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Postwildfire Soil Trajectory Linked to Prefire Ecosystem Structure in Douglas-Fir Forest

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Abstract

Changes in soil C and N pools following wildfire are quite varied, but there is little understanding of the causes of the variation. We examined how the legacies of prefire ecosystem structure may explain the variation in soil trajectories during the first decade following wildfire. Five years prior to wildfire in a southwestern Oregon forest dominated by mature Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], ecosystem structure was experimentally manipulated by thinning or clearcutting for comparison with unthinned forest. Repeated measurements of replicated experimental units were made before wildfire and during the first decade following wildfire. In the unthinned forest, the O-horizon soil C and N pools were decreased to 24–39% of prefire levels by wildfire, then increased to 53–70% during the first year postwildfire by deposition of fire-killed needles from overstory trees. The mineral soil (0–6 cm depth) C pool was decreased by wildfire, then increased in the following decade, while no change in the N pool was detected. In contrast, in the clearcut treatment, the O-horizon soil C and N pools were nearly totally consumed during the wildfire, lacked fire-killed overstory as a source of needle and fine and coarse wood inputs, but regained 20% of prefire masses in the following decade via foliar and root inputs from regenerated shrubs and herbaceous vegetation. Surface mineral soil C and N pools were decreased 35–50% by wildfire and showed no sign of recovery during the following decade. In contrast to wildfire, unburned ecosystem structures showed no changes in O horizon and increased mineral-soil N pool in the clearcut. We propose a conceptual model of soil C and N response following wildfire that includes legacy influences resulting from prefire ecosystem structures: residual live trees that generate continual litterfall and root turnover; fire-killed trees that produce needle-fall, dead roots, and fine- and coarse-wood detritus; and surviving roots and burls that contribute to postwildfire shrub regeneration. Consideration of prefire ecosystem structure and legacies in quantitative models may improve forecasts of postwildfire C budgets at stand to regional scales.

Key words: fine woody debris; forest management; legacy; postwildfire change; soil carbon; soil nitrogen; wildfire.

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Introduction

Forest wildfire has immediate and substantial ecosystem effects, including decreases in soil organic matter, C and N in many forests (Bormann and others 2008; Fernandez and others 1999; Homann and others 2011; Leduc and Rothstein 2007). These soil components have multiple important functions. Soil C is a major ecosystem C pool and reflects a source of energy and nutrients for decomposers. Soil N is a critical nutritional source for vegetation. In some cases, wildfire-induced N losses are of sufficient magnitude to prompt concern about exacerbating N limitation and influencing long-term ecosystem functioning (Bormann and others 2008; Durán and others 2009). In the decade following wildfire, soil C and N pools may begin to recover, with the postwildfire soil trajectory varying among sites, fire-severity, and soil horizons (Fernandez and others 1999; Martin and others 2012; Keyser and others 2008).

Prefire ecosystem structure—including amount and distribution of live and detrital biomass—can influence the immediate wildfire-induced losses of soil C and N. In Minnesota pine forest, salvage logging of blown-down trees increased subsequent wildfire effects on the forest floor (Fraver and others 2011). In west-coast USA Douglas-fir forest, wildfire caused greater loss of soil C and N in thinned than unthinned stands (Homann and others 2011). Greater amounts of prefire fine wood, a component of ecosystem structure, yield greater soil losses for both wildfire (Homann and others 2011) and experimental fires (Granged and others 2011).

How prefire ecosystem structure affects postwildfire soil recovery is less clear. In the absence of legacy vegetation in Ponderosa pine forest, Ross and others (2012) hypothesized a conceptual model in which soil C following stand-replacing fire would decrease during a plant-colonization period and subsequently increase during a phase of substantial C inputs from regenerated plants. But several studies indicate legacies from the prefire ecosystem may influence the soil recovery. In Minnesota pine forest, wildfire increased the snag C pool (Bradford and others 2012), which could serve as a source of C to fallen woody debris and the forest floor. In a wildfire-affected Spanish pine forest, the legacy of fire-generated coarse woody debris yielded greater soil organic matter, C, and N compared with area lacking coarse woody debris (Maranon-Jimenez and Castro 2013). In another Spanish pine forest, increases in mineral soil C and N during the first year following wildfire were attributed to the incorporation of legacy unburned plant residues (Martin and others 2012). In Florida scrub forest, Alexis and others (2012) recognized the importance of prescribed-fire-generated uncharred litterfall from legacy vegetation, as well as fresh litter input from regenerating vegetation.

Our objective of this study was to determine how different prefire ecosystem structures, through their legacies, influence soil C and N pools in the first decade following wildfire. We addressed the hypothesis that prefire ecosystem structure influences both the rate and the processes of postwildfire soil recovery. This led to an expansion of the conceptual model of soil C following stand-replacing fire (Ross and others 2012) to include multiple types of detrital inputs from legacy vegetation in both stand- and non-stand-replacing wildfire. To address our objective and hypothesis, we evaluated postwildfire soil changes associated with three prefire ecosystem structures: mature unthinned, mature thinned, and clearcut in Douglas-fir dominated forest (Figure 1). Our study is unique because its repeated measures of replicate experimental units follow the trajectories of soil properties from prefire to 1- and 9-years postwildfire, thereby extending our analysis of wildfire effects on soils under multiple ecosystem structures (Bormann and others 2008; Homann and others 2011).

Methods

Study Site and Design

The site is located 25 km southeast of Gold Beach, Oregon, USA, at an elevation between 750 and 900 m in the Rogue River—Siskiyou National Forest. The native forest is dominated by 80-to-110-year-old Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) that regenerated naturally after stand-replacing wildfire in 1881 (Little and others 1995). Additional tree species include knobcone pine (*Pinus attenuata* Lemmon), sugar pine (*Pinus lambertiana* Dougl.), and a second story of hardwoods (tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Rehd.; giant chinquapin, *Chrysolepis chrysophylla* (Dougl. ex Hook.) Hjelmqvist var. *chrysophylla*; and madrone, *Arbutus menziesii* Pursh). When the study site was established in 1992, live trees ($>$3.5-cm diameter) averaged 1,300 stems ha^{-1} and their basal area averaged 77 m^2 ha^{-1}. Conifers accounted for 81% of the stems and 96% of the basal area, and had a quadratic mean diameter of 30 cm. Mean January temperature is 4°C, mean July temperature is 18°C, and annual precipitation is approximately 190 cm, of which only 10 cm falls between June and September (Homann and others

Figure 1. 1 year after wildfire, legacies of prefire ecosystem structure are evident in conifer forest, Rogue River—Siskiyou National Forest. Thinned (*foreground*), clearcut (*middle*), and unthinned (*background*) prefire treatments influenced the prefire ecosystem structures and their postwildfire legacies.

2011). Additional site details are available in Little and others (1995) and Raymond and Peterson (2005).

