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Fire effects on temperate forest soil C and N storage

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Abstract. Temperate forest soils store globally significant amounts of carbon (C) and nitrogen (N). Understanding how soil pools of these two elements change in response to disturbance and management is critical to maintaining ecosystem services such as forest productivity, greenhouse gas mitigation, and water resource protection. Fire is one of the principal disturbances acting on forest soil C and N storage and is also the subject of enormous management efforts. In the present article, we use meta-analysis to quantify fire effects on temperate forest soil C and N storage. Across a combined total of 468 soil C and N response ratios from 57 publications (concentrations and pool sizes), fire had significant overall effects on soil C (−26%) and soil N (−22%). The impacts of fire on forest floors were significantly different from its effects on mineral soils. Fires reduced forest floor C and N storage (pool sizes only) by an average of 59% and 50%, respectively, but the concentrations of these two elements did not change. Prescribed fires caused smaller reductions in forest floor C and N storage (−46% and −35%) than wildfires (−67% and −69%), and the presence of hardwoods also mitigated fire impacts. Burned forest floors recovered their C and N pools in an average of 128 and 103 years, respectively. Among mineral soils, there were no significant changes in C or N storage, but C and N concentrations declined significantly (−11% and −12%, respectively). Mineral soil C and N concentrations were significantly affected by fire type, with no change following prescribed burns, but significant reductions in response to wildfires. Geographic variation in fire effects on mineral soil C and N storage underscores the need for region-specific fire management plans, and the role of fire type in mediating C and N shifts (especially in the forest floor) indicates that averting wildfires through prescribed burning is desirable from a soils perspective.

Key words: carbon sinks; fire; forest management; meta-analysis; soil carbon; soil nitrogen; temperate forests.

Introduction

Roughly half of Earth's terrestrial C is in forests, and of this amount, about two-thirds is stored in soils (Dixon et al. 1994, Nave et al. 2010). Fire is one of the most important disturbances affecting forest soil C accumulation and loss, yet the effects of fire on soil C storage are poorly understood from a large-scale perspective. Fire effects on soil C storage are especially important within the temperate zone, since forests of this region are a major part of the terrestrial C sink that mitigates rising atmospheric CO_2 and climate change (Schimel 1995, Liski et al. 2003). Temperate forests, especially in the northern hemisphere, are home to globally unique interactions between disturbance history, climate, and N cycling that make these ecosystems significant C sinks (Goodale et al. 2002, Luyssaert et al. 2008). Understanding the effects of disturbances like fire on soil C and N storage is consequently imperative to the science, policy, and practice of forest management in the temperate zone.

The management of fire in temperate forests is important not just because it impacts the global C cycle, but also because fire affects forest productivity and hydrology. Fire pyrolizes and volatilizes C and N from litter and soil organic matter (SOM), which are the principal storehouses of these elements in forest soils (Certini 2005). Fire also alters the composition and structure of remaining litter and SOM, leading to changes in C and N cycling processes that form the basis of plant nutrition (Wan et al. 2001, Gonzalez-Perez et al. 2004). Consequently, through its effects on SOM amount, composition, and soil C and N cycling, fire may affect forest productivity (Jurgensen et al. 1997, Grigal and Vance 2000). Fire-induced litter and SOM losses, increased soil hydrophobicity, and shifts in soil C and N cycling drive hydrologic changes, including decreased soil water retention, increased surface runoff and sediment loading to surface water, and N export in surface and ground water (DeBano 1998, Neary et al. 1999, Shakesby and Doerr 2006). Predicting changes in soil C and N storage due to fire will therefore allow

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anticipation of changes in ecosystem services including water quality protection, C sequestration, and the supply of forest products.

Many sources of variability mediate the effects of fire on soil C and N storage, which limits the generality of conclusions drawn from individual studies. In addition to the inherent spatial and temporal heterogeneity of soil C and N storage (Magrini et al. 2000, Homann et al. 2001, 2008), variation in geographic features, fire characteristics, and soil structure and morphology may influence the observed effects of fire on forest soils. For example, in one study of prescribed burns in the Appalachian region of the United States, landscape position and fire intensity had significant effects on the magnitude of forest floor C and N losses, while mineral soils were unaffected by prescribed fire (Vose et al. 1999). Organic (forest floor) and mineral soil horizons have divergent responses to fire that have been noted throughout the literature, with forest floors typically showing greater C and N shifts than mineral soils (Binkley et al. 1992, Rothstein et al. 2004, Murphy et al. 2006, Johnson et al. 2007). Studies examining the role of fire intensity on soil processes and properties have found different levels of change following prescribed vs. wildfires, with prescribed fires either having smaller impacts, or mitigating the effects of wildfires (Choromanska and DeLuca 2001, Wan et al. 2001, Grady and Hart 2006). Finally, in addition to geographic effects operating at fine spatial scales, such as within a study site (e.g., Vose et al. 1999), regional geography may also influence fire effects on forest soils. For example, Hatten et al. (2005) pointed to the interaction between seasonal precipitation deficits and thunderstorm activity as a driver of wildfire occurrence in the northwest United States, a region increasingly prone to severe fires (Bormann et al. 2008). In the present study, we sought to determine whether there is a consistent, overall effect of fire on temperate forest soil C and N storage, to quantify the magnitude of these changes, and to identify the most important sources of variability among studies of fire and temperate forest soils.

