CSIRO PUBLISHING

RESEARCH PAPER
https://doi.org/10.1071/WF21064

International Journal of WILDLAND FIRE
International Association of Wildland Fire

How interactions between wildfire and seasonal soil moisture fluxes drive nitrogen cycling in Northern Sierra Nevada forests

Mary K. Brady[A], Erin J. Hanan[A,*], Matthew B. Dickinson[B], Jessica R. Miesel[C,D], Laura Wade[A] and Jonathan Greenberg[A]

For full list of author affiliations and declarations see end of paper

***Correspondence to:**
Erin J. Hanan
Department of Natural Resources and Environmental Science, University of Nevada - Reno, Reno, NV, USA
Email: ehanan@unr.edu

Received: 14 May 2021
Accepted: 2 June 2022
Published: 8 July 2022

Cite this:
Brady MK *et al.* (2022)
International Journal of Wildland Fire
31(8), 786–798. doi:10.1071/WF21064

ABSTRACT

As wildfires become larger and more severe across western North America, it grows increasingly important to understand how they will affect the biogeochemical processes influencing ecosystem recovery. Soil nitrogen (N) cycling is a key process constraining recovery rates. In addition to its direct responses to fire, N cycling can also respond to other post-fire transformations, including increases or decreases in microbial biomass, soil moisture, and pH. To examine the short-term effects of wildfire on belowground processes in the northern Sierra Nevada, we collected soil samples along a gradient from unburned to high fire severity over 10 months following a wildfire. This included immediate pre- and post-fire sampling for many variables at most sites. While season and soil moisture did not substantially alter pH, microbial biomass, net N mineralisation, and nitrification in unburned locations, they interacted with burn severity in complex ways to constrain N cycling after fire. In areas that burned, pH increased (at least initially) after fire, and there were non-monotonic changes in microbial biomass. Net N mineralisation also had variable responses to wetting in burned locations. These changes suggest burn severity and precipitation patterns can interact to alter N cycling rates following fire.

Keywords: fire, nitrogen cycling, post-fire soil properties, pre- and post-fire sampling, Sierra Nevada, soil, soil biogeochemistry, soil timeseries, Walker Fire, wildland fire.

Introduction

Wildfires shape coniferous forests across western North America, in part through their effects on soil biogeochemical processes such as nitrogen (N) cycling (Knelman *et al.* 2015; Alcañiz *et al.* 2018). Although such belowground processes can vary substantially following fire, two trends stand out as particularly robust: increases in pH, and accelerated net N mineralisation and nitrification (Certini 2005; Neary *et al.* 2005; Hanan *et al.* 2016*b*; Alcañiz *et al.* 2018). The magnitude of these increases generally grows with burn severity (DeLuca *et al.* 2006; Verma and Jayakumar 2012; Alcañiz *et al.* 2018; Kranz and Whitman 2019). However, we still lack a strong mechanistic understanding of how wildfire and other environmental factors interact to influence biogeochemical cycles as ecosystems recover.

There are several interconnected processes that influence net N mineralisation and nitrification rates after fire. For one, fire increases soil pH by (1) depositing ash and char on soil surfaces, which are rich in ammonium (NH_4^+), readily decomposable organic N, and base-forming cations, and (2) destroying organic acids in surface soils (Hanan *et al.* 2016*b*). Increases in soil pH can in turn increase nitrification rates by increasing the ratio of ammonia (NH_3) to NH_4^+, which is the N substrate used by nitrifying bacteria and archaea (Prosser 1990; De Boer and Kowalchuk 2001; Hanan *et al.* 2016*b*). However, other factors can counteract increases in N availability. For example, readily decomposable materials deposited on soil surfaces with ash can stimulate heterotrophic microbial biomass, which has been linked with N immobilisation in N-limited ecosystems (Aoyama and Nozawa 1993; Gallardo and Schlesinger 1995). Additionally, even though fire typically increases immediate N availability, it also oxidises, volatilises, and transports N away from burned ecosystems, which over time can reduce N supply to plants and microbes.

Fire characteristics such as energy release affect many tangible changes to forest systems post-fire, including the degree of forest floor combustion, ash and char deposition, and the presence and depth of hydrophobic soil layers (Gustine *et al.* 2022). These effects can influence the extent to which fire affects biogeochemical processes and which processes dominate in a given location (Neary *et al.* 1999; González-Pérez *et al.* 2004; Knicker 2007; Knelman *et al.* 2015; Whitman *et al.* 2019). Because direct measurements of fire characteristics are challenging to obtain across large spatial scales, burn severity metrics are frequently used to indirectly categorise the extent to which fire transforms an ecosystem or landscape. Generally, the severity metric is a category: low, moderate, or high severity. The categories are based primarily on the amount of charring and combustion evident in the vegetation and surface soils (Turner *et al.* 1994; Keeley 2009).

It is extremely challenging to directly link or model relationships between burn severity categories and below-ground N cycling because wildfires are complex and rarely provide opportunities to compare homologous burned and unburned areas. Despite the importance of quantifying how fire affects N dynamics, few wildfire studies have true pre-fire samples, and instead rely on space-for-time substitutions, which increases uncertainty in a variety of ways. For instance, because soil properties can vary at fine spatial scales (e.g. less than 30 m; Campbell 1978; Ste-Marie and Paré 1999; Morgan *et al.* 2014), chronosequences (e.g. comparing recently burned, young, and mature stands) confound spatial and temporal differences among sites. Ignoring spatial variation is problematic because site heterogeneity can have a strong effect on soil processes following fire, sometimes even stronger than the fire itself (Kranz and Whitman 2019; Santos *et al.* 2019). Other studies have relied on opportunistic pre-fire samples that were intended for another use before a study area burned (Homann *et al.* 2011; Pingree *et al.* 2012). However, in many cases, these samples had been collected weeks, months, or even years before the fire, which can confound the effects of fire with other environmental drivers, such as weather and hydrology.