The soils are mapped as the Saddlepeak–Threetrees complex, which are loamy-skeletal, mixed, superactive, frigid Typic Dystrupdepts developed on a parent material of weathered sandstone and schist–phyllite. They had been identified previously as Typic Dystrochrept and Typic Hapludult (Homann and others 2001). Mean depth of soils to a stony C horizon is about 35 cm. Based on measurements of our samples, of the total soil inorganic material, 56% is <2 mm, 7% is 2–4 mm, and 37% is >4 mm. Of the <2 mm inorganic mass, 26% is clay, 37% is silt, and 36% is sand.

The study site has two forest management experiments that were established prior to wildfire (Homann and others 2011). In one experiment, clearcut, thinned, and unthinned treatments (Table 1) were applied to experimental units within each of three blocks. Clearcut and thinned units had various amounts of coarse woody debris, and clearcut units had various post-harvest vegetation manipulations (Table 1). In the second experiment, thinned and unthinned treatments were applied in two blocks. The thinning and clearcutting took place in 1997 (Table 1). The 2002 Biscuit Complex Wildfire and associated backburns burned portions of both experiments as a surface fire (Raymond and Peterson 2005), thereby disrupting the original experimental designs. As a consequence, 21 postwildfire experimental units are categorized by structure and burn characteristics: 2 unthinned unburned, 3 unthinned wildfire-burned, 3 thinned unburned, 3 thinned wildfire-burned, 4 clearcut unburned, and 6 clearcut wildfire-burned. Four additional unburned experimental units that were not measured in 2003 and two other units that underwent prescribed burning were not considered in this wildfire analysis. Postwildfire vegetation C pools are summarized in Table 2.

Measurements and Data Synthesis

Each experimental unit is 6–8 ha, consisting of a central 1.5-ha sampling area surrounded by buffer. For each experimental unit at each of three sampling times (prefire, 1 year postwildfire, and 8–9 years postwildfire), an experimental-unit value was determined for each C and N pool (mass per m^2) based on multiple samples and measurements taken within the unit, as described below. The experimental-unit values were then subjected to statistical analysis.

Prefire surface coarse (>10 cm diameter) and fine wood (1–10 cm diameter) measurements were made in 1998–2000, and postfire measurements in 2003 and 2010. Coarse wood was measured on eight or ten 25-m transects per experimental unit by the method of Brown and others (1982). Masses per m^2 were corrected for slope, based on slope measurements at the time of sampling. The C pool was estimated as mass per m^2 times an assumed C concentration of 50%. Fine wood was collected from 15 1-m^2 plots per experimental unit, oven-dried at 70°C and weighed (Raymond and Peterson 2005). For 2003 and 2010, samples were separated into three size classes: 1–2.5 cm (part of 10-h fuel class), 2.5–7.6 cm (100-h fuel class), and 7.6–10 cm diameter (part of 1,000-h fuel class). The fine wood masses per m^2 were slope-corrected based on slope measurements at time of sampling. The C and N pools were calculated as mass per m^2 times the following concentrations. Composite fine wood samples from several experimental units in 2003 and 2010 were analyzed for C and N concentration with a Thermo NC 1112 Analyzer (CE Elantech, Inc., Lakewood, New Jersey). Carbon concentration was consistent across units and size classes (mean = 50.1%, SD = 1.4%, n = 11), and the

Table 1. Experimental Treatments in Conifer Forest Prior to Wildfire at the Siskiyou Long-Term Ecosystem Productivity Study, Rogue River—Siskiyou National Forest, Oregon

Treatment	Treatment description
Unthinned	Unmanaged mature stands, dominated with 80- to 110-yr-old Douglas-fir, with some knobcone pine and secondary story of tanoak. Averaged 1,100 total live stems ha^{-1} and total live basal area 60 m^2 ha^{-1}. Conifers accounted for 67% of the stems and 92% of the basal area, and had quadratic mean diameter of 31 cm
Thinned	Mature forest thinned and helicopter-logged in 1997. Averaged 240 remaining live stems ha^{-1} and total live basal area 23 m^2 ha^{-1}, approximately 38% of unthinned. Conifers accounted for 69% of the stems and 97% of the basal area, and had quadratic mean diameter of 41 cm. Some units had 15% of the merchantable harvest (10–15 stems ha^{-1}) left on the ground as woody debris; other units removed all downed woody material greater than 3 m in length and greater than 5 cm in diameter at the small end
Clearcut	Clearcut and helicopter-logged in 1997. Some units had 15% of the merchantable harvest (30–40 stems ha^{-1}) left on the ground as woody debris; other units removed downed woody material. Some units were planted with Douglas-fir and knobcone pine; other units planted with Douglas-fir, and shrubs cut in 1999 to reduce competition

Table 2. Aboveground C Pools of Conifer Trees and Understory Vegetation in Wildfire-burned Forest at the Siskiyou Long-Term Ecosystem Productivity Study, Rogue River—Siskiyou National Forest, Oregon

Stratum	Time (yr postwildfire)	C Pool, mean (SE)[a] (kg m^{-2}) in		
		Unthinned	Thinned	Clearcut
Fire-killed conifer trees[b]				
Foliage	0	0.23 (0.08)	0.20 (0.04)	0
Branch	0	0.45 (0.16)	0.41 (0.09)	0
Bole	0	6.7 (2.4)	5.3 (1.1)	0
Residual live conifer trees[b]				
Foliage	0	0.28 (0.15)	0.002 (0.002)	0
Branch	0	0.55 (0.31)	0.005 (0.005)	0
Bole	0	7.9 (4.3)	0.06 (0.06)	0
Understory[c]	1	0.002 (0.001)	0.002 (0.001)	0.020 (0.002)
	8	2.0 (0.1)	3.2 (0.7)	1.9 (0.3)
n experimental units		3	3	6

[a]*Mean is the average of the n experimental units. SE is based on variation among the n experimental units.*
[b]*Conifer biomasses were calculated from site-specific biomass equations (Nay and Bormann 2014 in press), diameters of trees measured in five 18- by 18-m plots in each experimental unit prior to the wildfire, and assessment of proportion of trees that were killed by the wildfire. Biomass was assumed to be 50% C. Trees are defined as >3.5-cm diameter at breast height.*
[c]*Understory biomass (1-year postwildfire) was calculated from biomass equation (Homann and others 2011), vegetation coverage on sixteen 3- by 3-m plots per experimental unit, and height determined by photointerpretation at six points per experimental unit. Understory biomass (8-year postwildfire) was based on destructive sampling of 28 3- by 3-m plots to calibrate observations on sixteen 3- by 3-m plots per experimental unit (Bormann and others in prep). Biomass was assumed to be 50% C.*

average was applied to all fine wood masses. N concentration varied with size class: mean 0.182%, SD 0.009%, $n = 4$ for 1–2.5 cm; mean 0.130%, SD 0.031%, $n = 4$ for 2.5–7.6 cm; mean 0.095%, SD 0.018%, $n = 4$ for 7.6–10 cm; these mean values were applied to 2003 and 2010 fine wood size-class masses. For 1998–2000, for which only total fine wood masses are available, the following N concentrations were used: unthinned 0.153%, thinned 0.138%, clearcut 0.142%; these are based on weighted concentrations for 2003 unburned experimental units.

