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The effect of fire on microbial biomass: a meta-analysis of field studies

Sandra R. Dooley · Kathleen K. Treseder

Abstract Soil microbes regulate the transfer of carbon (C) from ecosystems to the atmosphere and in doing so influence feedbacks between terrestrial ecosystems and global climate change. Fire is one element of global change that may influence soil microbial communities and, in turn, their contribution to the C dynamics of ecosystems. In order to improve our understanding of how fire influences belowground communities, we conducted a meta-analysis of 42 published microbial responses to fire. We hypothesized that microbial biomass as a whole, and fungal biomass specifically, would be altered following fires. Across all studies, fire reduced microbial abundance by an average of 33.2% and fungal abundance by an average of 47.6%. However, microbial responses to fire differed significantly among biomes and fire types. For example, microbial biomass declined following fires in boreal and temperate forests but not following grasslands fires. In addition, wildfires lead to a greater reduction in microbial biomass than prescribed burns. These differences are likely attributable to differences in fire severity among biomes and fire types. Changes in microbial abundance were significantly correlated with changes in soil CO_2 emissions. Altogether, these results suggest that fires may significantly decrease microbial abundance, with corresponding consequences for soil CO_2 emissions.

Keywords Biome · Fire · Fire severity · Fungi · Global climate change · Meta-analysis · Microbial biomass · Soil CO_2 emissions

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Introduction

Soil microbes play a critical role in mediating feedbacks between terrestrial ecosystems and global climate change. Bacteria and fungi regulate the transfer of carbon (C) from terrestrial ecosystems to the atmosphere via the decomposition of organic material in soil (Swift et al. 1979). In doing so, microbes directly influence the concentration of CO_2 in the atmosphere. Microbes are also sensitive to global change factors, including changes in temperature (Allison and Treseder 2008; Frey et al. 2008; Rustad et al. 2001), soil nutrients (Allison et al. 2010; Allison et al. 2008; Demoling et al. 2008), and moisture availability (Hawkes et al. 2011; Salamanca et al. 2003). Fire is one additional aspect of global climate change that may impact soil microbial communities and, in turn, the way that ecosystem C dynamics recover following fire. Fires are a pervasive disturbance in natural ecosystems, and the frequency

and severity of wildfires is anticipated to increase in forest biomes under future warmer and drier climate patterns (Balshi et al. 2009; Flannigan et al. 2009; Pechony and Shindell 2010). Climate-linked increases in wildfire activity are already evident in forests across the western United States (Miller et al. 2009; Westerling et al. 2006) and boreal forests especially (Kasischke and Stocks 2000). A more complete understanding of the way in which fire affects soil microbes is necessary for predicting ecosystem C dynamics under future global change.

Fires may negatively affect total soil microbial abundance through both direct and indirect mechanisms (Fig. 1). Direct heat transfer to soils during fire may lead to heat-induced microbial mortality (Cairney and Bastias 2007; Hart et al. 2005). Both laboratory and field studies have indicated that fatal temperatures for microbes can be less than 100°C (DeBano et al. 1998), which is below the surface and subsurface temperatures achieved during many fires (Frandsen and Ryan 1986; Hernandez et al. 1997; Neary et al. 1999). Fires also alter soil physical and chemical properties like hydrophobicity, nutrient concentrations, and C quality and these changes may in turn have negative consequences for microbes (Certini 2005). For example, burning has been shown to increase soil water repellency and hydrophobicity, resulting in soil drying (DeBano 2000; O'Donnell et al. 2009). Additionally, nutrient volatilization during intense fires decreases long-term nutrient availability in soil (Wan et al. 2001), which may inhibit microbial growth. Declines in microbial abundance following fires may also be attributable to post-fire changes in soil C. Indeed, the quantity and quality of soil C is reduced following fires in boreal forests (Neff et al. 2005) and these changes are associated with a concurrent decline in microbial biomass (Waldrop and Harden 2008).

Alternatively, post-fire changes in soil properties may increase total microbial abundance (Fig. 1). Ash deposition following fires increases the availability of inorganic nitrogen (N) in soil (Grogan et al. 2000; Peay et al. 2009; Wan et al. 2001). Post-fire N availability may also increase due to higher rates of N mineralization. This pulse of available soil N could stimulate microbial growth by alleviating nutrient limitations. In addition, post-fire decreases in aboveground vegetation reduce evapotranspiration, which may in turn increase soil moisture content (Moore and Keeley 2000). Furthermore, decreases in soil shading can lead to higher soil temperatures in the years following a fire (Treseder et al. 2004). Higher soil temperatures following fires may promote the growth of bacteria and fungi, especially in ecosystems where microbial growth is strongly limited by temperature.

Soil fungal responses to fire may differ from the response of the microbial community as a whole.