In addition to the difficulties associated with pre-fire sampling, sampling immediately after wildfire is challenging because of safety and access limitations. As a result, many studies rely on longer post-fire time intervals. In these studies, the first post-fire sampling may not occur until weeks or months after fire, even in the case of prescribed burns (Stephens *et al.* 2004; Weber *et al.* 2014; Kranz and Whitman 2019). These time-lags in post-fire sampling may cause researchers to miss ephemeral changes that occur immediately after fire. However, such changes may still influence ecosystem N budgets and post-fire recovery trajectories, particularly following low severity burns where compounding effects of multiple fires are likely to occur (Pellegrini *et al.* 2021).

This case study uses a combination sampling approach with both immediate pre- and post-fire samples, in addition to unburned control areas, to circumvent many of the uncertainties associated with space-for-time substitutions and long time-lags between pre- and post-fire sampling (Supplementary Fig. S1). We studied the Walker Fire, which burned in Plumas National Forest, CA in 2019, by sampling within 4 days before and after the fire burned a given location, as well as 1.5, 6, and 9 months after the fire. We sampled sites that did not burn in the Walker Fire, and sites that burned at low, moderate, and high severities. We measured soil characteristics including pH, microbial biomass, total C:N ratios, water content, NH_4^+, nitrite (NO_3^-), and net N mineralisation and nitrification rates to address two questions: (1) how does N cycling change with burn severity in the first year following this fire? And (2) does this sampling design provide unique data to advance methodology for future research?

Methods

Site description

The northern Sierra Nevada experiences a mediterranean climate, with more than half its annual precipitation falling mostly as snow in January, February, and March (van Wagtendonk *et al.* 2018). Summer precipitation, when it occurs, often comes as afternoon thunderstorms, and annual precipitation is approximately 125 cm. Average summer high temperatures are 25°C and winter high temperatures are −5°C. The portion of Plumas National Forest included in this study is *Pinus ponderosa* (Douglas ex C. Lawson) dominated, with some *Calocedrus decurrens* (Torr.) Florin and infrequent lower montane conifers such as *Pinus lambertiana* Douglas (van Wagtendonk *et al.* 2018). Understory vegetation is grass and forb dominated with few shrubs. The soils are either sandy, mixed, frigid Entic Xerumbrepts (for plots C1 and C2, described below), mixed, frigid Dystric Xeropsamments (for plots L1, L2, and M1), or clayey, smectitic, frigid, shallow Typic Argixerolls (for plots C3 and H1; NRCS and UC Davis 2020). Sampling site aspect varied, and slope ranged from <5 to 17°. The site elevations ranged from 1650 to 1700 m above sea level.

Sampling design

The Walker Fire burned in Plumas National Forest, California in September 2019. It burned approximately 55 000 acres from September 4 to 15 (Fig. 1; Dickinson *et al.* 2019). While the fire was active, the US Forest Service Fire Behavior Assessment Team (FBAT) sampled six plots prior to fire arrival at those sites. The plot size, 30 m by 30 m, was established for vegetation and fuel surveys in a complementary study (Greenberg, unpublished). The plots were selected

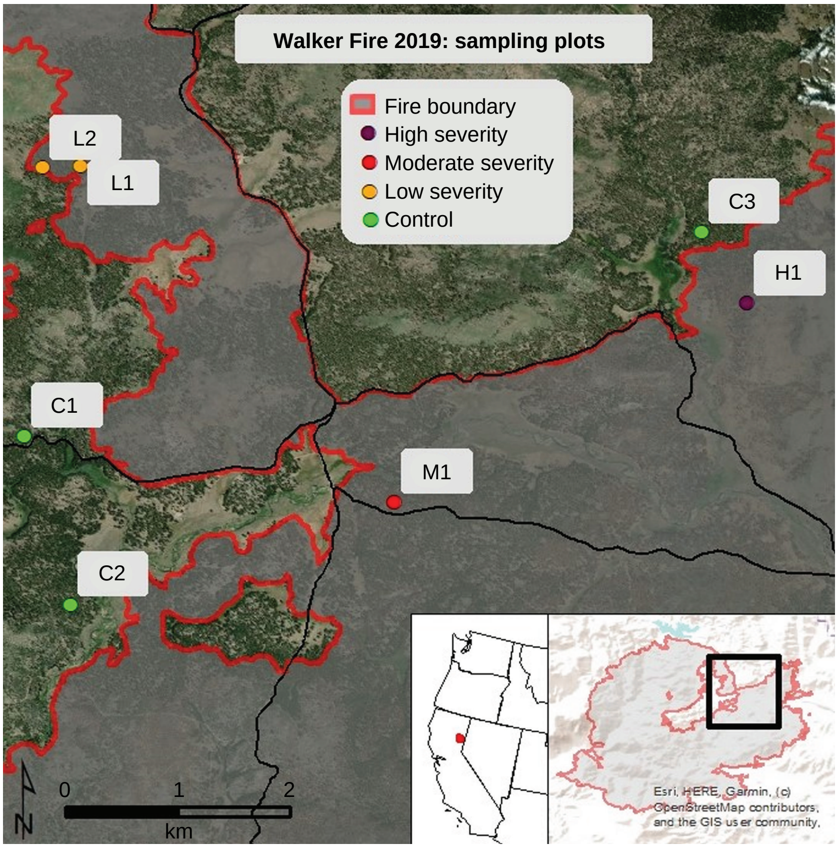

Fig. 1. Map of plot locations and Walker Fire perimeter in the vicinity of Murdoch Crossing Spring, Plumas National Forest, CA. Coordinates for the southwest corner of each plot are given in Supplementary Table S4.