Prefire soil measurements were made in 1992 on most experimental units and in 1995 on others. Postfire measurements were made in 2003 and 2011. Soil samples at an average of 13 points per experimental unit were collected as described in detail by Homann and others (2001) and Bormann and others (2008). At each point, O layer from within a 30-cm-diameter ring was collected in 1992 and 1995 and from within a 21-cm-diameter ring in 2003 and 2011. Then the mineral soil was sampled with a corer that had a rectangular cross-section of 10 by 15 cm. In 1992, 1995, and 2003, mineral soil sampling depth was 30 cm, and the soil was separated into three layers with average depths of 0–3, 3–15, and 15–30 cm. In 2011, mineral soil sampling depth was 6 cm, and the soil was separated into 0–3 and 3–6 cm layers. The O-layer samples were hand-sorted into >4-mm rocks, >6.4-mm diameter woody debris, and residual material, which we call soil. Mineral soil samples were sieved at 4 mm, with the <4-mm-fraction defined as soil; rocks were separated from the >4-mm fraction in 1992, 1995 and 2003. Fractions were oven-dried and weighed, and masses of fractions per m^2 were calculated based on the cross-sectional sampling areas and slope measurements at time of sampling. The C concentration of >6.4-mm wood in the O layer was assumed to be 50%. For each experimental unit, the soil C and N pools were calculated as average layer mass per m^2 times the following concentrations. For each experimental unit and for each soil layer, a mass-weighted composite of the soil was made from the sampling points. Composites were analyzed for total C and N with a Thermo NC 1112 Analyzer. Concentration of soil organic matter was calculated as C concentration divided by 0.53, which is the ratio of total C to loss-on-ignition (Homann and others 2001), and soil inorganic matter concentration as 1,000 mg g^{-1} soil minus soil organic matter concentration.

The C and N pools of the O horizon were estimated by correcting the sampled O layers for mineral soil that contaminated them, as follows.

$$\mathrm{CPool}_{\mathrm{O horizon}} = \mathrm{CPool}_{\mathrm{sampled O}} - \mathrm{CPool}_{\mathrm{mineral in sampled O}},$$

where

$$\mathrm{CPool}_{\mathrm{mineral\ in\ sampled\ O}} = M_{\mathrm{sampled\ O}} \times F_{\mathrm{mineral}} \times \mathrm{CConc}_{\mathrm{mineral}},$$

$$F_{\mathrm{mineral}} = \left(I_{\mathrm{sampled\ O}} - I_{\mathrm{O\ horizon}}\right)/\left(I_{\mathrm{mineral}} - I_{\mathrm{O\ horizon}}\right).$$

$\mathrm{CPool}_{\mathrm{O\ horizon}}$, $\mathrm{CPool}_{\mathrm{sampled\ O}}$, and $\mathrm{CPool}_{\mathrm{mineral\ in\ sampled\ O}}$ are the C pools (kg m^{-2}) of the O horizon, the sampled O layer, and the contaminating mineral soil, respectively; $\mathrm{M}_{\mathrm{sampled\ O}}$ is the mass (kg m^{-2}) of the sampled O layer; $\mathrm{CConc}_{\mathrm{mineral}}$ is the C concentration (kg C kg^{-1} soil) of the mineral soil beneath the sampled O layer; $\mathrm{F}_{\mathrm{mineral}}$ is the unitless fraction of the sampled O layer mass that is contaminating mineral soil; $\mathrm{I}_{\mathrm{sampled\ O}}$, $\mathrm{I}_{\mathrm{O\ horizon}}$, and $\mathrm{I}_{\mathrm{mineral}}$ are the inorganic matter concentrations (mg g^{-1}) of the sampled O layer, uncontaminated O horizon, and mineral soil beneath the sampled O layer, respectively. $\mathrm{I}_{\mathrm{O\ horizon}}$ was taken to be 119 mg g^{-1}, which is the lowest inorganic matter concentration of the O layer samples and is consistent with inorganic matter concentration of partially decomposed Douglas-fir needles (Homann 2012). The N pools of the O horizon were calculated similarly. In addition, the O horizon pools immediately after the 2002 wildfire in the thinned and unthinned wildfire-burned units were estimated by removing from the 2003 composites the fresh needle litter that fell between the wildfire and the 2003 sampling, quantifying that fresh needle litter, and subtracting it from 2003 values to yield 2002 O horizon estimates.

The C and N pools for the upper mineral soil were quantified with a comparable-layer approach that accounts for soil volume change and soil loss resulting from fire, as described in detail by Bormann and others (2008). In this approach soil pools are standardized by mass of soil inorganic matter per unit area rather than by depth. This approach was taken because of the large amount of soil organic and inorganic matter that was lost due to the fire. In this study, we used 30 kg m^{-2} of <4-mm inorganic matter to define the surface comparable layer. Beginning with the mineral soil that contaminated the sampled O layer and proceeding down through the mineral soil layers, the cumulative soil inorganic pool of 30 kg m^{-2} was reached, as follows:

$$30\ \mathrm{kg\ m^{-2}}\ \text{of inorganic matter} = \mathrm{IPool}_{\mathrm{lost}} + \mathrm{IPool}_{\mathrm{mineral\ in\ sampled\ O}} + \mathrm{IPool}_0 + \mathrm{IPool}_3$$

where $\mathrm{IPool}_{\mathrm{lost}}$, $\mathrm{IPool}_{\mathrm{mineral\ in\ sampled\ O}}$, and IPool_0 are masses of <4-mm inorganic matter (kg m^{-2}) lost due to wildfire, in the mineral soil contaminating the O layer, and in the 0–3 cm mineral soil, respectively. Values for $\mathrm{IPool}_{\mathrm{lost}}$ averaged 2.2 kg m^{-2} for unthinned, 7.6 kg m^{-2} for thinned, and 8.5 kg m^{-2} for clearcut. IPool_3 is the inorganic mass contribution from the 3–15 cm (for 1992, 1995, and 2003) or 3–6 cm mineral soil (for 2011) that is needed to yield the total 30 kg m^{-2} of inorganic matter.

The C pool of the comparable layer was then calculated, as follows:

$$\mathrm{CPool}_{\mathrm{comp\ layer}} = \mathrm{CPool}_{\mathrm{mineral\ in\ sampled\ O}} + \mathrm{CPool}_0 + \int_0^{\mathrm{IPool3}} ae^{-b\,\mathrm{IPool}}$$

where $\mathrm{CPool}_{\mathrm{comp\ layer}}$, $\mathrm{CPool}_{\mathrm{mineral\ in\ sampled\ O}}$, and CPool_0 are the C pools (kg m^{-2}) of the comparable mineral soil layer, the mineral soil contaminating the O layer, and the 0–3 cm mineral soil, respectively. The integral is the C pool of the portion of the 3–15 or 3–6 cm mineral soil layer that contributes to the comparable layer, assuming an exponential decrease in C concentration (kg C per kg inorganic matter) within the layer; IPool is cumulative inorganic matter mass, beginning at zero at the top of the layer and increasing with depth. The coefficient *b* was determined to be 0.00611 for our site, based on fitting the integral to the 3–15 and 15–30 cm soil C pools for 2003 in each of three unburned and three wildfire-burned units. The coefficient *a* is the C concentration at the top of the 3–15 or 3–6 cm layer and is determined by fitting the integral to the C pool for that layer. The same approach was used for N, but *b* was 0.00364.