Fig. 1 Potential direct and indirect mechanisms through which fire may increase (+) or decrease (−) microbial abundance. (Solid arrows) direct mechanism, (dashed arrows) indirect mechanism
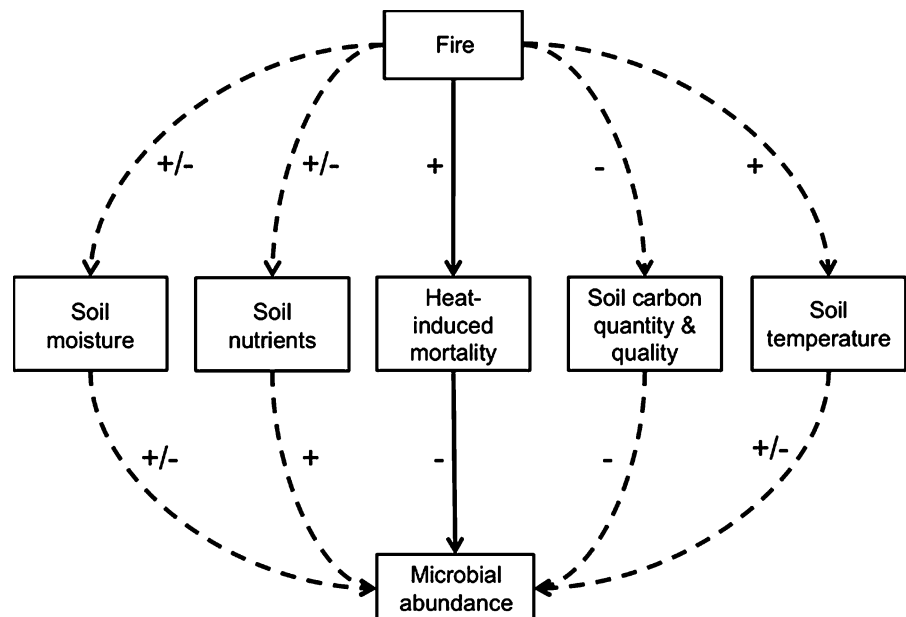
Fungi are tolerant of acidic soils and are typically dominate members of the microbial community in soils with low pH, while bacterial abundance in soil increases from low to high pH (Bárcenas-Moreno et al. 2011; Rousk et al. 2010). Ash deposition following fires increases soil pH (Peay et al. 2009), which may favor the growth of bacteria and result in fungal declines. In soil heating trials, fungi also appear to be more heat sensitive than bacteria (Bollen 1969), suggesting that fungi may be more severely affected by fire than the microbial community as a whole. However, reported decreases in fungal abundance following fires (Hamman et al. 2007; Rutigliano et al. 2007) are difficult to reconcile with the observation that certain fungal species are fire-adapted and fruit abundantly following fires (Wicklow 1973, 1975). Thus, changes in total soil fungal abundance following fires remain unclear. Since fungi are important decomposers of recalcitrant C compounds in soil, fire-induced changes in soil fungal abundance may affect the turnover and storage of recalcitrant soil C.

Post-fire changes in soil chemical and physical properties vary in their duration and this may have consequences for the recovery of microbial biomass following fires. For example, the rapid regeneration of fire-adapted vegetation may nullify changes in soil moisture and soil temperature within the first few years following a fire (Cave and Patten 1984). Moreover, increases in inorganic N availability may be transient if plants and soil microbes can readily assimilate this nutrient pulse. Conversely, nutrient volatilization during fires may decrease total ecosystem N for decades following a fire (Harden et al. 2003). Soil organic C also recovers slowly, especially following intense fires that consume the majority of the organic horizon (González-Pérez et al. 2004). We currently have a limited understanding of how soil microbial communities recover from fire.

Numerous studies have measured changes in microbial abundance following fires, but the results among these studies are inconsistent. Some studies find increases in microbial abundance following fires, while others report negative microbial responses to fire. In addition, few studies have examined microbial responses to fire over longer timescales (i.e., years to decades). Consequently, it is unclear how projected increases in fire activity will affect microbial biomass on short and long timescales. Because soil microbes regulate C loss from ecosystems, this is a key uncertainty that hinders our ability to predict the magnitude and duration of feedbacks between fire and global climate change. In this study we synthesize the existing literature regarding how fire alters soil microbial abundance by conducting a meta-analysis of published microbial responses to fire. We hypothesized that fires would alter microbial abundance, but that wildfires would elicit greater changes in microbial biomass than prescribed burns due to differences in burn severity. Furthermore, we expected that microbial responses to fire would vary by biome, owing to differences in fuel loads across ecosystem types. In this meta-analysis we specifically examined microbial responses to fire in boreal forests, temperate forests, grasslands, and woodland/shrublands because these were the only biomes in the literature with sufficient replication to include. We also predicted that the effect of fire on microbial biomass would diminish as the time since fire increased. Finally, we hypothesized that changes in microbial abundance would be associated with parallel changes in CO_2 emissions from soils. We tested these hypotheses separately for studies that targeted fungi separately and the microbial community as a whole (fungi + bacteria) since these major classes of microbes may have different responses to fire.