Table 1. Plots and number of replicate sampling locations per burn severity category and at each sampling event.

Severity category	Plot names (FBAT plot numbers)	Number of samples				
		Immediately pre-fire	Immediately post-fire	1.5 months post-fire	6 months post-fire	9 months post-fire
Control	C1 (2)	9	0	9	9	9
	C2 (3)					
	C3 (7)					
Low severity	L1 (4)	6	6	6	6	6
	L2 (5)					
Moderate severity	M1 (8)	3	3	3	3	3
High severity	H1 (NA)	0	0	0	3	3

Three sampling locations were nested within each plot. Sampling locations were treated as replicates within a burn severity category and plot was treated as a random effect. The sampling timeline covers immediately pre-fire through 9 months after the fire. 'Plot names' shows the plot names used in this study alongside their respective plot numbers from the FBAT report; plot H1 was not included in that report.

based on ease of access and a high likelihood of burning within a few days. For the sake of continuity with the FBAT datasets and report (Dickinson *et al.* 2019), Table 1 cross references our plot names (named for burn severity categories) with their FBAT plot numbers (numbered in the order sampled).

Severity categories were assessed visually using the mixed conifer forest classification system described in Parson *et al.* (2010): in low severity areas, fire charred the surface litter and partially consumed fine fuels; in moderate burn severity areas, fire consumed most of the fine fuels and scorched most tree canopies; and finally, in high burn severity areas, fire completely consumed surface and understory fuels and nearly or completely consumed canopies (i.e. no needles or leaves remained; Parson *et al.* 2010).

Plots L1 and L2 burned at low severity and plot M1 burned at moderate severity. Plot H1, added to the study in the spring following the fire, burned at high severity and was likely a crown fire (Supplementary Fig. S2). Plots C1, C2, and C3 did not burn and will be referred to as control locations (Supplementary Fig S2; Table 1). We did not observe ash or char in the control sites; there were small amounts of char in low severity sites, thin layers of ash and char scattered throughout sites that burned at moderate severity, and more substantial ash and char in sites that burned at high severity.

There were three sampling locations per plot – one in the northeast, one in the southeast, and one in the southwest corner, except for plot C1, which was always sampled in the centre of the plot instead of the southeast corner. Each time a location was re-sampled, the sample was within 1 m of the original, pre-fire sample, but did not overlap with previous sampling. Plot level data on land-use history, fuel loading, and stand assessments can be found in Supplementary Tables S1–S3.

We focused on mineral soils because forest floor consumption was inconsistent, ranging from no combustion in the control locations to almost completely consumed in the moderate and high severity sampling locations. At each sampling location, fifteen 3.5 cm diameter by 5 cm depth mineral soil cores were collected from within a 30 cm diameter sampling ring. Samples were kept cool and brought back to the laboratory for immediate processing and analysis.

Pre-fire and immediate post-fire samples were collected over the course of 1 week. All pre-fire sampling occurred over 4 days and, in the locations that burned, no more than 4 days prior to fire arrival. Immediate post-fire samples were collected within 3 days of burning. Samples were then collected at 1.5, 6, and 9 months post-fire at the burned and unburned locations (Table 1; see Supplementary Fig. S3 for weather at sample collection times). Sample collection at 6 months post-fire occurred during the spring snowmelt.

Laboratory analysis

In the laboratory, soils were sieved using a 4.7 mm mesh. Samples were then composited by sampling location, and homogenised such that subsamples used for each of the laboratory analyses would be equivalent. We determined water-holding capacity and fractional water content by weighing 10 g field moist subsamples, then saturating them with water. We dried them at 58°C for 48 h, at which point all samples had reached a constant mass. Water-holding capacity was calculated as saturated weight minus dry weight divided by dry weight. Fractional water content, the water fraction of the field moist sample weight, was determined by subtracting dry weight from field wet weight then dividing by field wet weight. Soil pH was measured by adding deionised water to 10 g field moist soil subsamples to create a 1:1 ratio slurry. We recorded pH using a Fisher Scientific AE 150 pH meter.

Heterotrophic microbial biomass was estimated using substrate induced respiration (SIR) in a method adapted from West and Sparling (1986). We added 1.67 mL of a 12 g L^{-1} glucose/deionised water solution to each soil sample, and measured the CO_2 concentrations immediately and then again after 4 h. We measured the CO_2 concentration in the headspace of the sealed jars by using a glass syringe to extract air samples through septa in the jar lids then fed those samples through a LiCOR infrared gas analyser. The change in CO_2 concentration was converted to μg carbon (C) per gram of dry soil per hour. Although it is not a direct measure of microbial abundance, SIR rates strongly correlate with estimates from direct chloroform fumigation methods (Fierer 2003), and therefore provide a useful index for relative changes in heterotrophic microbial biomass (West and Sparling 1986; Beare *et al.* 1990; Bailey *et al.* 2002).

