and how these factors influence total soil respiration post-harvest. While

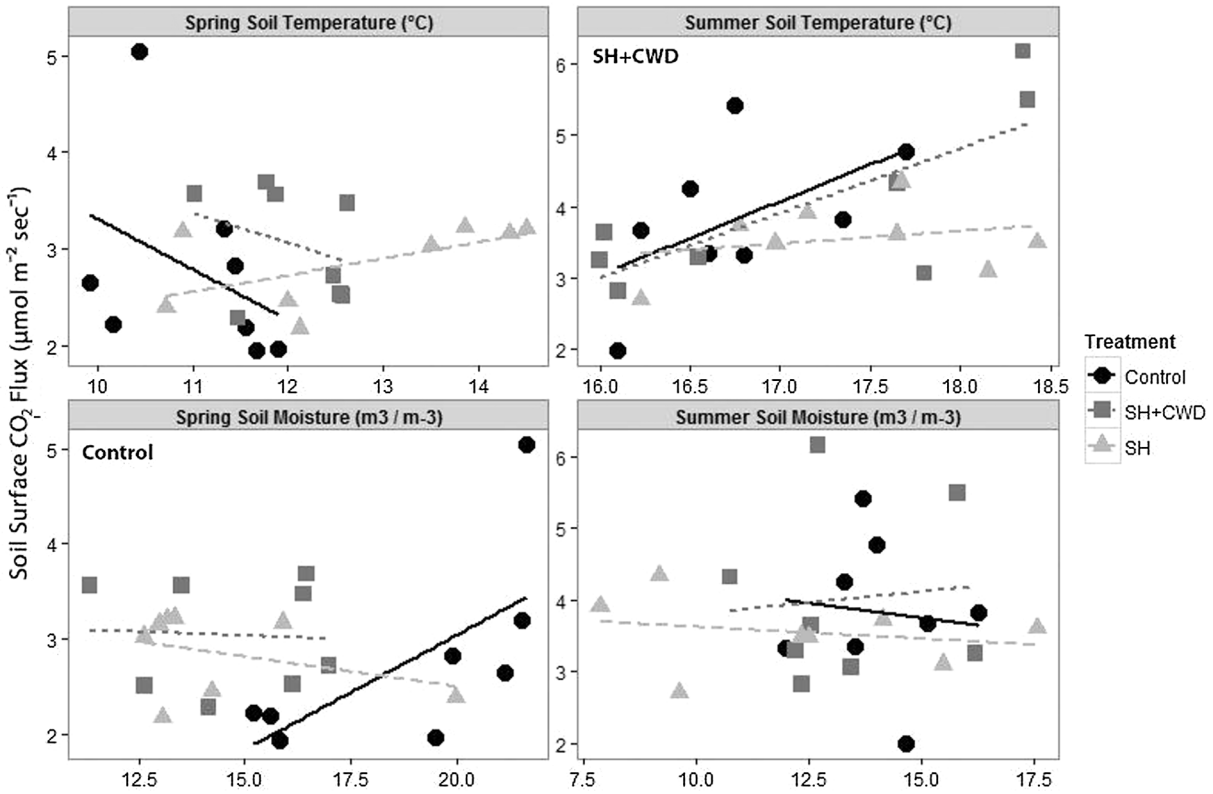

Fig. 5. Linear regressions among soil moisture and temperature and soil respiration during the spring and summer in control, shelterwood harvests (SH), and shelterwood harvests plus CWD supplementation (SH + CWD). This analysis was performed at the plot-level with eight samples per treatment. Treatments that have significant regression relationships ($p < 0.1$) are indicated in the upper corner within each graph. X-axis labels and units are indicated in the bar above the graph.

these relationships are correlational and not causative, we felt these results contribute to the current body of literature regarding the different sources of soil respiration by providing an interesting insight into the relationships between a key soil process and the *in situ* soil microbial community. The resulting numerous positive linear relationships with the absolute abundances of individual microbial groups reflect the idea that increasing microbial biomass leads to greater respiration. The multiple regression analyses indicated biotic variables were significant predictors of respiration in both seasons, while environmental factors were only influential in the summer.