Methods

In order to address the objectives of our study, we conducted a meta-analysis following the general methods of Curtis (1996), Johnson and Curtis (2001), and Nave et al. (2009). We searched the peer-reviewed and gray literature (i.e., government technical reports) using Boolean keyword searches within the online databases ISI Web of Science, BIOSIS, Agricola, and CAB Direct. Keyword search strings were permutations of terms including: forest, fire, burn, burning, management, soil C, and soil N. In the process of inspecting >6500 references returned by our literature searches, we found 57 publications that met our inclusion criteria of: (1) reporting control (unburned) and treatment (burned) soil C and N values, and (2) being conducted in a temperate forest (4–8 months of mean air temperature >10°C [Köppen 1931]). Acceptable controls for unburned forest soils were either pre-burn soil C and N values, or soil C and N observations from nearby reference stands that were not burned. The latter type of control value included both simultaneous measurements of burned and unburned soils, and chronosequences, in which case the oldest stand was treated as the control. As a minimum, control stands were those that had not been burned within the past 30 years, although some publications had control stands that had not been burned for 1–2 centuries. Therefore, our meta-analysis does not bear specifically on the consequences of long-term fire suppression, nor does it focus on the effects of frequent fires in ecosystems with short fire return intervals. Rather, our analysis includes many different temperate forest types with diverse fire regimes, sampled across a range of time scales. Although they did not meet the temperate climate requirement, we included several publications from the southeast United States due to the importance of this region to U.S. forest management. We accepted soil C and N concentrations and pool sizes as metrics of soil C and N, and used meta-analysis to determine whether concentrations and pool sizes significantly differed in their responses to harvest. Among publications that reported both concentrations and pool sizes, we chose pool sizes as the response parameter, and we calculated soil C and N pool sizes for publications that reported concentrations and bulk densities. When used in reference to soil C and N, the term "storage" denotes C and N pool sizes only; we use the more general terms "soil C" and "soil N" when referring to soil C and N measurements that encompass both types of reporting units.

We extracted metadata (potentially useful predictor variables) from each publication, including temporal, climatic, soil chemical and physical data, measurement units, and treatment and analytical methods. One pertinent distinction in the soil physical data category was the soil layer sampled. We extracted data for organic and mineral soil layers separately, and coded the data so that we could test for differences between soil layers defined as forest floor (mostly organic horizons), surface mineral soil (uppermost 3–20 cm of mineral soil), deep mineral soil (20–100 cm), and whole mineral soil profile. We chose these coarsely defined layers based on the distribution of reported sampling depths during early literature assimilation with the goal of being able to detect small changes in soil C or N through high levels of within-layer replication. When initial meta-analyses revealed no significant differences between surface, deep, and whole mineral soils, we recoded the response ratios from these groups into a single category (mineral soil) for subsequent analyses. Regarding our classification of fire, we categorized studies as either prescribed burns or wildfires if meta-data were descriptive enough to ascertain which fire type occurred. In addition to

Table 1. Factors tested as predictor variables in the meta-analysis.

Factor	Levels
Reporting units	pool size; concentration
Soil layer	forest floor; mineral soil (range: 3–100 cm)
Soil texture†	coarse (mostly sand); fine (mostly silt or clay)
Soil taxonomic order	Alfisol; Andisol; Entisol; Inceptisol; Spodosol; Ultisol
Species composition	coniferous; mixed conifer–hardwood
Geographic group	northeast U.S.; northwest U.S.; southeast U.S.; southwest U.S.
Fire type	wildfire; prescribed fire
Time since fire	continuous (yr)
Mean annual temperature	continuous (°C)
Mean annual precipitation	continuous (cm)

Notes: The levels listed within each categorical factor define the response ratio groups contrasted in Q_b analysis in Table 2; factors without discrete levels were tested using continuous meta-analysis.
† Mineral soils only.

categorizing studies by fire type, we categorized fires according to whether they were of low or high intensity according to authors' descriptions. In the literature we assimilated, fires were occasionally described in qualitative terms like "low-intensity" or "stand-replacing," but quantitative measures of fire intensity were rarely reported. In the end, only one-third of the soil C and N response ratios we collected had any associated meta-data that allowed attribution of fire intensity. We deemed this rate of reporting too low to include fire intensity as a categorical variable in our final analysis, since small sample sizes that are based on a limited number of studies risk detecting significant effects that are in reality confounded with other factors specific to those studies. The complete list of factors by which we categorized the response ratios in the database before final analysis appears in Table 1.

Meta-analysis estimates the magnitude of change in a parameter (i.e., the "effect size") in response to an experimental treatment, which may be applied across a wide range of experimental systems and conditions. We used the ln-transformed response ratio R to estimate treatment effect size:

$$\ln(R) = \ln(\bar{X}_T/\bar{X}_C) \qquad (1)$$

where $\bar{X}_T$ is the mean soil C or N value of treatment (burned) observations and $\bar{X}_C$ is the mean soil C or N value of control observations for a given set of experimental conditions. The number of response ratios (k) from a given publication depends on how many sets of experimental conditions are imposed. For example, one publication with soil N storage data from a control soil and from two different levels of fire (prescribed and wild) would yield $k = 2$ response ratios, or "studies." Because it is unitless, the effect size R is a standardized metric that allows comparison of data between experiments reporting responses in different units (Hedges et al. 1999). After back transformation ($e^{\ln(R)}$), R can be conceptualized as the proportional or percentage change in soil C or N relative to its control value. When error terms and sample sizes are reported for each $\bar{X}_T$ and $\bar{X}_C$, a parametric, weighted meta-analysis is possible, but many publications we found did not report these data. Therefore, in order to include as many studies as possible, we used an unweighted meta-analysis, in which all studies in the data set are assigned an equal variance (1). In an unweighted meta-analysis, the distributional statistics of interest (mean effect sizes and confidence intervals) are generated with the nonparametric statistical method known as bootstrapping. Bootstrapping estimates a statistic's distribution by permuting and resampling (with replacement) the data set hundreds of times. Since it generates a statistic's distribution from the available data, bootstrapping is not subject to the assumptions of parametric tests, and typically produces wider, more conservative confidence intervals (Adams et al. 1997). We performed analyses using MetaWin software (Sinauer Associates, Sunderland, Massachusetts, USA), with 999 bootstrap iterations.