The cumulative soil inorganic pool of 30 kg m^{-2} corresponded to an average prefire mineral-soil depth of 6 cm, or a volume of 0.06 m^3 volume per m^2 area. Of this volume, 84.5% was occupied by <4-mm material and the remainder by >4-mm rocks and wood-plus-roots (for example, Homann and others 2001). The organic matter in the <4-mm fraction averaged 3.6 kg m^{-2}, which complemented the 30 kg m^{-2} of inorganic matter. The bulk density of the <4-mm fraction was (3.6 kg m^{-2} + 30 kg m^{-2})/(0.06 m^3 × 84.5%/100%) = 660 kg m^{-3} = 0.66 g cm^{-3}. This is consistent with an average bulk density of 0.72 g cm^{-3} in the surface mineral soil of 20 other forest research sites in Washington and Oregon USA (Homann and others 2004, 2008).

Statistical Analysis

The total detrital C pool 8–9 years postfire was determined for each experimental unit by adding the C pools associated with the coarse wood, fine wood, O wood, O horizon, and mineral soil comparable layer. For each combination of ecosystem structure and fire regime, the mean and standard error were calculated from the resulting experimental-unit values. The means of all six combinations of ecosystem structure and fire regime were compared with a Tukey multiple comparison test. A similar analysis was performed for the O-horizon C pool. To evaluate temporal change (prefire, 0–1 year postfire, 8–9 years postfire) in each structure-burn category, repeated measures ANOVA of log-transformed data was followed by Tukey multiple comparison test at $\alpha = 0.10$ and 0.05. For presentation, means of log-transformed data were back-transformed, and the ratio of back-transformed means at which the means differed at $\alpha = 0.05$ was calculated as

$$\text{Critical ratio} = 10^{[Q_{0.05} \times \text{sqrt}(\text{MSR}/n)]},$$

where $Q_{0.05}$ is the critical value from the Tukey test for $\alpha = 0.05$, MSR is mean square residual from ANOVA, and *n* is number of replicate experimental units.

Results

Surface and subsurface detrital C pools were greatly influenced by wildfire, but the direction and degree of alteration varied with prefire ecosystem structure. The total detrital C pool nearly a decade after wildfire was substantially less in wildfire-burned than unburned stands in the thinned and clearcut treatments, but not in the unthinned stands (Figure 2).

The influence of wildfire varied with time as well as ecosystem structure. Coarse wood C was decreased approximately 55% by wildfire in all

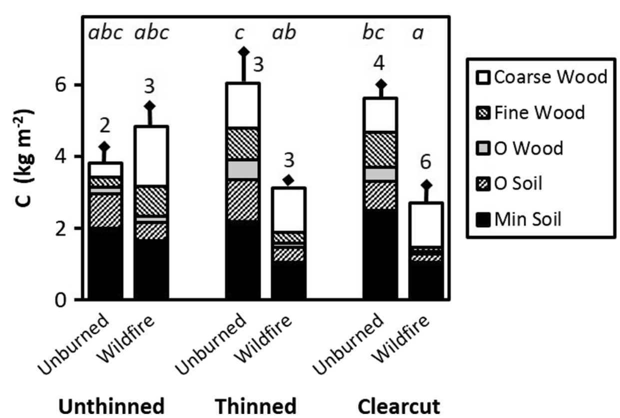

Figure 2. Wildfire effects on detrital C pools vary with prefire ecosystem structure (unthinned, thinned, clearcut) 8-to-9 years after wildfire in conifer forest, Rogue River—Siskiyou National Forest. For detrital C pools in each experimental unit, coarse wood (>10-cm diameter) is based on 10 transects per experimental unit; fine wood (1–10-cm diameter) is based on 15 quadrats per experimental unit; and O wood (wood within O horizon), O horizon soil, and mineral soil to a prefire depth of 6 cm are based on an average of 13 soil sampling points per experimental unit. The C pools of the various strata were summed to yield the total detrital C pool of each experimental unit. *Bar segments* represent strata averages of replicate experimental units, total bar height is average total detrital C pool, the *error bar* is the standard error of the total detrital C pool, and the value associated with each bar is the number of replicate experimental units. *Bars not identified by a same letter* are different at $\alpha = 0.05$, Tukey multiple comparison test.

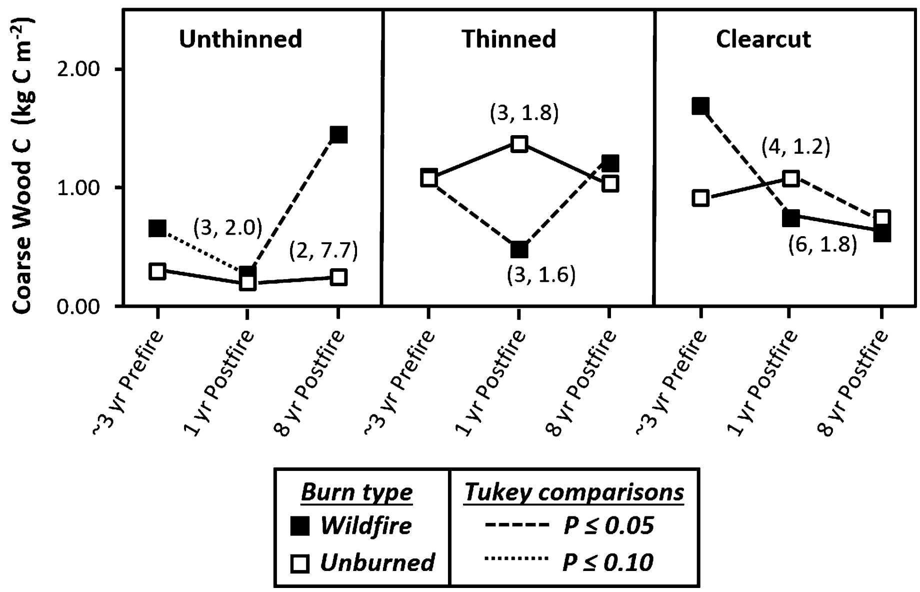

Figure 3. Coarse woody debris C (>10 cm diameter) in unburned and wildfire-burned conifer forest with different prefire ecosystem structure (unthinned, thinned, clearcut), Rogue River—Siskiyou National Forest. Within each structure-burn type combination, repeated measures ANOVA of log-transformed values was followed by Tukey multiple comparison test; comparisons of sequential points are shown. Points are back-transformed means; *numbers in parentheses* are the number of repeatedly measured experimental units and the critical ratio, which is the ratio at which two points within a structure-burn type combination differ at $P \leq 0.05$. Prefire coarse wood varied due to prefire experimental treatments (Table 1).

treatments (Figure 3), then it rebounded during the following 8 years in the unthinned and thinned stands. Fine wood C and N were decreased 97% by wildfire in the thinned and clearcut treatments, where prefire logging residues burned thoroughly (Figure 4). In the 8 years following wildfire, the fine wood pools increased in the unthinned wildfire-burned stands, but did not change in the clearcut (Figure 4).