To estimate net N mineralisation and nitrification rates at field moisture conditions, we incubated a set of 10 -g field moist subsamples from each sampling location for 1 week. The second and third incubations, 1-week wetted and 3-week wetted, were incubated at 40% water holding capacity for 1 and 3 weeks, respectively. When field moisture was above 40% water holding capacity, no water was added to the wetted incubations and the soils were incubated at their field moisture. This situation occurred in 7 of the 21 samples collected during the spring snowmelt at 6 months post-fire. To maintain humidity levels, we added approximately 2 cm of water to the jars that contained the vials of soil. Weights from individual tubes did not change significantly during the incubations. No incubations were conducted for the immediate pre- or post-fire samples.

The field-moist incubations provide rates of net N mineralisation (total inorganic N; change in μg NH_4^+ and NO_3^-) and nitrification (change in μg NO_3^-) at field moisture conditions. The rate from 1-week long wetted incubations provides clues about the soil microbial community composition by removing any water or diffusion limitations. The rate for the 3-week long wetted incubations, compared with the 1-week wetted incubations, can provide insights into microbial biomass dynamics and resource availability by showing how a prolonged release from water limitation can affect NH_4^+ and NO_3^- cycling.

We determined available NH_4^+ and NO_3^- concentrations for all incubated and unincubated (time = 0) samples by extracting the soil samples in 2 M potassium chloride (KCl; 40 mL) for 2 h, then vacuum filtering through a glass fibre filter (Pall Gelmann Type A/E 1.0 μm). The extractants were measured using UV absorbance at 650 nm for NH_4^+ and 540 nm for NO_3^- with a plate reader to determine the μg NH_4^+ and μg NO_3^- per g dry soil (Hood-Nowotny *et al.* 2010). Daily net N mineralisation rates were calculated as the amount of inorganic N at the end of a given week divided by seven. For the week-long incubations, the time zero extraction, immediately after collection in the field, was the starting value. For the 3-week incubations, the value at the end of the second week was the starting value. This enabled us to isolate what occurred in the third week of the incubation from the N cycling that occurred in the first and second weeks. Net nitrification rates were determined analogously but using only NO_3^-.

We were unable to assess net N mineralisation and nitrification rates immediately pre- and post-fire due to logistical constraints. A timeline of which soil properties were assessed at each sampling event is included in Supplementary Table S4.

Statistical approach

To examine the extent to which soil characteristics varied among locations that experienced different burn severities, we used linear mixed effects models. For each soil characteristic, we compared burn severity categories within a sampling event and sampling events within a burn severity category, and assessed interactions between burn severity and sampling events (time since fire). We used each soil characteristic as a response variable. Burn severity and sampling event were fixed effects and plot was a random effect, because (1) plots were randomly located within each severity level, (2) soil characteristics can vary significantly at distances smaller than the distance between our sampling locations (i.e. 30 m; Campbell 1978; Hudak *et al.* 2007; Morgan *et al.* 2014), and (3) plot had no significant effect on any of the soil characteristics we measured before the fire (Table 2). Each sampling location was a replicate within a given burn severity category. Due to the low sample size, we would not extrapolate these results to other locations, but this approach enabled us to assess fire-induced changes across burn severity categories on the Walker Fire and the utility of immediate sampling events before and after wildfires. High severity was not included in the third analysis due to the short sampling timeline at those locations, and the immediate post-fire sampling event was excluded because the control sampling locations were not sampled at that time.

All statistics were run in R version 4.0.3 (R Core Team 2020), using the following packages: ggplot2 (Wickham 2016), nlme (Pinheiro *et al.* 2020), car (Fox and Weisberg 2018), lme4 (Bates *et al.* 2015), RLRsim (Scheipl *et al.* 2008), and multcomp (Hothorn *et al.* 2008). Due to the relatively small sample sizes, normality of residuals was assessed visually using histograms. We used an alpha of 0.1 to determine statistical significance in all analyses to offset the risk of type II errors due to low sample size.

Results

Plot effects

Soil characteristics did not vary significantly by plot before the fire (Table 2). Following fire, plot affected various soil characteristics at times, but significant effects were not consistent and confounded with spatial patterns of the fire in the low severity category (Table 2).

Soil moisture and pH

Immediately post-fire, low and moderate severity sampling locations had high fractional water content following the fire-ending rain. At 6 months post-fire, during the spring thaw, all sampling locations had high fractional soil water content (Fig. 2, Supplementary Table S5).

The sampling event–severity interaction had a significant effect on soil pH ($P < 0.01$; Supplementary Table S6). Soil pH increased by about 0.5 pH unit immediately after the fire in both low and moderate severity sampling locations (Fig. 3, Supplementary Table S5). In moderate severity locations, pH continued to increase until 1.5 months after the fire while low severity locations levelled off after the immediate post-fire sampling event. High severity had the highest pH of all categories at 6 and 9 months after the fire. The control sampling locations' pH changed less than any of the burned sites (Fig. 3, Supplementary Table S5).

Microbial biomass

The sampling event–severity interaction also significantly affected estimated microbial biomass ($P < 0.01$; Supplementary Table S6). The control locations had minimal

Table 2. *P*-values for restricted likelihood ratio tests (RLRT) for plot effects.