One of our primary goals in this analysis was to identify which commonly reported factors were the best predictors of variation in soil C and N responses to fire. Accomplishing this task with meta-analysis is similar to using ANOVA to partition the total variance of a group of observations (Q_t, the total heterogeneity) into two components: within- and between-group heterogeneity (Q_w and Q_b, respectively; Hedges and Olkin [1985]). In such a Q_b analysis, a categorical factor that defines a group of response ratios with a large Q_b is a better predictor of variation (or heterogeneity) than a categorical factor associated with small response-group Q_b. In order to determine which categorical factors were the "best" predictors of variation, we followed the hierarchical approach detailed in Curtis (1996) and Jablonski et al. (2002). Briefly, we performed the following steps independently for soil C and soil N data sets. First, we ran meta-analysis on the entire data set to determine which categorical factor among those in Table 1 had the lowest P value, and then divided the database into the categorical groups defined by the levels of that factor (e.g., soil layer had the lowest P value, so we subsequently divided the database into forest floor and mineral soil groups). Then, within each of these groups,

TABLE 2. Between-group heterogeneity (Q_b) among the k studies comprising each response parameter.

Response parameter	k	Reporting units†	Soil layer	Soil texture	Soil taxonomic order	Species composition	Geographic group	Fire type	Time	MAT	MAP
Overall soil C	240	6.7**	29.0**	NA	11.2**	4.2*	3.4	1.2	0.03	1.5*	<0.01
Forest floor C storage	72	5.9*	NA	NA	8.5**	7.4**	3.8	4.2*	4.5**	1.5	5.2**
Mineral soil C storage	73	0.5*	NA	<0.01	0.8*	<0.01	0.6**	0.04	0.5*	0.5*	0.2
Overall soil N	228	1.8*	14.0**	NA	6.9*	3.4*	3.7	3.9**	0.1	0.02	0.5
Forest floor N storage	64	4.9*	NA	NA	2.2	10.7**	8.4*	8.3**	2.9*	2.2	1.6
Mineral soil N storage	75	0.8*	NA	0.1	1.1**	0.05	0.6*	<0.01	0.1	0.1	0.4*

Notes: Overall soil C and N responses to fire include all studies in the database, regardless of reporting units (concentration or pool size). Forest floor and mineral soil C and N storage responses are pool sizes only, except for the reporting units column, which demonstrates significant differences between concentrations and pool sizes. Note that the values for continuously varying factors (time, MAT, MAP) represent Q_m, which is conceptually similar to but statistically distinct from Q_b. See Table 1 for the predictor variables tested in Q_b analysis. NA means "not applicable." Predictor variables showing statistically significant Q_b are denoted by asterisks.

* $P < 0.05$; ** $P < 0.01$.

† Soil C response data were reported as either concentrations or pool sizes.

we ran meta-analysis again for each remaining categorical factor, and identified the one with the lowest P value. We performed this variance-partitioning exercise twice as described above, at which point we felt it prudent to go no further due to limited sample sizes and possible confounding relationships. When, during the course of these Q_b iterations, we found multiple categorical variables with the same P value, we selected the one with the highest Q_b. Categorical groups with $k < 5$ were included in overall meta-analyses of fire effects on soil C and N, but were not included in the iterative Q_b analyses, since these poorly replicated groups sometimes had outlying effect sizes that artificially inflated the Q_b values. For example, while our database included studies from the United States, Europe, Asia, Australia, and South America, geographic group analyses were conducted only on U.S. regions.

In addition to identifying categorical variables that influenced soil responses to fire, we tested several continuously varying factors (e.g., time and climatic variables) as predictors of variation using continuous meta-analyses. Continuous meta-analysis is similar to the variance-partitioning process of Q_b analysis, in that the heterogeneity among k observations is partitioned into that which is explained by a linear regression model (Q_m), and that which constitutes the residual error variance (Q_e). In this way, continuous meta-analysis is analogous to the ANOVA F test for significance of linear regression models (Hedges and Olkin 1985). Continuous meta-analysis also estimates the coefficients for the intercept and slope terms of linear models, allowing estimation of linear relationships between predictor variables and response parameters. In all tests, including overall, hierarchical Q_b, and continuous meta-analyses, we accepted test results with $P < 0.05$ as statistically significant.

While our literature search was not exhaustive, the database we developed for this analysis is quite large, comprising 468 soil C and N response ratios from 57 papers published between 1975 and 2008. These publications correspond to studies of forest fire conducted in temperate forests around the world, and the full data set is *available online*.[6]

RESULTS

Overall effects and principal sources of variation

Fires significantly reduced soil C (−26% ± 6%) and soil N (−22% ± 6%) in the temperate forests included in this analysis, although many sources of variation mediated this overall effect (Table 2). Fires had significantly different effects on pool sizes vs. concentrations of soil C and soil N, demonstrating that the units of measurement used to report soil C and N values are an important source of variation. Fires reduced both pool sizes and concentrations, but with significantly greater reductions in pools. On average, soil C storage declined by 35% following fire, and soil C concentrations decreased by 9%. Fires reduced soil N storage by 28%, while soil N concentrations declined by 12%. Fire had fundamentally different impacts on forest floors and mineral soils. Indeed, soil layer was the strongest of all predictor variables tested in our analyses, in terms of both level of significance and Q_b values. The significant effect of soil layer ($P < 0.01$) explained 25% of the variation among soil C response ratios ($Q_b = 29.0$, $Q_t = 115.6$), and 14% of the total heterogeneity among soil N response ratios ($P < 0.01$, $Q_b = 15.6$, $Q_t = 106.2$).