The O soil C and N were decreased approximately 70% by wildfire in the unthinned stands and by more than 97% in the clearcut (Figure 5). They then increased to about 50% of prefire level in the unthinned during the first year following the fire and increased to around 20% of prefire levels in the clearcut between 1 and 9 years postfire.

Mineral soil C was decreased by wildfire in all ecosystem structures (Figure 6). This is attributed both to loss of some soil and to a lower concentration of C in the remaining soil (Appendix A in supplementary material). The large decrease in the clearcut is associated with large amounts of harvest-generated fine wood (Figure 4) that produced high intensity wildfire, combustion of organic matter in the mineral soil, and soil erosion (Homann and others 2011). Mineral soil C subsequently increased in the unthinned wildfire stands between 1 and 9 years postfire. In contrast, no change in mineral soil C was observed in the unburned stands (Figure 6). In the clearcut, mineral soil N was decreased by wildfire, but it increased in the unburned stands.

Discussion

Potential Processes driving C and N Change

Our study supports the premise that legacies from prefire ecosystem structures influence the dynamics of soil C and N pools following wildfire. Key legacies are dead overstory vegetation (Table 2), which provides deposition of fire-killed needles, roots, fine wood and coarse wood over different periods; residual living overstory (Table 2), which provides continual aboveground litterfall and root turnover, as well as influencing soil decomposition processes through microclimate and microbial interactions; and roots and burl structures from which some shrub and tree species regenerate (Bormann, personal observation).

Multiple processes of losses and gains contributed to the various responses of soil and woody debris that were exhibited by the different prefire eco-

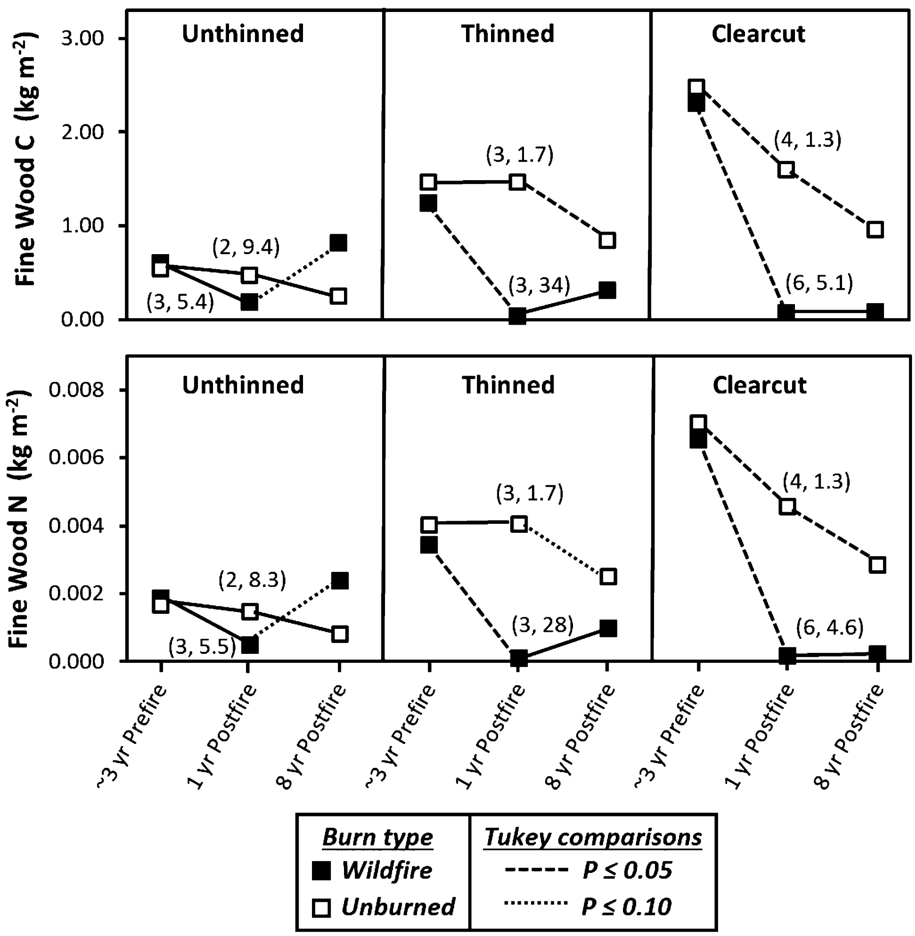

Figure 4. Fine woody debris C and N (1–10 cm diameter) in unburned and wildfire-burned conifer forest with different prefire ecosystem structure (unthinned, thinned, clearcut), Rogue River—Siskiyou National Forest. Within each structure-burn type combination, repeated measures ANOVA of log-transformed values was followed by Tukey multiple comparison test; comparisons of sequential points are shown. Points are back-transformed means; *numbers in parentheses* are the number of repeatedly measured experimental units and the critical ratio, which is the ratio at which two points within a structure-burn type combination differ at $P \leq 0.05$.

system structures. In the burned unthinned and thinned treatments, fire-killed trees provided a source of C (Table 2) and N deposition. In unthinned wildfire treatment, branch-fall from fire-killed trees increased fine wood C and N to prefire masses in the following decade (Figure 4) and bole deposition of fire-killed trees elevated coarse wood C far above prefire amounts (Figure 3). Similarly, in Ponderosa pine forests, fine woody debris in moderate- and high-severity burns recovered to unburned levels within 5 years (Keyser and others 2008) and tripled in mass between 3 and 9 years postfire (Passovoy and Fule 2006). Also in Ponderosa pine forests, many fire-killed snags fell within 8 years after wildfire, leading to elevated surface fuels (Ritchie and others 2013). In the thinned wildfire treatment, fire-killed trees also provided postfire sources of coarse (Figure 3) and fine wood. Postfire fine wood pools increased in each of the thinned wildfire experimental units, but high variation among the units precluded observing a statistically significant change between 1 and 8 years postfire. The clearcut wildfire stands lacked postfire sources of coarse and fine wood; these pools did not change in the decade following the wildfire (Figures 3, 4).