	Imm. pre-fire		Imm. post-fire		1.5 months post-fire		6 months post-fire		9 months post-fire	
	All plots	Control	Low sev.	Low sev.	Control	Low sev.	Control	Low sev.	Control	Low sev.
Water content	0.41	0.34	1.00	0.37	0.25	0.19	0.42	1.00	**0.09**	0.37
pH	0.42	1.00	1.00	0.24	0.36	0.34	**0.02**	**<0.01**	0.10	0.37
Microbial biomass	0.35	**0.02**	1.00	1.00	0.28	0.34	0.42	1.00	**0.07**	0.16
NH_4^+	0.34	0.42	1.00	0.36	**0.02**	0.29	0.42	**<0.01**	0.28	**0.07**
NO_3^-	0.31	1.00	1.00[A]	1.00	1.00	0.14	0.25	0.14	1.00	0.26

Control locations were not sampled immediately post-fire. Values less than 0.1 are bolded and indicate that plot had a significant effect on the soil characteristic. Value of 1 indicates that the RLRT statistic was equal to 0 – model fit with the null and alternative hypothesis were indistinguishable. NH_4^+ and NO_3^- refer to the available NH_4^+ and NO_3^- at the time the sample was collected.

[A]This ratio test was designated not calculated as 1.00, because the concentrations were all zero.

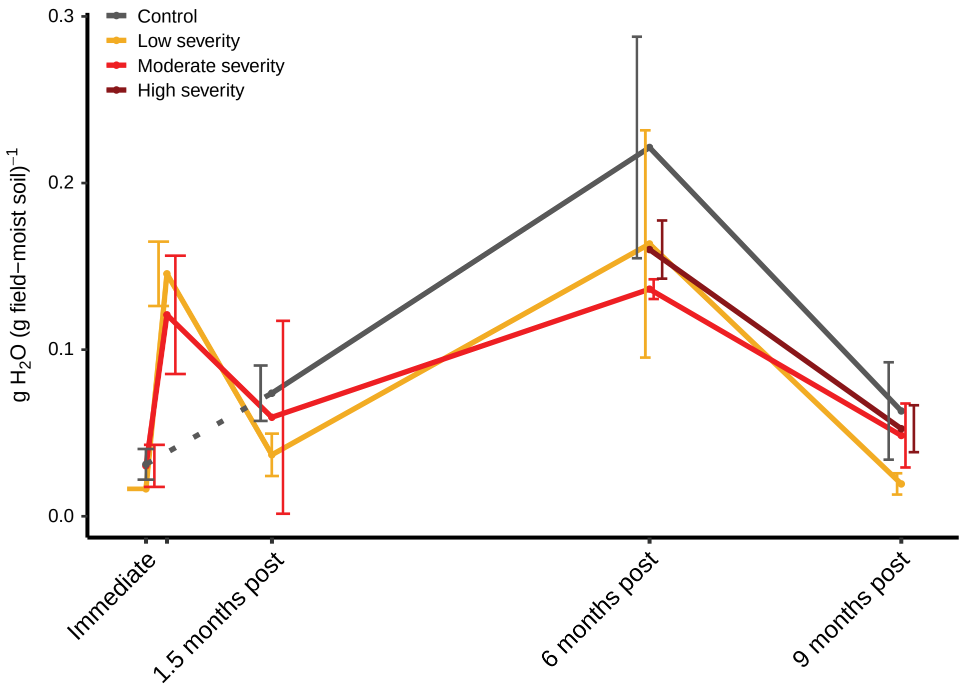

Fig. 2. Fractional water content of field-moist soils from the four burn severity categories over time. The *x*-axis is scaled with time. The two tick marks labelled 'immediate' are immediately pre- and post-fire samples. Control sites were not sampled immediately post-fire. Error bars show standard deviation within severity categories.

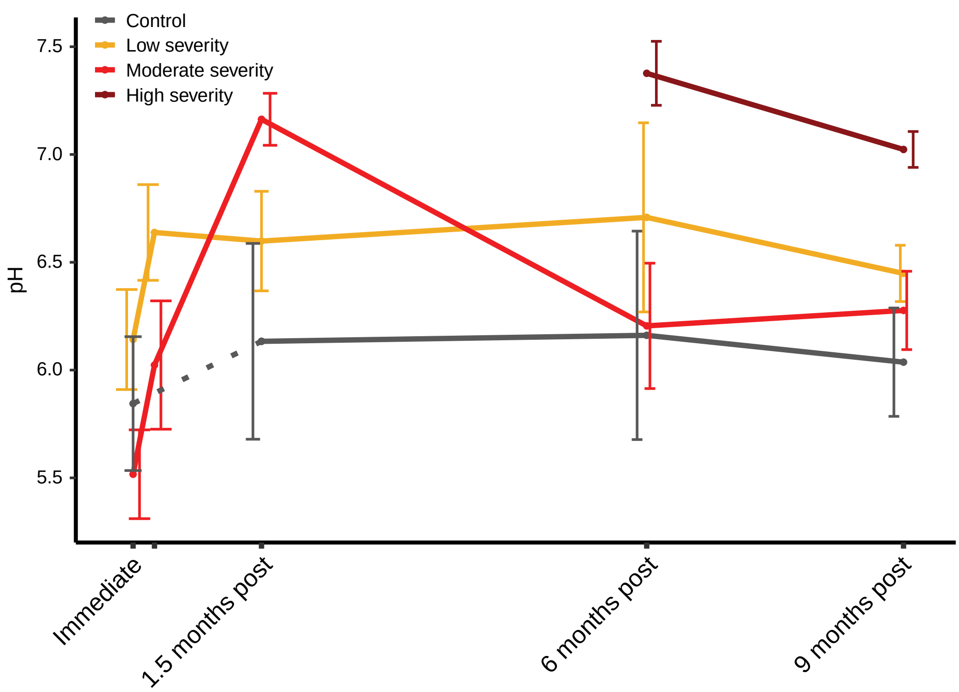

Fig. 3. Soil pH values over time from the four burn severity categories. The *x*-axis is scaled with time. The two tick marks labelled 'immediate' are immediately pre- and post-fire samples. Control (unburned) sites were not sampled immediately post-fire. Error bars show standard deviation within severity categories.