Materials and methods

Literature survey and selection criteria

We searched the biological literature for studies that reported microbial abundance measurements in burned and unburned soils. Literature searches were conducted using the ISI Web of Science database with the keywords: fire or burn and microb* or fung* or bacteri*. Studies were collected for analysis until 1 October 2010.

Meta-analyses were performed on a subset of articles that met our search criteria (see Online Resource 1 in Supplementary Material). We focused on studies reporting microbial abundance measurements following a fire in comparison to an unburned control. If a particular study utilized a chronosequence approach in which the study sites varied in their time since fire, we assumed that the oldest site in the chronosequence functioned as the control site.

Given our focus on the ecosystem-level implications of fire-induced changes in microbial abundance, we excluded studies in which fire was simulated in the laboratory. In addition, we limited our data collection to results in which the mean, standard deviation (SD), and replicate numbers (n) of microbial abundance measurements were reported or could be determined.

Because one critical assumption of meta-analyses is that studies are independent from one another (Gurevitch and Hedges 1999), we primarily used only one data set from a given publication. For example, if a given study reported changes in microbial biomass over time, the sampling date closest in time to the fire was used. However, when testing for a relationship between microbial responses and the time since fire, we included all sampling points reported within studies. In addition, if a particular study sampled from a variety of soil depths, we used data from the uppermost soil layer (0–5 cm). If a study reported the effect of multiple levels of fire severity, we chose the most severe treatment because global change is anticipated to increase fire severity (Westerling et al. 2006).

Data acquisition

For each study, the mean, SD, and n of microbial abundance were recorded for the unburned control as well as the burned area. In addition to recording changes in microbial abundance with fire, we also noted the type of fire (wildfire or prescribed burn) and the biome in which the study took place. The only biomes with sufficient replication to include in the meta-analysis were boreal forests, temperate forests, grasslands, and woodland/shrublands. When means and errors were presented in a graph, we digitized the data by using Engauge Digitizer 4.1 (http://digitizer.sourceforge.net). If standard errors (SEs) were presented instead of standard deviations, they were converted using the formula: $SD = SE\ (n^{1/2})$. Any unidentified errors bars in graphs were assumed to represent standard errors. There were a total of two studies (Garcia and Rice 1994; Jensen et al. 2001) in which error bars were not identified.

Indices of microbial abundance

To characterize microbial abundance in soils, authors employed a variety of techniques. To estimate total microbial biomass, studies used chloroform fumigation extraction or incubation for microbial C (Brooks et al. 1985), total amounts of phospholipid fatty acids (PLFAs) in soil (Frostegard and Bååth 1996), substrate-induced respiration (Anderson and Domsch 1978), or total abundance of ATP in soil (Eiland 1983). Studies characterized fungal abundance using microscopy, fungal-specific PLFAs, total amounts of ergosterol in soil (Djajakirana et al. 1996), and quantitative PCR with universal fungal primers (Borneman and Hartin 2000). We excluded studies that focused on specific groups of bacteria or fungi (e.g., ammonia oxidizers, mycorrhizal fungi) to avoid biasing our results towards subsets of bacterial or fungal communities.

Soil CO_2 emissions

Where possible, we also recorded concurrent changes in soil CO_2 emissions following fires. Authors measured soil CO_2 emissions via laboratory incubations of soil or using chambers in the field (Kutsch et al. 2009).

Statistics

Meta-analyses were used to determine the significance of microbial biomass responses to fire. For each study and each target group of microorganisms (microbes or fungi) the effect size was calculated as the natural log of the response ratio ('R'). R is calculated as the mean of the treatment group (i.e., burn group) divided by the mean of the control group and an R of 1 indicates that fire had no effect on microbial abundance. The estimate of variance within each study was represented by v_{lnR} and is computed using the means, SD, and replicate numbers of the control and treatment group (Hedges et al. 1999).