We see a number of explanations for the positive relationship between soil respiration and soil moisture, the bacterial stress ratio, and AMF absolute biomass. Under stressed conditions, such as those due to soil rewetting that could be caused by the spring thaw or precipitation events, GmN bacteria alter their resource allocation from growth to survival pathways causing an increase in the bacterial stress ratio, which ultimately results in greater CO_2 respiration and less C stored in soil organic matter (Schimel et al., 2007). The positive relationship between respiration and AMF could also be related to moisture in the controls, as higher moisture during the spring has been shown to stimulate root respiration (Carbone et al., 2011). Root respiration, which is controlled by the availability of recent photosynthate (Heinemeyer et al., 2006; Högberg et al., 2001) is directly related to the respiration of AMF (Moyano et al., 2007). The increase in belowground labile C during the spring due to vegetation leaf-out could also contribute to the positive correlation between AMF biomass and soil respiration in the control. We would be less likely to see this relationship in the shelterwoods due to the reduction in overstory vegetation. During the summer, respiration in the controls is significantly and positively correlated with fungal and GmN bacterial biomass, and the bacterial stress ratio. This could be caused by the fact that controls are significantly cooler than harvested areas, and compared to the harvested treatments, soil moisture in the controls skews higher. The cool and moist spring-like conditions in controls support soil fungi, while the added rhizodeposition from trees promotes GmN bacterial biomass, a higher bacterial stress ratio, and greater total soil surface respiration.

In the SH + CWD treatment, the positive correlations between soil respiration and actinomycete bacteria and soil fungi are most likely because these microbial groups are able to decompose recalcitrant C sources such as woody debris (Deslippe et al., 2012; Nakatsu, 2005; Wolf and Wagner, 2005). The negative correlation between soil respiration and the bacterial stress ratio is more difficult to explain as this does not fit with the current literature (Schimel et al., 2007); more sampling may be needed to validate the significance of this relationship. The lack of correlations between soil respiration and microbial groups in the SH treatment could be due to this treatment being the driest of the three treatments, resulting in a reduction in heterotrophic activity leading to reduced soil respiration (Carbone et al., 2011; Moyano et al., 2007).

4.4. Conclusion

The purpose of this research was to understand the effect of ecological forestry practices, including living and dead biological legacies, on composition, biomass, and metabolic activity of the SMC, and total soil respiration. We found seasonality that influences microclimatic patterns, describes most of the variation in the SMC composition and biomass. Bacterial groups comprised the highest relative abundance of the community, though fungal abundance increased in the summer sampling period. The SMC composition differed among canopy treatments, with fungal groups more abundant in the unharvested controland bacterial groups more abundant in harvested treatments. The changes in microclimatic conditions caused by harvesting, resulted in changes in soil CO_2 flux. While typically, higher soil temperatures correspond with increased soil CO_2 flux, we measured lower fluxes in the hotter harvest only treatment (SH). These patterns reflect a shifting

balance of autotrophic and heterotrophic compononents of soil respiration. Total soil respiration in the modified shelterwood with standing dead wood addition (SH + CWD) more closely paralleled total soil respiration in unharvested controls, presumably because roots from girdled trees that were still living contributed to autotrophic soil respiration. Soil respiration in unharvested controls was most significantly correlated with microbes that relate to autotrophic respiration sources, while respiration in SH + CWD was most significantly correlated with heterotrophic microbes. These results indicate that although ecological forest harvesting practices changed the SMC composition, the addition of standing dead wood effectively maintained SMC function, measured as total soil respiration, which is an important component of ecosystem function.

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Appendix A

See Tables A1 and A2.

Table A1
Relative abundance (%) of microbial groups by treatment during the spring (n = 24) and summer (n = 24). Total biomass is an absolute abundance (μmol lipid/g soil).

	Spring			Summer		
	Control	SH	SH + CWD	Control	SH	SH + CWD
Total biomass	0.222	0.217	0.225	0.179	0.215	0.193
Fungi	3.250	3.070	3.640	4.246	3.907	3.261
AMF	3.536	3.136	3.694	7.228	7.338	6.433
Actinomycete	4.856	5.099	5.260	3.815	4.319	4.465
Gram positive	13.000	13.210	13.788	12.792	12.818	13.778
Gram negative	17.127	18.670	18.029	16.085	17.870	17.178
CYC	0.395	0.339	0.324	0.424	0.358	0.368

Table A2
Regression table reporting results of stepwise multiple regression analyses performed to evaluate the relationship of environmental and biotic parameters with soil CO_2 flux in the spring ($R^2 = 0.304$) and summer ($R^2 = 0.599$). Both analyses included a sample size of 24 observations.

Season	Variable	*B*	*SE B*	β	*t*	*p*
Spring	Intercept	1.47	0.47	0	3.12	0.005
	AMF	184.11	59.47	0.55	3.10	0.005
Summer	Intercept	−6.07	2.98	0	−2.04	0.055
	Soil temp	0.51	0.18	0.43	2.78	0.012
	Fungi	204.07	61.58	0.51	3.31	0.004
	Treatment	−0.80	0.29	−0.41	−2.75	0.012

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