changes in microbial biomass estimates after an initial decrease at 1.5 months after the fire. Estimated microbial biomass had a non-monotonic response in the burned locations: immediately following fire, microbial biomass estimates decreased in low severity sampling locations by 74% and increased by 70% in moderate severity locations (Fig. 4, Supplementary Table S5). Estimated microbial biomass in the low severity samples levelled off whereas moderate severity plots increased through 1.5 months post-fire before declining. At 6 and 9 months after fire, high severity locations had the highest estimated microbial biomass of any severity category (Fig. 4, Supplementary Table S5).

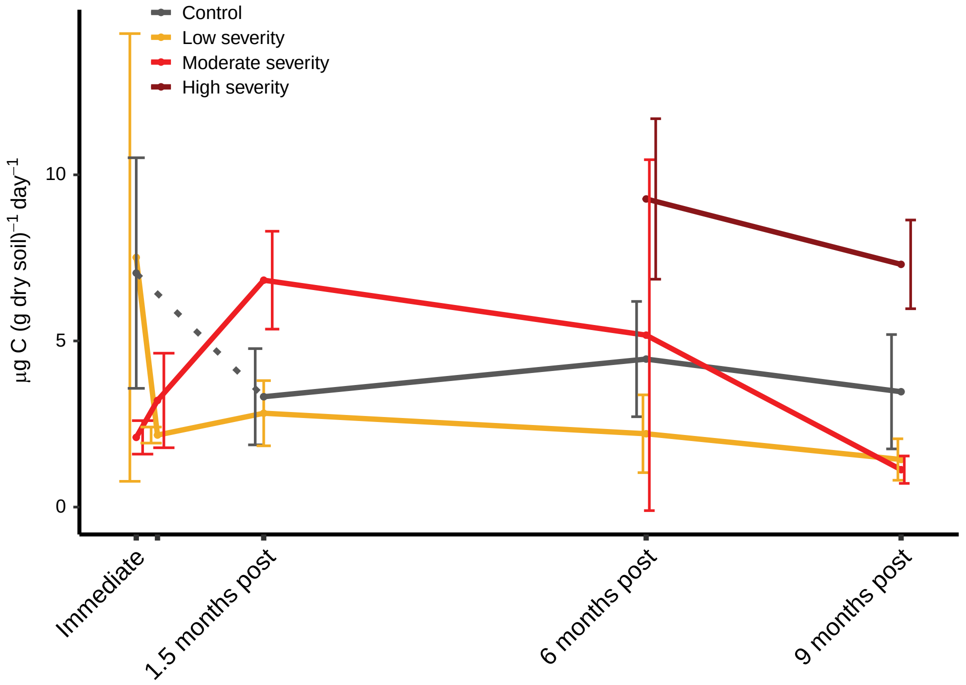

Fig. 4. Microbial biomass was estimated via substrate induced respiration. Respiration was measured before and after a 4-h incubation with glucose. The *x*-axis is scaled with time. The two tick marks labelled 'immediate' are immediately pre- and post-fire samples. Control (unburned) sites were not sampled immediately post-fire. Error bars show standard deviation within severity categories.

Net N mineralisation

The sampling event–severity interaction had a significant effect on rates of net N mineralisation in the field-moist incubations ($P = 0.02$; Supplementary Table S6). High severity sampling locations were the only locations with positive net mineralisation rates in the field-moist incubations at rates 0.9 μg inorganic N g^{-1} dry soil day^{-1} for both 6 and 9 months post-fire (Fig. 5, Supplementary Table S5). The field-moist incubations for the control sampling locations exhibited some net immobilisation but they did not substantially differ from zero at any sampling event (Fig. 5, Supplementary Table S5). The low severity locations had rates similar to the control sites, differing most at 1.5 months post-fire when low severity locations were 0.08 μg inorganic N g^{-1} dry soil day^{-1} lower than the control locations. The moderate severity locations, on the other hand, had lower net mineralisation rates than the control and low severity sampling locations at all sampling events although the difference decreased over time post-fire as the rates at moderate severity locations rates increased. Only the high severity locations had net N mineralisation rates (in field-moist incubations) that were substantially different from the control rates at any time, with rates 1 μg of inorganic N g^{-1} dry soil day^{-1} higher than those in the control locations at both 6 and 9 months post-fire (Fig. 5).

The addition of water caused different responses among the burned categories. Although the control locations showed little response to the water additions in the 1- and 3-week wetted incubations, net mineralisation increased for the low severity samples following water addition, on average by 0.37 μg inorganic N g^{-1} dry soil day^{-1} for 1-week and 1.30 μg inorganic N g^{-1} dry soil day^{-1} for 3-week incubations (Fig. 5). In contrast, the moderate severity locations had a non-monotonic reaction to water additions, where net mineralisation rates slightly increased in the 1-week incubations, and decreased substantially in the 3-week incubations, dropping to -3.82 μg inorganic N g^{-1} dry soil day^{-1} at 9 months post-fire (Fig. 5). The moderate severity samples showed stronger, although negative, responses in net mineralisation rates in the 3-week water incubations than the low severity throughout the study. Net mineralisation rates were highly variable in the incubations for soils that burned at high severity with the lowest rate at -7.30 μg inorganic N g^{-1} dry soil day^{-1} for the 3-week incubation at 6 months post-fire and the highest rate at 2.98 μg inorganic N g^{-1} dry soil day^{-1} for the 3-week incubation at 9 months post-fire (Fig. 5, Supplementary Table S5). The sampling event–severity interaction had a significant effect on net N mineralisation rates in the 1-week wetted incubations and severity had a significant effect on rates in the 3-week wetted incubations ($P < 0.01$, < 0.01; Supplementary Table S6).