Variation in fire effects within soil layers

Forest floors.—In a pattern similar to that observed in the overall analysis, the effects of fire on forest floors depended on the units used to report C and N values (Table 2; $P < 0.01$ for soil C, $P < 0.05$ for soil N). However, forest floors differed from the overall analysis in that neither C nor N concentrations changed in response to fire (Fig. 1). Forest floor C and N storage both declined significantly, with mean effect sizes of

[6] ⟨http://www.nrs.fs.fed.us/niacs/tools/soil_carbon/⟩

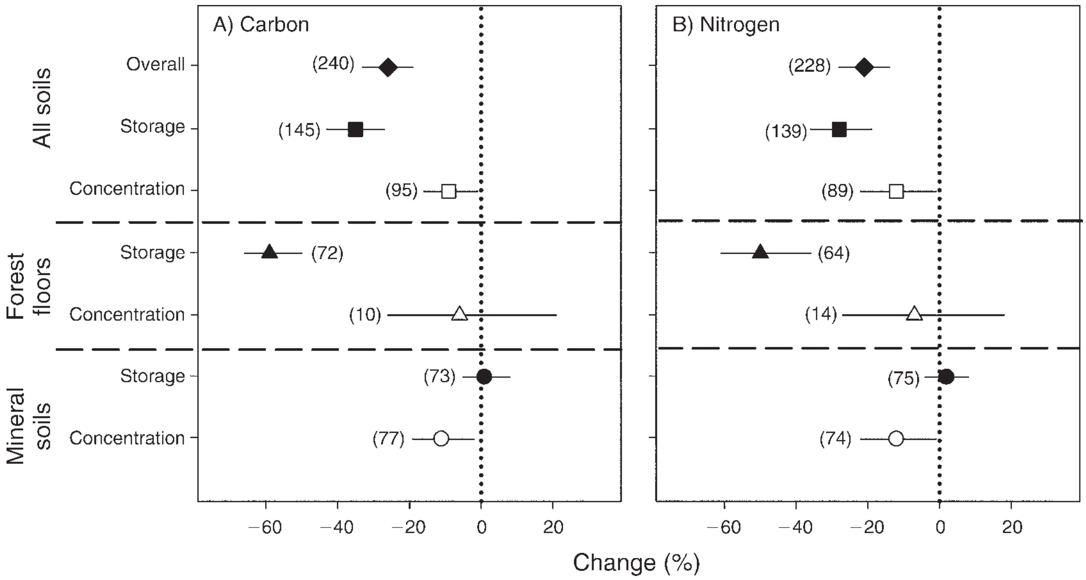

FIG. 1. Changes in soil C and N due to forest fires, overall and by soil layer. All points are mean effect sizes with bootstrapped 95% confidence intervals, with the number of studies (*k*) in parentheses. Groups with confidence intervals overlapping the dotted reference line (0% change) show no significant change in soil C or N due to fire. At the top of each panel, the solid diamond shows the overall effect of fire, including C and N pool sizes and concentrations from forest floors and mineral soils. Within each soil layer, mean effect sizes are shown separately for C and N pool sizes (storage; solid symbols) and C and N concentrations (open symbols).

−59% and −50% for the two response parameters, respectively. Since we were primarily concerned with changes in C and N storage due to fire, we restricted further forest floor analyses to those studies reporting C and N pool sizes (and those reporting sufficient data to calculate pool sizes). Among these studies, fire effects were impacted most by species composition (Table 2, Fig. 2), with mixed hardwood–conifer forests losing significantly less C and N (−37% and −12%, respectively) than purely coniferous stands (−68% and −64%). In spite of the large magnitude of these fire-induced C and N losses, reductions in forest floor C and N storage did not appear to be permanent. Continuous meta-analyses demonstrated that time was a significant predictor of variation among forest floor C and N storage response ratios (Table 2). For these two elements, linear models generated through continuous meta-analysis suggested recovery times of 100–130 years (Fig. 3).

Mineral soils.—As with the overall analysis, and forest floors, fire effects varied significantly according

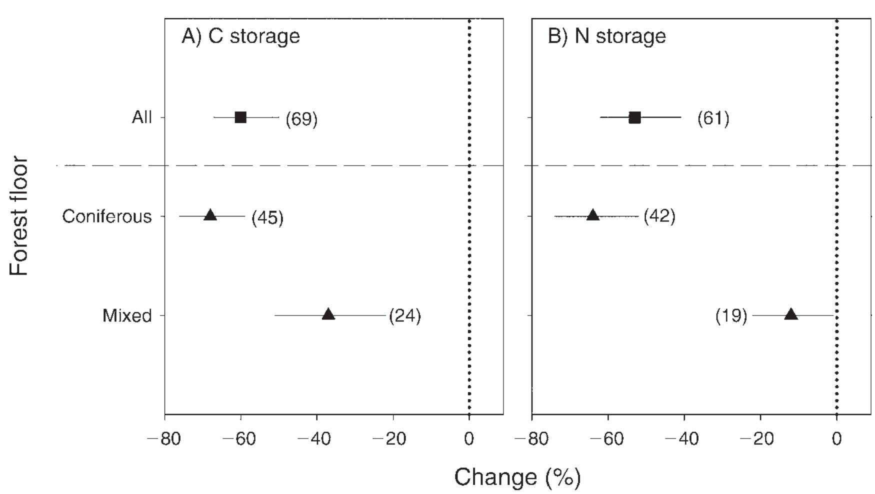

FIG. 2. The effects of fire on forest floor C and N storage, overall and by species composition group. All points are mean effect sizes with bootstrapped 95% confidence intervals, with the number of studies (*k*) in parentheses. Groups with confidence intervals overlapping the dotted reference line (0% change) show no significant change in forest floor C or N storage due to fire.