To determine if fire had a significant effect on microbial abundance, we applied a random effects model using MetaWin software (Rosenberg et al. 2000). Bias-corrected bootstrap 95% confidence intervals (CIs) were calculated for each mean R. If the 95% CIs of R did not overlap with 1, then responses were significant at $P < 0.05$. Random effects models allow for comparisons among groups in a framework similar to analysis of variance (ANOVA). Using this framework, we compared microbial abundance responses to fire among biomes,

type of fire, and the method of measurement used to estimate microbial abundance. Furthermore, we applied continuous randomized effects model meta-analyses to test for relationships between R and the time since fire and replicate number. Tests for the relationship between R and the time since fire were done separately for each biome, owing to the fact that the time required for an ecosystem to recover from fire varies substantially between biomes. Statistical results reported include R; 95% CIs for R (CI); total heterogeneity in R among studies (Q_T); and in the case of comparisons among groups, the difference among group cumulative effect sizes (Q_M), and the residual error (Q_E) (Rosenberg et al. 2000). We also conducted a Kendall's tau rank correlation test (Sokal and Rohlf 1995) to test for the relationship between replicate number of each study and the standardized effect size. Such a relationship would be indicative of a publication bias in which larger effects of fire were more likely to be published than smaller effects. Finally, we applied a Pearson's correlation to analyze

the relationship between R of microbial abundance and R of soil CO_2 emissions for studies in which both were reported. We also analyzed the relationship separately for measurements made in the laboratory and measurements made in the field.

Results

Total microbial biomass

Microbial biomass declined significantly following fires, by an average of 33.2% across all studies (Table 1). However, microbial responses to fire were inconsistent among studies, as indicated by a significant Q_T value ($Q_T = 52.86$, $P = 0.006$). The response of microbes to fire differed significantly by fire type (Table 1, $P = 0.023$). When examined separately, wildfires lead to a significant reduction in microbial biomass while prescribed fires had non-significant effects (Table 1). Microbial responses to

Table 1 Results of statistical comparisons among and within groups

Comparison	Group	R	95% CI	Number of studies	Q_M	Q_E	P-value among groups[a]
Microbes	All microbe studies*	0.668	0.480–0.847	31			
Fire type	Prescribed fire	0.857	0.658–1.102	20	9.673	42.715	0.023
	Wildfire*	0.400	0.197–0.647	11			
Biome	Boreal forest*	0.452	0.342–0.591	7	13.312	36.459	0.087
	Temperature forest*	0.430	0.183–0.773	9			
	Grassland*	1.175	1.033–1.341	8			
	Woodland/shrubland	0.867	0.429–1.365	7			
Measurement	Chloroform fumigation*	0.638	0.449–0.847	25	2.921	46.229	0.409
	PLFA*	0.729	0.649–0.838	2			
	SIR*	1.234	1.060–1.338	3			
Fungi	All fungi studies*	0.524	0.382–0.729	11			
Fire type	Prescribed fire*	0.495	0.375–0.681	7	0.187	9.200	0.685
	Wildfire	0.597	0.187–1.281	4			
Biome	Boreal forest*	0.368	0.318–0.413	4	19.998	12.061	0.008
	Temperate forest	0.885	0.433–1.483	4			
	Woodland/shrubland*	0.600	0.417–0.606	3			
Measurement	Ergosterol*	0.358	0.298–0.418	2	10.102	11.281	0.079
	Microscopy	0.788	0.537–1.188	6			
	PLFA*	0.417	0.373–0.526	2			

PLFA phospholipid fatty acid, *SIR* substrate induced respiration

* Significant effect of fire on group ($P < 0.05$)

[a] Only groups represented by two or more studies were included in comparisons

fires did not differ significantly across biomes ($P = 0.087$) or methods of measurement ($P = 0.409$, Table 1). Within biomes, fire effects were significantly negative in boreal forests and temperate forests. Conversely, fire effects in grasslands were significantly positive. Estimates of microbial biomass derived from chloroform fumigations and total amounts of PLFAs in soil were associated with a significant decline in microbial biomass, while studies that utilized the substrate-induced respiration technique found a significant 23% increase in microbial biomass (Table 1). However, very few studies utilized PLFA analysis ($n = 2$) and substrate-induced respiration ($n = 3$).

Fungi

Across all studies, fires significantly reduced fungal abundance by an average of 47.6%. In addition, fungal abundance response ratios were not significantly heterogeneous among studies ($Q_T = 9.75$, $P = 0.463$). Fungal responses to fire differed significantly among biomes (Table 1, $P = 0.008$). Responses were significantly negative in boreal forests and woodlands/shrublands but non-significant in temperate forests. However, the study by Kara and Bolat (2009) conducted following a wildfire in a temperate forest was associated with a strong positive response of fungal abundance to fire ($R = 1.6$). This study utilized dilution-plating to characterize fungal abundance following fire. Because the majority of soil microbes do not grow readily in culture, this technique may not accurately reflect microbial abundance in soil. When Kara and Bolat (2009) was removed from the analysis, fungal responses were also significantly negative following fire in temperate forests; response ratios ranged between 0.376 and 0.888. There were no significant differences in fungal responses across fire types ($P = 0.685$) and measurement assay ($P = 0.079$, Table 1). Prescribed fires were associated with a significant 50% decline in fungal abundance. When Kara and Bolat (2009) was excluded, fungal abundance declined significantly following wildfires, by an average of 64%. Ergosterol and PLFA based estimates of fungal abundance yielded significantly negative responses while microscopy-based counts were non-significant. However, it is important to note that ergosterol ($n = 2$) and PLFA ($n = 2$) based estimates of fungal

abundance following fire had low replication in the literature.