The increase in O soil C and N in the year following the fire in the unthinned wildfire stands (Figure 5) is ascribed to deposition of heat-killed needles and natural needle senescence of surviving trees. The 0.28 kg C m^{-2} increase in O soil C (Figure 5) compares favorably with needlefall sources of 0.23 kg C m^{-2} from dead needles on fire-killed trees (Table 2) plus 0.06 kg C m^{-2} from a 20% per year turnover of needles of surviving trees (Table 2). The deposition of fire-killed needles is consistent with the observations of other studies (Alexis and others 2012; Cerdà and Doerr 2008; Keyser and others 2008; Rodríguez and others 2009). Thereafter, C remained stable but N decreased, resulting in an increased C/N ratio. Input of high-C/N material likely contributed to this pattern, with decomposition residue of fine wood, and possibly coarse wood, being a potential source of this material. Fine wood had C/N ratios of 270–530; its decomposition residues would

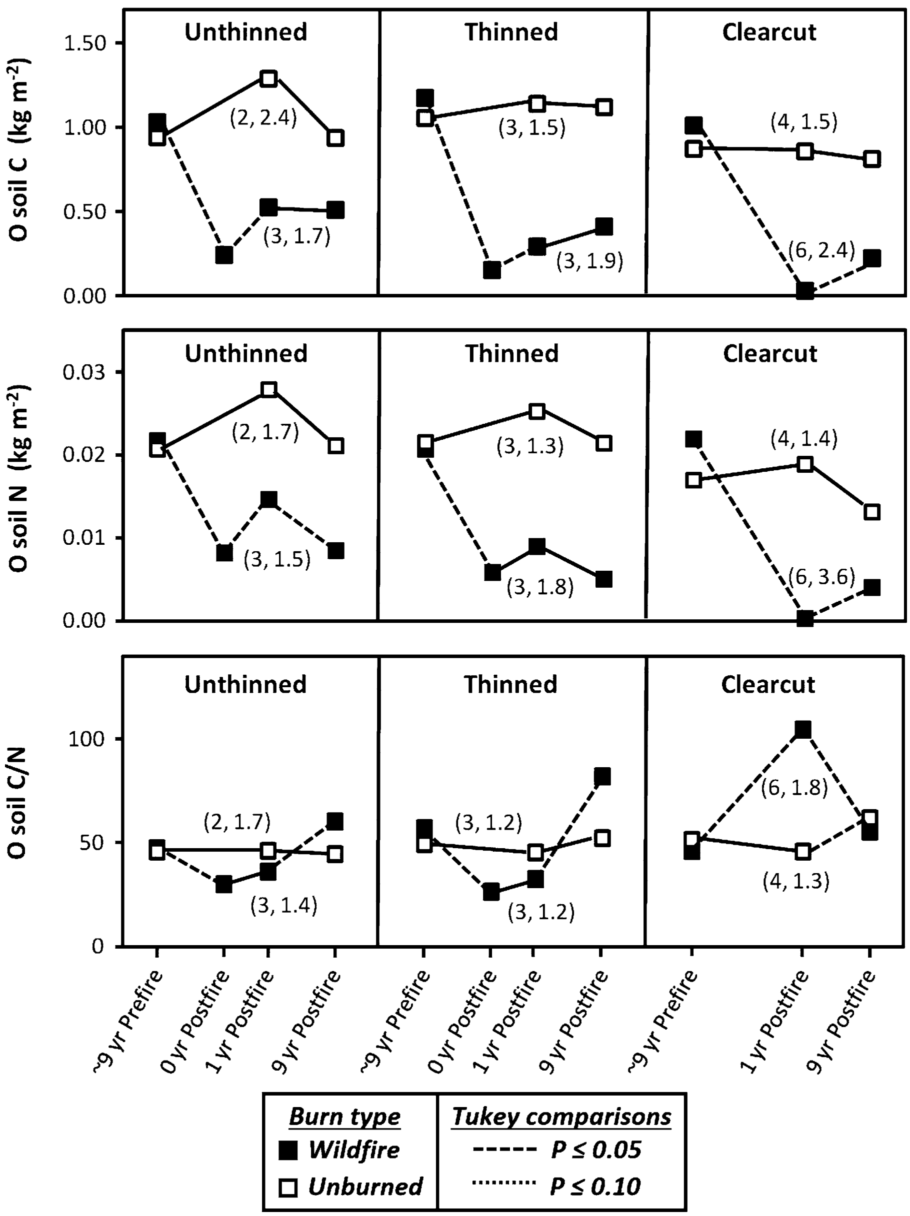

Figure 5. O horizon soil C and N in unburned and wildfire-burned conifer forest with different prefire ecosystem structure (unthinned, thinned, clearcut), Rogue River—Siskiyou National Forest. Within each structure-burn type combination, repeated measures ANOVA of log-transformed values was followed by Tukey multiple comparison test; comparisons of sequential points are shown. Points are back-transformed means; *numbers in parentheses* are the number of repeatedly measured experimental units and the critical ratio, which is the ratio at which two points within a structure-burn type combination differ at $P \leq 0.05$.

likely have somewhat lower, but still high, ratios. Inputs of fresh litter from residual trees and postfire shrubs and herbs (Table 2) would be expected to contribute, too, but with lower C/N ratios. Output of N from the O horizon by leaching, plant uptake, or erosion could have contributed to an increase in C/N ratio. A similar substantial increase in the C/N ratio in the thinned wildfire stands support the concept of input of fine and coarse wood decomposition residue with high C/N ratio to the O horizon. Further, the lack of substantial postfire build-up of fine wood in the thinned wildfire treatment (Figure 4) suggests deposition of fine wood was balanced by its decomposition, thereby providing decomposed material to the O horizon.

In the clearcut, more than 97% of O soil C and N was lost in the wildfire, leaving only minimal amounts of charred residues with high C/N ratio. This is consistent with the charred residues being derived from high-C/N-ratio fine and coarse wood. There was no dead overstory source for postfire input of needles or fine wood. Between 1 and 9 years postfire, O soil C and N increased to approximately 20% of prefire values. The C/N ratio declined to values consistent with inputs from litterfall from postfire vegetation.

The substantial losses of mineral soil C as a result of wildfire have been attributed to combustion, convective transport during the fire and postfire erosion (Bormann and others 2008; Homann and others 2011). In addition, heating causes solubili-