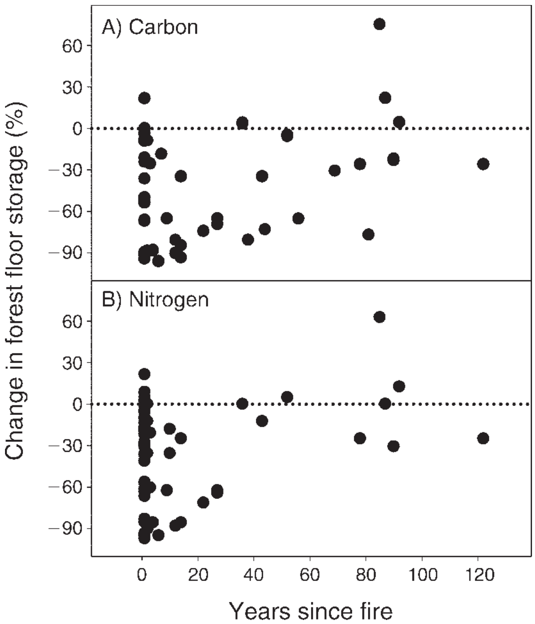

FIG. 3. Recovery of forest floor (A) carbon and (B) nitrogen pools following forest fires. Each point represents one response ratio. Some response ratios in the database could not be assigned a time value; these studies are not plotted.

to the units used to report mineral soil C and N data (Table 2). Fire did not change mineral soil C or N storage, but %C and %N declined by an average of 11% and 12%, respectively (Fig. 1). Soil taxonomic order and geographic location explained more of the variation among mineral soil C and N storage response ratios than any other predictor variables, but because these two predictors were not independent in our data set, we chose to explore and interpret variation among C and N response ratios according to only one of them. To determine which variable was a stronger predictor of variation in fire effects on mineral soil C and N storage, we aggregated the response ratios from both response parameters, which had statistically indistinguishable responses to fire. Tests of the two predictors on the aggregated C and N response ratios subsequently demonstrated that geographic location was a more important determinant of C and N storage shifts (Q_b = 3.9, $P < 0.01$) than soil taxonomic order (Q_b = 1.7, $P < 0.01$). When considered in a geographic context, fires had a significant impact only on mineral soil C pool sizes in forests of the northwest United States, where C storage declined by an average of 19% (Fig. 4). While other geographic groups differed from one another in their responses to fire, none showed significant changes in mineral soil C or N storage.

Variation in fire effects due to fire type

Fire type was another important source of variation in fire effects on soil C and N (Table 2). While fire type was not among the most important sources of variation in the overall analysis, the distinction between wildfires and prescribed burns was significant for forest floor C storage ($P < 0.05$) and forest floor N storage ($P < 0.01$). In both cases, wildfires caused greater declines than prescribed fires (Fig. 5). Wildfires reduced forest floor C storage by 67%, compared to an average of –46% for prescribed burns, and the effect was quite similar for forest floor N storage (–69% vs. –45%).

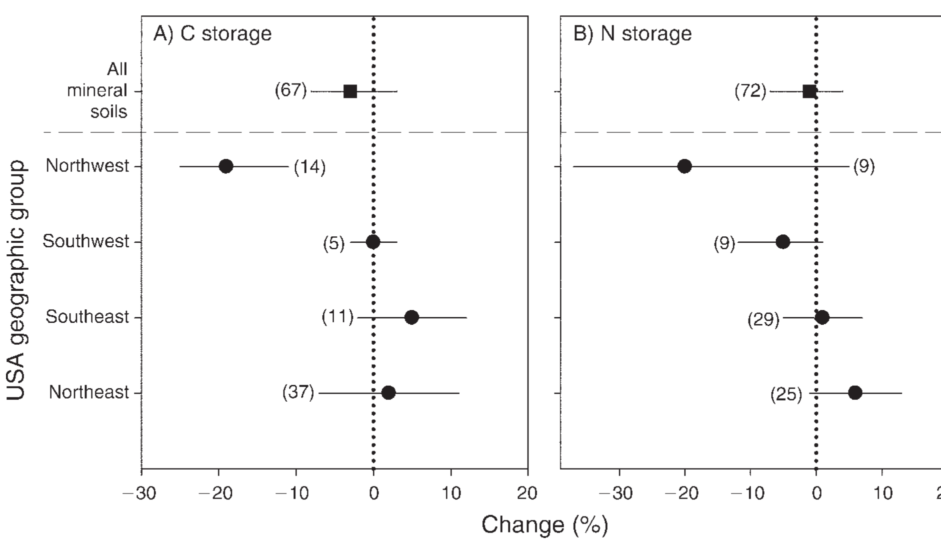

FIG. 4. The effects of fire on mineral soil C and N storage, overall and by geographic group. All points are mean effect sizes with bootstrapped 95% confidence intervals, with the number of studies (k) in parentheses. Groups with confidence intervals overlapping the dashed reference line (0% change) show no significant change in forest floor C or N storage due to fire. Geographic groups shown are from the United States. The small numbers of observations from Australian, European, and South American geographic groups are not plotted.

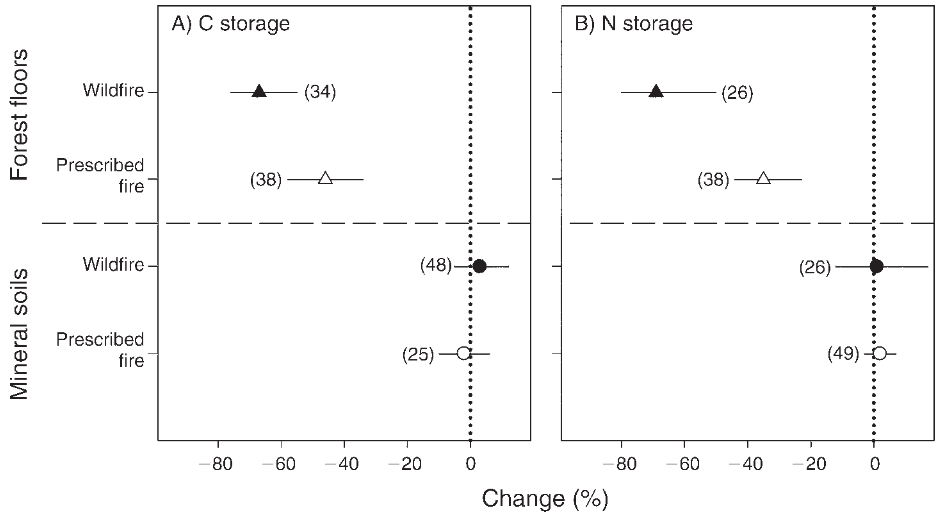

FIG. 5. Changes in soil C and N storage due to forest fires, by soil layer and fire type. All points are mean effect sizes with bootstrapped 95% confidence intervals, with the number of studies (k) in parentheses. Groups with confidence intervals overlapping the dashed reference line (0% change) show no significant change in soil C or N storage due to fire. Within each soil layer, mean effect sizes are shown separately for wildfires (solid symbols) and prescribed fires (open symbols).