Recovery of microbial abundance following fire

There was a non-significant relationship between microbial response ratios and the time since fire when data from all biomes were combined ($P = 0.206$, data not shown). In boreal forests, as the time since fire increased, the effect of fire on microbial biomass became significantly less negative (Fig. 2). Responses to fire in boreal forests were generally negative in the first 15 years following fires; while after 15 years microbial responses to fire were positive (Fig. 2). Microbial response ratios were not significantly related to the time since fire in temperate forests ($P = 0.763$), grasslands ($P = 0.568$), or woodland/shrublands ($P = 0.280$, Fig. 2). Additionally, we did not detect a significant relationship between fungal responses to fire and the time since fire across all biomes combined ($P = 0.920$) and for each biome when examined individually ($P = 0.440$, 0.629, 0.863 for boreal forests, temperate forests and woodland/shrublands, respectively; data not shown).

Microbe and fungi studies combined

Across all microbial and fungal studies included in this meta-analysis, there was a marginally significant relationship between response ratio and replicate number ($P = 0.057$, data not shown). However, this pattern was primarily driven by three studies that were associated with a large negative response ratio and a low replicate number. When these studies were excluded, the relationship between response ratio and replicate number was non-significant ($P = 0.389$). The Kendall's tau rank correlation test for publication bias was non-significant ($\tau = 0.139$, $P = 0.190$), indicating that stronger effects of fire were no more likely to be published than weaker effects.

Soil CO_2 emissions

A limited number of studies reported changes in soil CO_2 emissions in concert with changes in microbial biomass ($n = 13$). Across all studies that reported both, there was a significant positive correlation between the R of microbial biomass and the R of soil CO_2 emissions ($n = 13$, $r = 0.616$, $P = 0.025$,
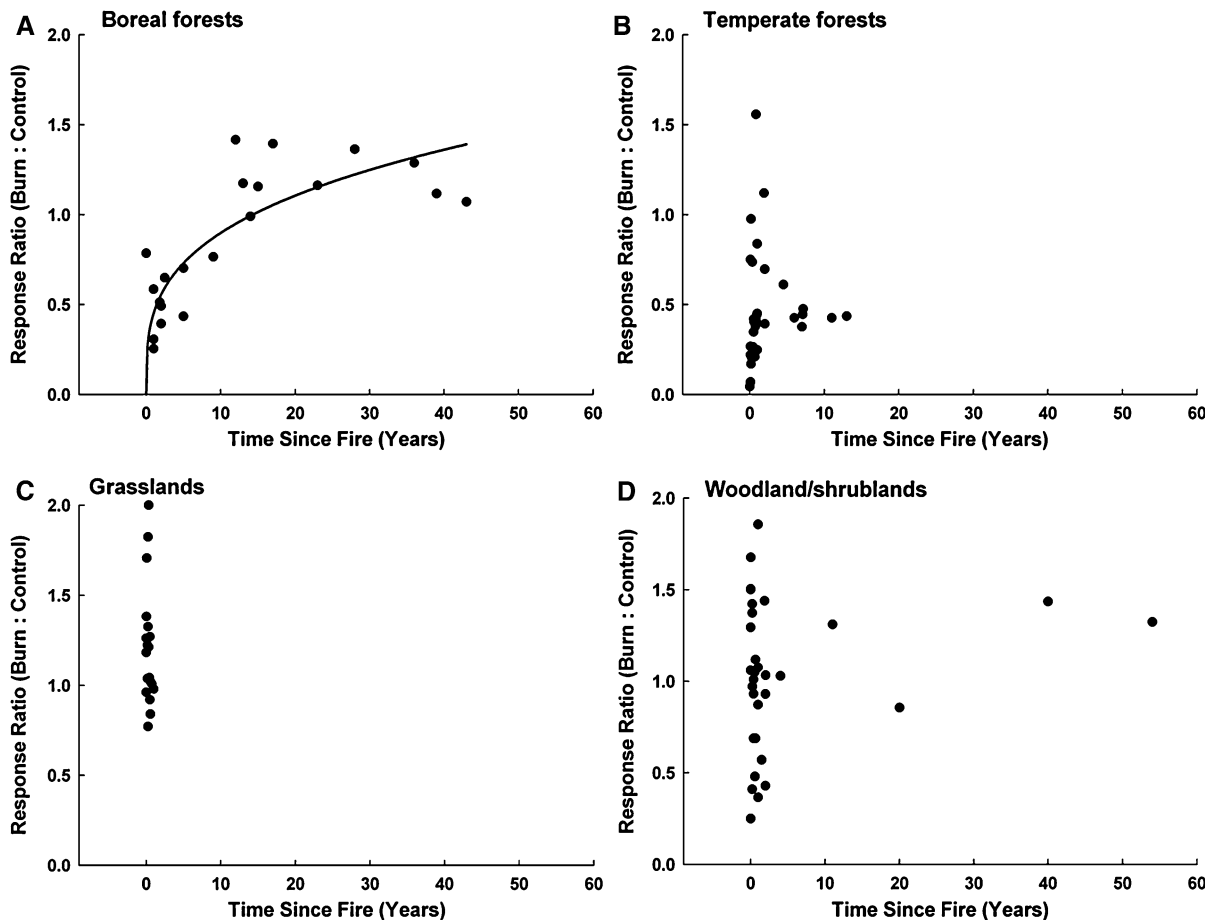
Fig. 2 The response ratio of microbial biomass as a function of the time since fire in boreal forests (**a**), temperate forests (**b**), grasslands (**c**), and woodland/shrublands (**d**). Response ratios were not significantly related to the time since fire in **b–d**. In boreal forests, the response ratio of microbial biomass increased significantly as the time since fire increased ($R = 0.31 \times \ln[\text{time since fire}] + 0.44$, $r^2 = 0.72$, $n = 21$, $P < 0.001$)