Net nitrification

The sampling event–severity interaction had a significant effect on the field-moist incubation net nitrification rates ($P < 0.01$; Supplementary Table S6). The control sampling locations had net nitrification rates for the field-moist incubations that did not differ significantly from zero over the course of the study (Fig. 6, Supplementary Table S5). The low and moderate severity sampling locations did not differ substantially from the control sites at any point. The sampling locations that burned at high severity had the highest

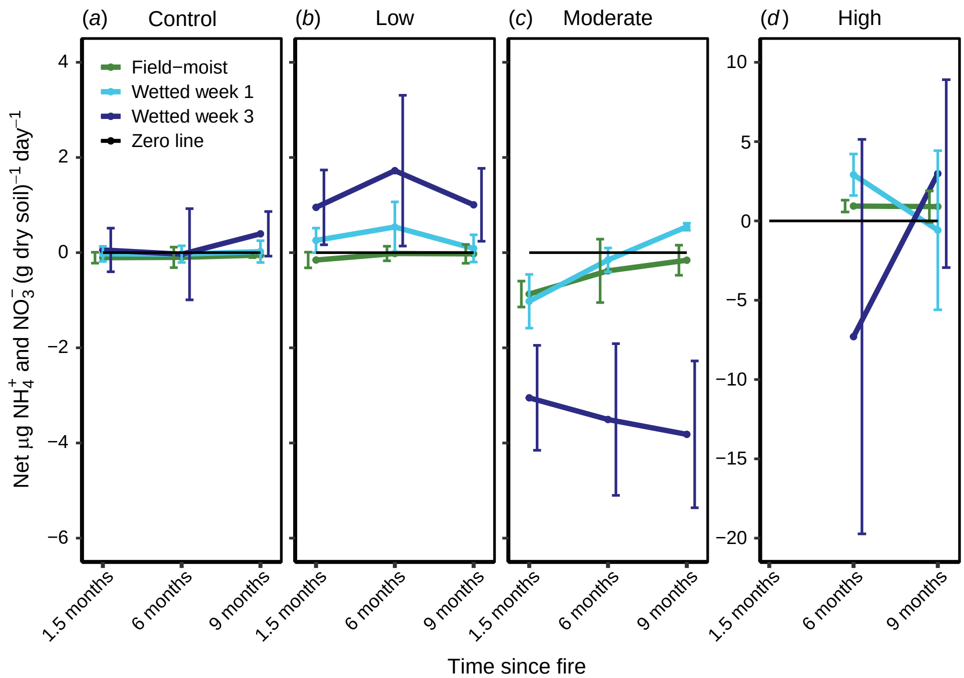

Fig. 5. Mean net N mineralisation (μg NH_4^+ plus NO_3^-) per gram dry soil per day for the weeklong field moist incubations, the 1-week 40% water holding capacity incubations (wetted week one), and the 3-week 40% water holding capacity incubation (wetted week three) for the four burn severity categories. The error bars show standard deviation within the burn severity category. (*a*) Control sampling locations, (*b*) Low severity sampling locations, (*c*) Moderate severity sampling locations, and (*d*) High severity sampling locations; note different *y*-axis scale. Negative numbers indicate net immobilisation.

net nitrification rate for the field-moist incubations at 6 months and the lowest rate at 9 months after fire (Fig. 6, Supplementary Table S5).

Sampling event, severity, and the sampling event–severity interaction did not significantly affect the 1-week wetted incubation net nitrification rates ($P = 0.91$, 0.57, 0.75 respectively; Supplementary Table S6). However, the sampling event–severity interaction did significantly affect net nitrification rates in the 3-week wetted incubation ($P = 0.01$; Supplementary Table S5). The control sampling locations had the lowest nitrification rates for both the 1- and 3-week incubations with values ranging from 0.00 to 0.41 μg NO_3^- g^{-1} dry soil day^{-1} (Fig. 6, Supplementary Table S5). The low severity locations had slightly higher net nitrification rates than the control locations. Low severity values were mostly within 0.2 μg of the control rates but got as high as 1.10 μg NO_3^- g^{-1} dry soil day^{-1} more than the control rates in the 1-week incubations at 9 months post-fire (Fig. 6, Supplementary Table S5). Moderate severity locations, by contrast, typically had lower net nitrification rates than either the control or low severity locations. The moderate severity rates ranged from −0.02 in the 1-week incubation at 6 months post-fire up to 0.08 μg NO_3^- g^{-1} dry soil day^{-1} in the 3-week incubation at 1.5 months post-fire. As with net mineralisation rates, net nitrification rates were highly variable for the high severity locations. The net nitrification rates were substantially higher in both the 1- and 3-week incubations at 6 months post-fire than they were at 9 months post-fire when the values dropped 2.91 μg NO_3^- g^{-1} dry soil day^{-1} for the 1-week incubation and 2.35 μg NO_3^- g^{-1} dry soil day^{-1} for the 3-week incubation (Fig. 6, Supplementary Table S5). The full suite of statistical results and additional analyses are described in Supplementary Section S3.