Neither type of fire affected mineral soil C or N storage (Fig. 5), but wildfires reduced mineral soil %C and %N by 17% and 18%, respectively (Table 4). Prescribed fires had no effect on mineral soil %C or %N.

Soil C and N budgets

The effects of fire on soil C and N budgets were driven not only by the magnitude of the changes, but also by the relative pool sizes of C and N in the forest floor vs. the mineral soil (Table 3). Fires caused forest floors to lose substantial amounts of their C and N pools, but the impacts of these losses on overall soil C and N budgets were tempered by the relatively small proportion of total soil C and N stored in the forest floor in these forests. In unburned forests, forest floor C and N storage constituted approximately one-third of total soil C and N pools. Following fire, forest floors accounted for only ~15% of total soil C and N storage. On average, fires reduced forest floor C storage from 18 to 7 Mg/ha, although the lack of any change in the mineral soil meant that the relative decline in total soil C storage was much less: 55 Mg C/ha in the control and 46 Mg C/ha in the burned forests. Forest floor and mineral soil N pools were much smaller, but the impacts were quite similar to those on C pools. Fire decreased forest floor N storage from an average of 0.5 to 0.2 Mg/ha, but the lack of any

TABLE 3. C and N budgets for unburned (control) and burned (treatment) soils included in the meta-analysis.

Parameter and soil layer†	k	Control (Mg/ha)		Burned (Mg/ha)	
		Mean	95% CL	Mean	95% CL
C storage					
Forest floor	72	18	13, 23	7	6, 9
Mineral soil	73	37	25, 49	37	35, 40
Sum		55	38, 72	46	43, 49
N storage					
Forest floor	64	0.5	0.4, 0.6	0.2	0.2, 0.3
Mineral soil	75	1.1	0.9, 1.3	1.1	1.1, 1.2
Sum		1.6	1.3, 1.9	1.3	1.2, 1.5

Notes: The number of observations in each response parameter–soil layer group is the same as in Table 2. Unburned means and 95% confidence limits were calculated directly from the control data provided by papers included in the meta-analysis. Burned means and 95% CLs were calculated as products of the unburned means and the ($e^{\ln(R)}$) and 95% CL values calculated by meta-analysis and described in *Methods*.

† C and N budgets for the two soil layers are derived from various publications with different levels of sampling and replication. These differences preclude direct comparisons of C budgets to N budgets.

change in mineral soil N storage meant that the soil profile total changed from an average of 1.6 to 1.3 Mg/ha following fire.

Discussion

Overall effects and primary sources of variation

Soil C and N changes frequently are reported in primary studies of forest fire, although the magnitude of these changes varies substantially within and among studies (e.g., Baird et al. 1999, Boerner et al. 2005, Ferran et al. 2005, Gundale et al. 2005). By using meta-analysis to synthesize the results of many individual studies across temperate forests, we demonstrate that fires have relatively consistent effects on soil C and N at the global scale, even as site-to-site exceptions do occur (see Plate 1). This is even the case for temperate forest floors, which we expected to have more dynamic responses to disturbance than mineral soils due to their exposed position at the top of the soil profile, which make them susceptible to direct combustion and postfire erosion, as well as their relatively small organic matter mass and sensitivity to litter and detritus inputs (Robichaud and Waldrop 1994, Binkley and Giardina 1998, Currie 1999). These differences probably underlie the highly significant distinction between forest floor and mineral soil responses to fire implicated in our analysis (Table 2). In particular, since forest floors are exposed and mineral soils are insulated from all but the most extreme surface fires, combustion probably has a much stronger direct effect on forest floor organic matter. Furthermore, the smaller organic matter pool of forest floors (Table 3) means that losing a small absolute quantity of organic matter has a larger proportional effect on C and N storage in this component of the soil profile than in the mineral soil. If we had been able to populate soil layer categories of finer vertical resolution with a sufficient number of response ratios, it is possible that near-surface mineral soils would have shown significant postfire changes in C and N storage as well. Nonetheless, the results of our analysis suggest that mineral soils generally do not exhibit net changes in C or N storage following fire (Fig. 1). In this regard, the effects of fire on soil C and N storage are distributed throughout the soil profile in a very similar way to the effects of forest harvesting on soil C storage, which reduces C storage in the forest floor but not the mineral soil (Nave et al. 2010).

Variation in fire effects within soil layers

Forest floors.—While combustion was probably the most important process directly influencing forest floor C and N reductions among the studies included in our analysis, other mechanisms likely contributed as well (Certini 2005). For example, postfire stimulation of decomposition and N cycling rates suggest that microbial action may be responsible for some forest floor C and N losses (Fernandez et al. 1997, Fierro et al. 2007). On the other hand, pyrolysis is known to produce organic compounds highly resistant to microbial and chemical action ("black carbon"), which may subsequently be lost from the forest floor and exported to deeper horizons by soil water percolation, mesofauna activity, and other causes. (Schmidt and Noack 2000, Gonzalez-Perez et al. 2004, 2008). Forest floor C and N reductions may also occur due to erosion by wind or water (Swift et al. 1993, Murphy et al. 2006). In the case of fires that kill vegetation, postfire reductions in aboveground litterfall can have major effects on forest floor C and N pools (Belanger et al. 2004, Rothstein et al. 2004). However, it is important to consider that while tree mortality may reduce leaf litterfall, dead trees produce substantial woody detritus that typically is not sampled as a forest floor component. Coarse woody debris may cover 25–60% of the forest floor following stand-replacing fires, although it is not certain how much of this material ultimately persists as soil organic matter (Hely et al. 2000, Tinker and Knight 2000, Spears et al. 2003, Turner et al. 2003).