Fig. 3). When examined separately, measurements of soil CO_2 emissions in the laboratory were significantly positively correlated ($n = 9$, $r = 0.718$, $P = 0.029$, Fig. 3), while measurements made in the field showed no significant relationship ($n = 4$, $r = -0.901$, $P = 0.099$).

Discussion

Microbial responses to fire have been studied extensively, but inconsistencies among studies have hampered our ability to draw general conclusions. We performed a meta-analysis of published microbial responses to fire in order to improve our ability to predict how projected increases in fire frequency and severity will alter microbial biomass. Across all studies, total microbial biomass declined by an average of 33.2% following fires. These results are in agreement with our first hypothesis, that fires would alter soil microbial abundance. The negative response of microbial biomass following fires can be explained by several potential mechanisms. Burning of the organic layer and heat-transfer to soil during fires may lead to microbial mortality (Cairney and Bastias 2007; Hart et al. 2005). Alternatively, declines in microbial abundance following fires may be attributable to C substrate-limitation. Post-fire decreases in above- and belowground net primary productivity (NPP) work in concert to reduce labile C
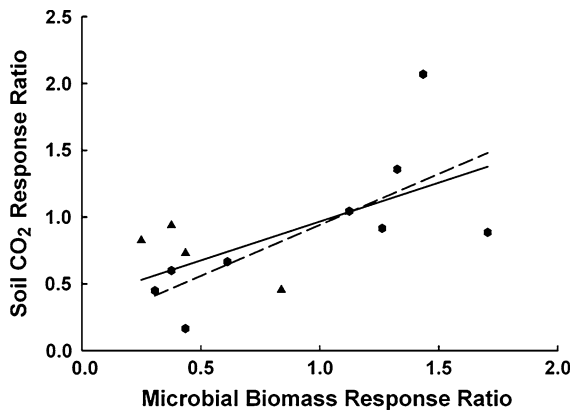
Fig. 3 The relationship between the response ratio of soil CO_2 emissions and the response ratio of microbial biomass. Each symbol designates one study, triangles-field measurement, circles-laboratory measurement. *Lines* are the best-fit regressions for all studies combined (*solid*, CO_2 $R = 0.58 \times$ microbial $R + 0.38$, $r^2 = 0.38$, $P = 0.025$) and measurements made in the laboratory only (*dashed*, CO_2 $R = 0.76 \times$ microbial $R + 0.18$, $r^2 = 0.52$, $P = 0.029$). The response of soil CO_2 emissions is significantly related to the response of microbial biomass when measured in the laboratory but not when measured in the field

inputs into soil and this in turn may cause microbes to become C limited (Choromanska and DeLuca 2001; Neff et al. 2005). Reductions in microbial biomass following fires may also be mediated by changes in soil moisture and soil nutrients (Capogna et al. 2009; O'Donnell et al. 2009; Smith et al. 2008).