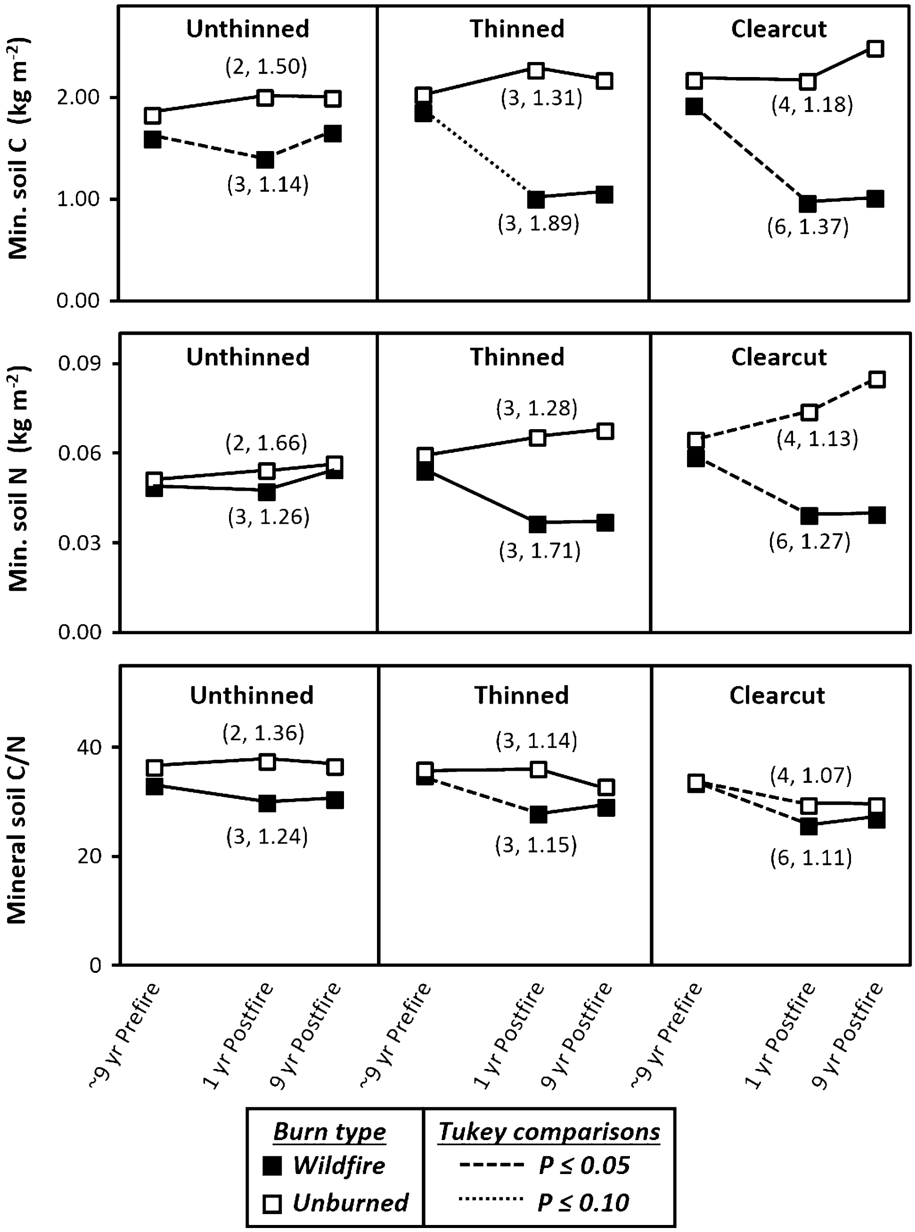

Figure 6. Mineral soil C and N (prefire depth = 6 cm) in unburned and wildfire-burned conifer forest with different prefire ecosystem structure (unthinned, thinned, clearcut), Rogue River—Siskiyou National Forest. Within each structure-burn type combination, repeated measures ANOVA of log-transformed values was followed by Tukey multiple comparison test; comparisons of sequential points are shown. Points are back-transformed means; *numbers in parentheses* are the number of repeatedly measured experimental units and the critical ratio, which is the ratio at which two points within a structure-burn type combination differ at $P \leq 0.05$.

zation of soil organic C (Homann and Grigal 1992), which could have resulted in enhanced leaching losses immediately following the fire.

Our observations of the O horizon and surface mineral soil support the hypothesis that prefire ecosystem structure influences the rate of postwildfire soil recovery. Rapid postwildfire change in O horizon C and N occurred in the burned unthinned and thinned treatments compared with a slower response in the burned clearcut (Figure 5). Postwildfire increase in mineral soil C occurred in the burned unthinned treatment, but not in the burned thinned and clearcut treatments (Figure 6).

Our observations also support the hypothesis that prefire ecosystem structure influences the processes of postwildfire soil recovery. The increase in mineral soil C in the unthinned wildfire treatment between 1 and 9 years postfire (Figure 6) may be from sources internal or external to the soil volume. Internal sources are decomposition of buried wood, prefire dead roots, dead roots from fire-killed trees and normal root turnover of surviving trees. In prefire unthinned forest at our site, root-plus-buried wood C is equivalent to about 7% of soil C in the surface mineral soil (Homann and others 2008). External sources include mixing of O horizon material into mineral soil; root decay; and organic leachates from vegetation, O horizon, and fine and coarse wood (Maranon-Jimenez and Castro 2013). O-horizon 0.5–4-mm charcoal particles averaged 0.023 kg C m^{-2} in the burned unthinned and thinned treatments 1 year after wildfire (Pingree and others 2012). In addition, 4–20-mm charcoal particles contributed 0.006 kg C m^{-2}. If all of this material were incorporated into the mineral soil C pool by transport, mixing and disintegration of the large particles, it would represent 10% of the postwildfire increase in the burned unthinned treatment (Figure 6). In the clearcut wildfire areas, these processes would have been of lesser importance, because of more limited O horizon, fine wood, and vegetation, resulting in stability of mineral soil C following the dramatic decrease caused by wildfire.

Soil microbial respiration depends on the amount and type of microorganisms and their related enzymes; the amount of organic matter substrate and its lability; and environmental factors such as moisture and temperature. Fire generally reduces soil microbial biomass, hydrolytic extracellular enzymes, and heterotrophic respiration (Holden and Treseder 2013; Holden and others 2013). Fire consumes soil organic matter, but produces pyrogenic organic matter that may be more recalcitrant (Knicker and others 2013).

In our study, postwildfire microbial respiration rates likely varied among the prefire structures. We suspect that immediately after the wildfire the burned clearcut had the lowest postfire areal respiration rates, because of the nearly complete loss of O horizon substrate and substantial loss of mineral soil substrate (Figures 5, 6). Soil temperature in the burned clearcut would likely have been higher than in burned thinned and unthinned forest because the near absence of live and dead vegetation (Table 2) would have yielded high solar gain; and higher temperatures generally increase microbial respiration (Kirschbaum 2006). But, this could have been off-set by decreased moisture, which can result in lower respiration (Van Meeteren and others 2007).

A decade after wildfire, we suspect soil microbial respiration remained lower in the burned clearcut than burned thinned and unthinned forest, because of lesser increase of the O horizon (Figure 5). However, variation in litter decomposition rates among vegetation species (Valachovic and others 2004; Homann 2012) indicates the composition of the O horizon, as well as its mass, needs to be considered in predicting areal respiration rates.

The longer-term effect of these different legacies and the processes they influence remains to be determined, but our decade-scale observations may foreshadow future change. Chronosequence studies suggest postwildfire soil changes continue to occur over multiple decades (Alexander and others 2012; Driscoll and others 1999; Durán and others 2010; Guenon and others 2013; Kashian and others 2013; Kaye and others 2010; Lecomte and others 2006; Norris and others 2009; Rothstein and others 2004). In eastern Canadian boreal forests, accumulation of O horizon biomass during the first century following fire was greater for low-severity burns than high-severity burns (Lecomte and others 2006). Our study parallels this pattern, but over a shorter time frame. In our study the unthinned treatment burned at lower severity than the clearcut, as indicated by degree of O horizon and mineral soil losses (Figures 5, 6); and 9 years after fire the lower-severity unthinned averaged twice the O soil C than the higher-severity clearcut ($P < 0.05$, Tukey test across all burn–structure combinations). Further, forest floor may recover from fire more rapidly than surface mineral soil (Latty and others 2004). Our observations in the thinned and clearcut wildfire treatments during the first-decade postfire (Figures 5, 6) support this concept of differential recovery rates among soil layers.