Litterfall plays a fundamental role in recovering and maintaining forest floor C and N pools after fire, but it also influences the magnitude of fire-induced C and N losses. It is likely that the relationship between litterfall and fire C and N losses is driven by fuel type effects, since mixed hardwood–conifer forests lost significantly less C and N than forests dominated solely by conifers (Fig. 2). In addition to producing high C:N litter that resists decomposition and accumulates on the forest floor (Finzi et al. 1998, Cote et al. 2000, Silver and Miya 2001), litter and wood produced by many coniferous tree species contain flammable resinous organic compounds (Schwilk and Ackerly 2001, Kozlowski and Pallardy 2002). Whether present within a matrix of conifers at the patch or landscape scale, hardwoods mitigate fire intensity by producing less flammable foliage, litter, and woody detritus (Gustafson et al. 2002, Sturtevant et al. 2002, Kennedy and Spies 2005, Ryu et al. 2007, Nowaki and Abrams 2008, Lee et al. 2009).

Fires caused forest floors to lose significant amounts of C and N, although these pools appear to replenish with time (Fig. 3). On average, forest floor C and N storage in burned forests returned to pre-burn levels within 128 and 103 years, respectively, although there were legitimate exceptions to these point estimates of recovery time. In particular, as shown in Fig. 3, some forest floors showed a complete net recovery of C and N pools within 40 years of fire. Since we estimated this recovery time from net changes in forest floor C and N pools compared to unburned forests, this duration probably represents the postfire time period during which the accumulation of litter inputs equilibrates with losses of forest floor organic matter through decomposition. The variables controlling the balance of these two fluxes are very complex, and include forest productivity, litter quality, and climate, as well as spatial variation in the effects of fire on these variables (Facelli and Pickett 1991, Berg 2000, Gholz et al. 2000, Raich and

Tufekcioglu 2000). Results from our data set suggest an influence of productivity, because net changes in forest floor C storage following fire were positively correlated with mean annual precipitation (i.e., more precipitation meant smaller C losses; Table 2). Since measures of precipitation also are positively correlated with litter decomposition rates (Gholz et al. 2000), the fact that forests with higher precipitation showed smaller reductions in forest floor C pools suggests that these forests may have recovered forest floor organic matter pools more quickly due to moister soils and higher productivity (Haxeltine and Prentice 1996). An additional explanation for this result, not mutually exclusive to the first, could be that abundant precipitation had the direct effect of mitigating forest floor organic matter losses by increasing the moisture content of available fuel (Neary et al. 1999). Variability in recovery times may be due to different levels of fire intensity, as prescribed burns lost less forest floor C and N and would presumably require less time to recover those pools than forests affected by wildfire (Fig. 5). However, due to a general lack of long-term prescribed fire studies, there were too few data to conduct a conclusive, separate assessment of recovery times for prescribed burns and wildfires. As scientific and social awareness of prescribed burning as an alternative to wildfires increases, long-term prescribed fire studies hopefully will become more prevalent and allow future analyses to compare the effects of these two burning regimes over multidecadal time scales.

Mineral soils.—Fire did not significantly affect the net storage of mineral soil C or N (Fig. 1). However, declines in the concentrations of the two elements suggest that counteracting processes may be masking underlying complexity (Table 4). In order for mineral soil C and N storage to show no net change in spite of decreased %C and %N, there must have been a compensating increase in the bulk density of the increment of soil that was sampled. The increase in bulk density could have been caused by direct combustion or postfire microbial decomposition of SOM and consequent degradation of soil structure, soil loss through wind or water erosion, or some combination (Shakesby and Doerr 2006, Bormann et al. 2008). In each case, increment sampling would result in the sampling of a deeper portion of the soil profile after fire than before. Since bulk density increases, and %C and %N generally decrease with depth in forest soils, the result could be lower concentrations of C and N, but similar amounts.

Geographic setting significantly influenced the effects of fire on mineral soil C and N storage (Table 2). While there was no significant change in either parameter across temperate forests as a whole (Fig. 1), regional variation pointed to consistent mineral soil C losses in forests of the northwest United States (Fig. 4). This suggests that fires are particularly intense in this region, possibly due to interactions between high forest productivity, abundant coniferous fuels, and strong seasonal droughts that combine to create the conditions for severe fires (Miller et al. 2009). The mountainous topography of the region likely augments erosion, which could exacerbate mineral soil C losses (Wondzell and King 2003). In a broader sense, the significance of geographic location as a predictor variable indicates that effects of fire on soil C pools must be considered in a regional context. If soils are to be included in policies or management plans that promote terrestrial C sequestration, then this analysis demonstrates the need for a regional perspective on fire management.

Table 4. Effects of fire on mineral soil C and N concentrations, by fire type.

Response parameter and fire type	k	Change (%) Mean	Change (%) 95% CL
Mineral soil %C			
Prescribed burn	21	4	−11, 22
Wildfire	55	−17	−26, −8
Mineral soil %N			
Prescribed burn	21	−1	−12, 11
Wildfire	52	−18	−31, −3

Note: Groups with 95% confidence limits overlapping 0% change were not significantly affected by fire.

One factor important to consider in our analysis of how mineral soils varied in their C and N responses to fire involves the way we approached response ratio assimilation and coding during database development. As described in the Methods, we extracted separate response ratios for surface, deep, and whole mineral soils from publications whenever possible, in order to test for differences between mineral soil layers. Upon finding no such significant differences in the overall analysis, we recoded all of these response ratios as generic mineral soils in order to achieve maximum use of the data we had collected. In doing so, we violated a strict interpretation of the assumption of independent observations in meta-analysis. However, reanalyzing the mineral soil effect sizes and confidence intervals presented in this paper using only one of the mineral soil layers (surface mineral soils, which had the largest k) changes none of the results we present here. In other words, this internal sensitivity analysis showed that all significant findings regarding mineral soil C and N in this manuscript are robust to the violation of the independence assumption.