Soil fungal abundance declined by an average of 47.6% following fires, providing further support for the hypothesis that fires alter microbial abundance. Fungal responses to fire may be driven by the same mechanisms that govern the response of the microbial community as a whole. Alternatively, increases in soil pH following fires may favor bacterial growth over fungi (Bååth et al. 1995; Bárcenas-Moreno et al. 2011). In addition, mycorrhizal responses to fire may contribute to the decline in total fungal abundance following fires. Mycorrhizal fungi scavenge for nutrients in soil and transfer these nutrients to their host plant in return for photosynthesis-derived plant C (Hodge et al. 2001; Smith and Read 1997). The absence of vegetation in post-fire stands may sever the flow of plant C to mycorrhizae and result in mycorrhizal declines. Indeed, studies have reported declines in both arbuscular mycorrhizal fungi (Allsopp and Stock 1994; Dhillion et al. 1988; Rashid et al. 1997) and ectomycorrhizal fungi (Dahlberg et al. 2001;

Schoenberger and Perry 1982; Treseder et al. 2004) following fires in a variety of biomes. Although certain ascomycete fungi consistently fruit following fires (Wicklow 1975), we did not find evidence for an increase in total soil fungal abundance following fires.

Due to the limited number of studies meeting our search criteria that reported changes in bacterial abundance following fires ($n = 5$), we were not able to separately analyze bacterial responses to fires. Among those studies that did measure bacterial abundance following fires, bacterial responses were variable. Kara and Bolat (2009) found a four-fold increase in bacterial abundance in soil following fires. In contrast, Esquilín et al. (2007) observed a significant decrease in bacterial biovolumes after fire. The limited sample size and the variability in observed bacterial responses to fire make it difficult to draw general conclusions regarding how fire affects soil bacteria. Furthermore, most bacterial studies to date have been conducted in temperate forests. Our understanding of bacterial responses to fire would benefit from additional studies examining changes in bacterial abundance following fires across biomes.

In support of our hypothesis that wildfires would elicit greater changes in microbial biomass than prescribed burns, microbial responses to fire were significantly negative following wildfires but nonsignificant after prescribed burns. This result is likely driven by differences in fire severity, with wildfires being more severe than prescribed fires (Carter and Foster 2004; Certini 2005). High severity fires may elicit stronger microbial response because they burn at higher temperatures, consume a greater proportion of aboveground biomass and soil organic matter, and promote higher levels of nutrient volatilization (Hatten and Zabowski 2010). Choromanska and DeLuca (2001) provide a direct comparison of fire severity during a wildfire and prescribed burn in a temperate forest. The prescribed fire resulted in 42% fine fuel consumption and no mortality of overstory trees while the wildfire led to 100% fine fuel consumption and complete stand mortality. Similarly, the wildfire elicited a more severe reduction in microbial biomass C than the prescribed fire. A very limited number of studies have directly compared microbial responses to low and high severity fires. In general, these studies suggest that high severity fires cause greater reductions in microbial biomass than low severity fires (Fioretto et al. 2005; Hamman et al. 2007; Palese

et al. 2004). Taken together, these data suggest that it may be inaccurate to predict microbial responses to wildfires from observed microbial responses to prescribed burns.

Likewise, the effect of fire on total microbial biomass differed between biomes. Microbial responses were significantly negative in boreal forests and temperate forests and significantly positive in grasslands. The difference in microbial responses among biomes may also be attributable to differences in fire severity among biomes. Fuel loads vary widely among biomes, ranging from <1 Mg ha^{-1} in grasslands to >400 Mg ha^{-1} in woodlands and forests (Neary et al. 1999). Higher fuel loads in forests and woodlands may favor more severe fires in these biomes than in grasslands. Alternatively, the positive response of soil microbes in grasslands may represent microbial adaptation to fire. Temperate and boreal forests have fire return intervals of ~100 years (Agee 1993; Kasischke and Stocks 2000) while grassland ecosystems burn more frequently (Collins and Wallace 1990). Over time, frequent fires in grasslands may have selected for microbes that are fire-tolerant. Many biomes (e.g. arctic tundra, tropical forests) had insufficient replication to include in this meta-analysis. Additional fire studies in these biomes are critical for improving our understanding of how fires alter microbial abundance on a global scale.

Fungal responses to fire among fire types and biomes differed from the response of the microbial community as a whole. Fungal abundance was significantly reduced following prescribed fires while fungal responses to wildfires were highly variable and non-significant. This variability is largely driven by one study that reported a strong positive effect of fire on fungal abundance (Kara and Bolat 2009). In general, the limited number of studies measuring changes in fungal abundance following wildfires ($n = 4$) hampers our ability to draw general conclusions. In addition, fires in boreal forests and woodland/shrublands elicited significant declines in fungal abundance. Changes in fungal abundance following fires in temperate forests were non-significant due to the strong positive response of Kara and Bolat (2009). Again, low replication among all biomes ($n = 3–4$) may have limited our ability to detect significant patterns. We did not find any published studies that reported changes in fungal abundance

following fires in grasslands, tropical forests, or the arctic tundra. Docherty et al. (2011) present one of the first detailed studies of fungal responses to grassland fires. They found no significant difference in total soil fungal abundance, but a trend towards increased arbuscular mycorrhizal fungal abundance in burned plots. Additional studies documenting changes in fungal abundance following fires in these biomes are necessary to develop a complete understanding of fungal responses to fire.