Expanded Conceptual Model

The basic conceptual model (Figure 7) of soil C change following stand-replacing fire focuses on C inputs from postfire recolonizing vegetation (Ross and others 2012). Our analysis indicates the conceptual model needs to be expanded for conditions where the fire-killed tree canopy provides substantial postfire detritus, including fire-killed needles, dying roots, and decomposing coarse and fine wood derived from fire-killed branches and trees. Further, surviving trees provide continual aboveground litterfall after non-stand-replacing fire, and their root growth and death likely complement the aboveground detrital processes to provide important inputs into soil C.

These processes may act in succession, for example, needle fall, followed by branch fall and decomposition; snag formation and coarse wood deposition, followed by coarse wood decomposition and fragmentation (Bond-Lamberty and Gower 2008); and finally postfire vegetation litterfall. Or these processes may overlap temporally. Where some trees survive wildfire, such as in our unthinned wildfire stands, residual live trees may provide litterfall and root turnover before new postfire vegetation becomes established. The input processes interact with the C output processes of microbial respiration, erosion, and soluble organic leaching. The relative and absolute rates of the various processes change as the system evolves.

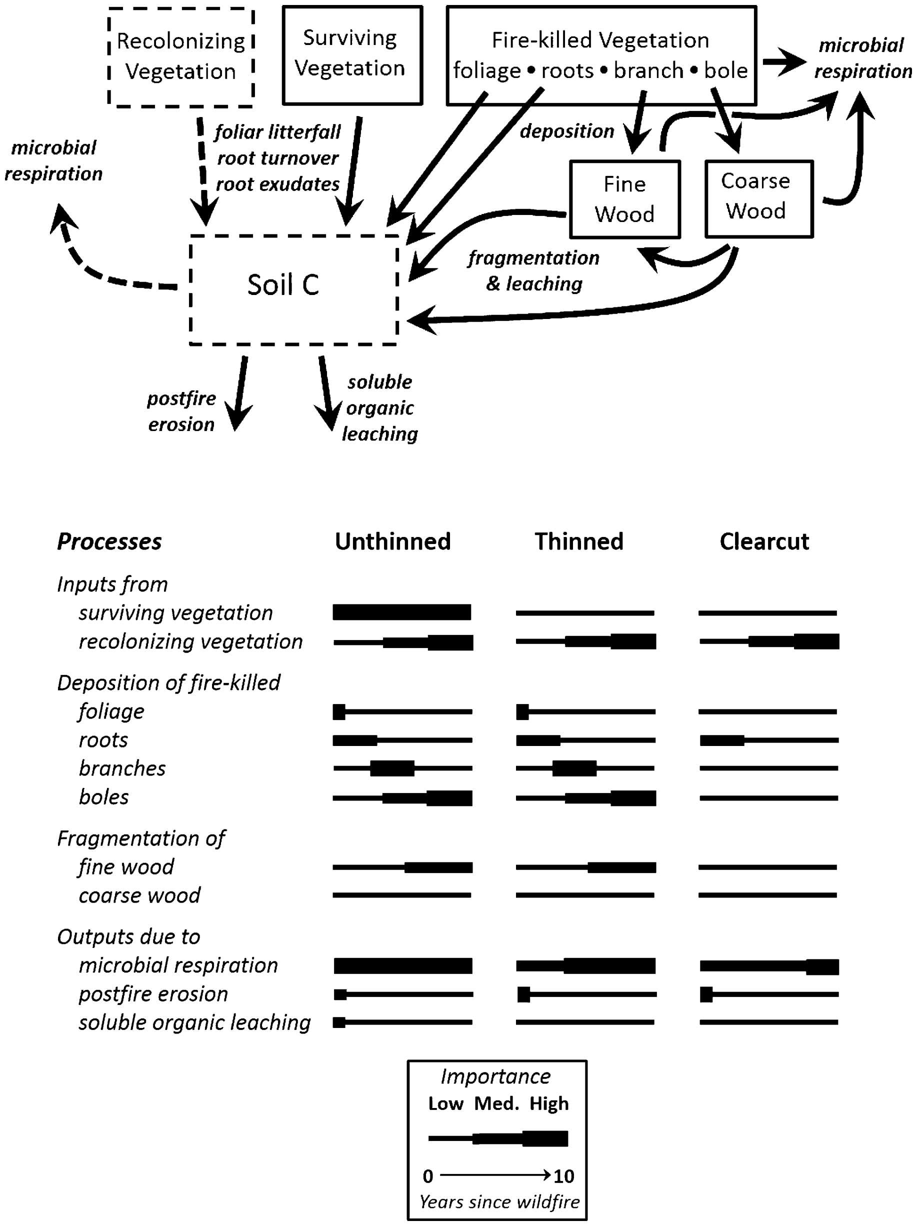

Figure 7. *Top* conceptual model of major pools and processes that influence soil C (O horizon plus mineral soil) after forest wildfire. *Dashed pools* and processes based on Ross and others (2012); *solid pools* and processes added in this study. *Bottom* hypothesized importance and duration of processes that influence soil C during the first decade after wildfire in unthinned, thinned and clearcut prefire ecosystem structures.

Ultimately, it is the imbalance of the rates of all the processes that results in the timing of increases and decreases in soil C.

In our study, the prefire ecosystem structure affected the relative importance of C input processes. The legacies of fire-killed needles, branches, and boles in the unthinned and thinned wildfire stands were important contributors to soil C (Table 2). The unthinned stands had the additional legacy of live residual trees that produce fresh litter (Table 2). These legacies were lacking in the clearcut, where input of litter from postfire vegetation took on greater relative importance. The consideration of prefire ecosystem structure, legacies, and multiple woody detrital and soil pools may improve postwildfire estimates of C budgets at spatial scales from individual stands to subcontinental regions (Alexander and others 2012; Balshi and others 2009; Kashian and others 2006; Smithwick and others 2009; Yue and others 2013).

Conclusion

This study used repeated measurements of replicated treatments to demonstrate the importance of ecosystem structure, not only on the immediate effects of wildfire, but also on the postwildfire trajectories on soil C and N. Our observations support the hypothesis that prefire ecosystem structure influences both the rate and the processes of postwildfire soil recovery. Critical legacies from the prewildfire ecosystem structures were residual live trees that generate continual aboveground litterfall and root turnover; dead trees with fire-killed canopies that produce needle-fall, dying roots, and fine- and coarse-wood detritus; and surviving belowground components that contribute to postwildfire shrub regeneration. In unthinned, mature conifer forest, all of these legacies produced potential sources of detrital inputs, resulting in increased C in the O horizon and surface mineral soil during the first decade following wildfire. In contrast, clearcut ecosystem structure had only postwildfire regeneration as a detrital source, resulting in a delayed increase in O-horizon C and N. These soil changes during the first decade may foreshadow century-long trajectories, as deposition and decomposition of additional branches and boles in burned mature forest influence the soil. A conceptual model of soil C and N response following wildfire must include legacy influences resulting from prefire ecosystem structures. Integration of this conceptual model into mathematical models may improve quantitative forecasts of postwildfire C and N budgets.

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