The importance of fire type

Fire type had a significant effect on C and N shifts in forest floors (pool sizes; Fig. 5) and mineral soils (concentrations; Table 4), with wildfires causing greater C and N declines than prescribed fires. Mineral soil C and N storage revealed no net changes after either type of fire, but wildfires significantly decreased mineral soil C and N concentrations, indicating that the biogeochemistry or nature of the C and N in these soils may have changed. Such changes

PLATE 1. Matrix of burned and unburned ground following the 1998 treatment at the University of Michigan Biological Station (USA) burn plot chronosequence. Spatial variation in fire intensity and soil organic matter content can obscure significant site-level soil C and N responses to fire, but a well-replicated sampling strategy surmounts this problem of heterogeneity. In similar fashion but on a much larger scale, meta-analysis constrains the effects of fire on soil C and N storage in temperate forests by testing hundreds of accumulated responses from dozens of studies, indicating with confidence that these effects are generally consistent and predictable based on site-level characteristics. Photo credit: Laura L. White, archived by the University of Michigan Biological Station.

in C and N chemistry and pool sizes are relevant to the capability of forests to maintain valuable ecosystem services such as nutrient retention, quantitative and qualitative water treatment, tree recruitment, and in some cases, forest productivity and C sequestration (Neary et al. 1999, Grigal and Vance 2000). Unfortunately, the mechanisms that underlie the greater C and N losses due to wildfire than prescribed fire are not clear from our analysis. One possibility is that wildfire studies more commonly originate from forests subjected to long-term fire suppression, which have greater aboveground fuel accumulation and an increased risk of severe fire (Stephens 1998, Schoennagel et al. 2004). Conversely, it may be that prescribed fires tend to be implemented under less extreme fuel and weather conditions than wildfires, and represent an effective tool for reducing aboveground fuel loads while mitigating the soil C and N losses that would occur in wildfire. Wildfires have increased in frequency in response to climate change and human land use practices (Attiwill 1994, Pinol et al. 1998, Kurz and Apps 1999, Westerling et al. 2006), and will continue to occur in temperate forests that have experienced them for millennia. Therefore, regardless of the underlying reasons for greater C and N losses with wildfire, the significant differences between the two types of fire suggest that proactive management, such as the prudent use of prescribed fire or other management tools, may be a preferable management alternative to losing larger quantities of C and N in wildfire. At the same time, expert judgment in the appropriate use of prescribed fire will be as important as ever, since some areas prone to severe wildfires rarely if ever provide the opportunity for a successful, contained prescribed fire.

Our findings differ from those presented in Johnson and Curtis (2001), which suggested that wildfires increase mineral soil C and N. These changes were attributed to the input of charcoal to the soil C pool, the downward transport of hydrophobic organic matter and its subsequent stabilization with mineral cations, and the frequent colonization of burned sites by Nfixing vegetation. Some of the divergence between these two meta-analyses arises from differences in sampling strategy. Specifically, in addition to considering elemental concentrations and pool sizes separately, and focusing solely on temperate forests, we used different depth categories than Johnson and Curtis (2001). An additional factor that differentiates the two analyses is the large increase in data availability since 1998, the year of the most recent paper included in Johnson and Curtis (2001). For example, the estimated soil C effect sizes of prescribed vs. wildfires from Johnson and Curtis (2001) were based on response ratios from 6 and 3 papers, respectively, while our present analysis includes prescribed fire response ratios from 24 papers and wildfire response ratios from 30 papers. Ultimately, the difference between these two meta-analyses illustrates the benefit of conducting meta-analysis as a cumulative process; as new data are published and added to the analysis, they increase the likelihood that this technique can detect the true, overall effect of fire on forest soils.

Soil C and N budgets

The absolute reductions in total soil C and N storage following fire were relatively small, since the soil layer most affected (the forest floor) was a small component of total soil C and N pools (Table 3). Furthermore, our analysis shows that fire-induced forest floor C and N losses are not permanent, but may require 100–130 years to recover. Since the forest floor plays vital roles in nutrient cycling and water retention (Tietema et al. 1992, Attiwill and Adams 1993, Schaap et al. 1997, Currie 1999), forest floor C and N losses may reduce soil productivity (and possibly new litterfall C and N inputs to soil) over the recovery period. The combination of direct C and N reductions, the length of C and N recovery, and the potential for reduced soil productivity should be considered in C and N management and accounting plans. Forest floor recovery may be accelerated somewhat by additions of C and N from coarse woody debris and tree mortality, although these inputs will often have a large C:N ratio and correspondingly low N availability. However, it is important to note that we did not include forest floor or mineral soil C:N ratios in this meta-analysis, and attempting to assess fire effects on either of those response parameters based on the C and N pool sizes in Table 3 would produce misleading conclusions. This is because the data available for calculating those pool sizes come from a diverse literature, and not all publications provide estimates of all pool sizes. For example, the mineral soil data in Table 3 include several publications with whole mineral soil profile C storage (large values), without a corresponding number of publications that include whole mineral soil profile N storage values. Hence, the mineral soil C:N ratios implied in Table 3 are rather high (>32).

Conclusions

In temperate forests, fires significantly reduced soil C (−35%) and N (−28%) storage, principally through effects on forest floors, which lost 59% and 50% of their C and N pools, respectively. Mineral soil C and N storage showed no overall changes in response to fire, in spite of significant declines in C (−11%) and N (−12%) concentrations. Prescribed fires caused smaller reductions in forest floor C and N storage than wildfires, and the presence of hardwoods also mitigated fire effects on forest floor C and N storage (compared to purely coniferous stands). In general, forest floors required 100–130 years to recover lost C and N pools. Among mineral soils, prescribed fires had no effect on C or N concentrations, while both of these parameters declined in wildfires. Finally, geographic variation in fire effects on mineral soil C and N storage indicate the need for region-specific fire management plans.

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APPENDIX

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