In addition to altering biomass, fires may shift the composition of soil microbial communities. Phospholipid fatty acid profiles have been used to detect changes in broad taxonomic groups of microbes following fires (Bååth et al. 1995; Docherty et al. 2011; Esquilín et al. 2007; Hamman et al. 2007). Using denaturing gradient gel electrophoresis, Waldrop and Harden (2008) documented changes in fungal community structure following fire in an Alaskan boreal forest. Bacterial community composition may also be sensitive to fire. Docherty et al. (2011) found decreases in Gram-negative and Gram-positive bacteria following a wildfire in a California annual grassland. In addition, *Bacteroidetes* abundance decreased following fire in a temperate grassland (Jangid et al. 2010) while Smith et al. (2008) report declines in *Chlamydiae* and *Nitrospirae* clades following fire in a boreal forest. These changes in microbial community structure following fire suggest that microbial species are differentially affected by fire. Shifts in microbial community composition following fires might either exacerbate or moderate the ecosystem-level effects of biomass changes, depending on the functional roles of individual species. Detailed investigations of changes in microbial community composition following fire (e.g., using high throughput sequencing) are rare, but would greatly contribute to our knowledge of microbial responses to fire.

We initially hypothesized that the effect of fire on microbial biomass would diminish as the time since fire increased. In boreal forests there was a significant positive relationship between microbial response ratios and the time since fire, providing partial support for this hypothesis (Fig. 2). The negative effects of fire persisted for ~15 years in boreal forests, after which time microbial response ratios increased. The fire return interval in boreal forests is ~100 years (Giglio et al. 2006). Given that microbial biomass can recover

within ~ 15 years of a fire, it is likely that microbial biomass will recover before another fire occurs. Studies on the recovery of NPP following fires in boreal forests indicate that aboveground NPP can recover in as little as 4 years (Mack et al. 2008). In contrast, soil organic matter accumulates slowly over time as C inputs from primary production outweigh C losses via decomposition. Taken together, these findings suggest that the recovery of microbial biomass following fires in boreal forests is more strongly related to the recovery of the soil organic layer than the recovery of aboveground biomass. There were non-significant relationships between microbial responses and the time since fire for all other biomes examined and for all fungal studies. This result may be partially due to the absence of long-term data in temperate forests and grasslands. Although, microbial biomass C remained lower in burned than unburned stands 13 years following a wildfire in a temperate forest (Litton et al. 2003), again suggesting that the effects of fire on soil microbes may persist long after aboveground vegetation regenerates.

The decrease in microbial abundance following fires may have consequences for C fluxes. Changes in microbial abundance were significantly positively correlated with changes in soil CO_2 emissions across all studies that measured both (Fig. 3). However, when changes in soil CO_2 emissions were examined separately for measurements made in the laboratory and field, the relationship was only significant for measurements made in the laboratory. The efflux of CO_2 from soils is comprised of both microbial and plant-derived sources. Measurements made in the laboratory primarily capture microbial respiration while measurements made in the field incorporate both sources. Plant root respiration is traditionally assumed to be low following fires (Richter et al. 2000). However, recent studies suggest that the autotrophic component of soil respiration following fire can be significant due to the survival of roots belowground and the rapid re-growth of fire-adapted vegetation (Bond-Lamberty et al. 2004; Czimczik et al. 2006; Singh et al. 2008). In addition, although microbial biomass may be one important control of soil CO_2 emissions, other abiotic factors will affect the efflux of CO_2 from soils following fires (e.g., soil temperature, soil moisture). Laboratory incubations that are conducted at standardized temperature and soil moisture do not capture the effect of these abiotic

factors on soil CO_2 emissions following a fire. The low number of studies ($n = 4$) reporting field measurements of soil CO_2 emissions following fires may have limited our ability to detect significant patterns. These results underscore our need to better understand both the autotrophic and heterotrophic contributions to soil respiration following fires.

Conclusions

In summary, overall fires had a negative effect on microbial and fungal biomass. However, the effect of fire on microbial biomass varied among fire types and biomes. The differential responses between biomes and fire types is likely related to fire severity, with more severe fires eliciting greater declines in microbial abundance. Our conclusions are necessarily limited to the studies we included in our analyses. Most studies were concentrated in Europe and North America, while other continents and biomes were underrepresented. Soil CO_2 emissions tended to respond in concert with microbial biomass. The frequency and severity of wildfires may increase as a result of climate warming, especially in forest biomes. These results imply that increases in fire activity may be associated with declines in microbial biomass, especially following severe wildfires. Declines in microbial biomass may lead to parallel declines in soil CO_2 emissions and constitute a negative feedback to climate warming.

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