Discussion

Burn severity and seasonal precipitation and/or snowmelt can synergistically affect N cycling the our Northern Sierra Nevada mountains (Supplementary Table S6). Following fire, we found that N mineralisation rates changed compared to control sites but the magnitude and direction of those changes, and the extent to which mineral N was nitrified, varied non-monotonically with burn severity and soil moisture. In addition to water content, other seasonal variables – such as temperature and plant phenology – can influence post-fire soil processes (MacDonald *et al.* 1995; Sierra 1997; Ren *et al.* 2020). However, in many studies seasonal variables are often confounded with fire effects. In

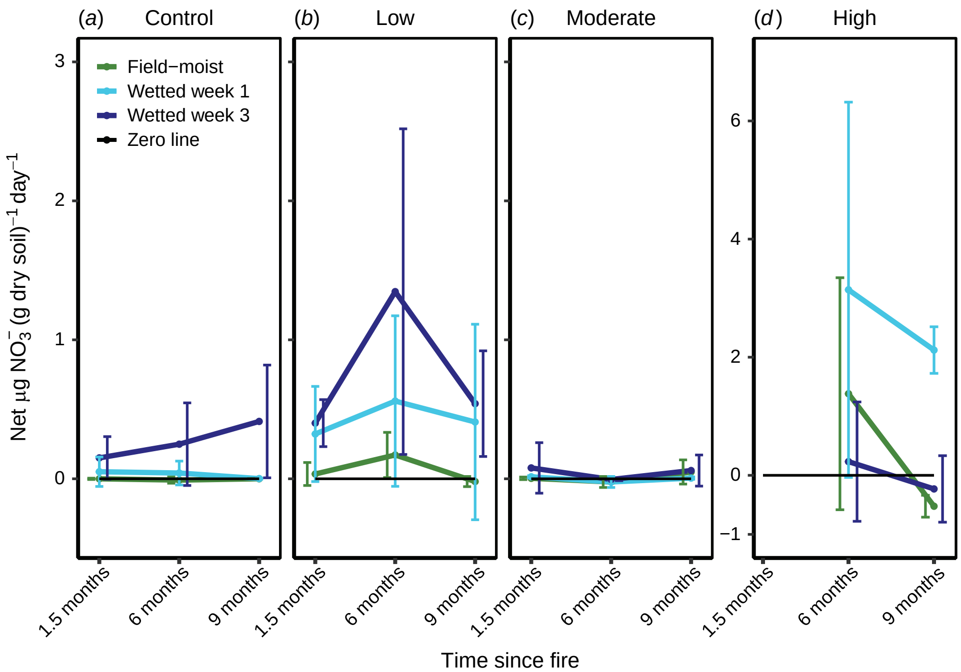

Fig. 6. Mean net nitrification (µg NO_3^-) per gram of dry soil per day for the weeklong field-moist incubations, the weeklong 40% water holding capacity incubations (wetted week one), and the 3-week long 40% water holding capacity incubation (wetted week three) for the four burn severity categories. The error bars show standard deviation. (*a*) Control sampling locations, (*b*) Low severity sampling locations, (*c*) Moderate severity sampling locations, and (*d*) High severity sampling locations; note different *y*-axis scale. Negative numbers indicate net nitrate immobilisation.

this study, we disentangled fire from other seasonal variables for many of the soil characteristics we investigated (i.e. soil moisture, pH, microbial biomass, and inorganic N) by comparing burned and unburned sites that had pre- and post-fire samples collected through different seasons. We found that moisture pulses had little effect on N cycling in unburned control locations, but had much larger effects in sites that burned (Fig. 5).

Net N mineralisation and nitrification

N oxidation, volatilisation, and the amounts of readily available N left on soil surfaces can vary with fire type (i.e. smoldering vs. crown-fire) and the movement of ash by wind and water post-fire (Grogan *et al.* 2000; Neary *et al.* 2005; Goodridge *et al.* 2018). As a result, N status immediately after fire can vary substantially among locations. Had we been able to measure N mineralisation and nitrification rates immediately post-fire, we may have seen variable short-term responses among sampling locations. However, the responses, 1.5 months after fire and beyond, showed consistently slow rates of net N immobilisation in the control, low severity, and moderate severity sampling locations incubated at field-moist conditions (net mineralisation rates ranged from −0.02 to −0.87 $\mu g\ g^{-1}$ dry soil day^{-1}). These findings suggest that any mobilised N was rapidly taken up by plants or immobilised by soil microbial biomass (in other words, N cycling was tight), despite the ash residues we observed following the fire (Fig. 5). We also found elevated net nitrification rates post-fire, particularly in locations that burned at low severity (Fig. 6). These findings suggest that, after fire, NH_4^+ is simultaneously being immobilised in some microsites, while being nitrified in others. These coupled processes can co-occur in locations where N-cycling is relatively tight (Schimel and Bennett 2004).

Microbial biomass

Microbial biomass in the low severity locations did not differ substantially from the control locations either before or after the fire, suggesting that low severity fire may not have lasting effects on microbial biomass, either through direct mortality or by providing nutrients from ash and char that can sustain a population boom. On the other hand, locations that burned at moderate severity experienced an initial spike followed by a decrease in microbial biomass after fire. This can result from an influx of C and N with ash and char that is deposited during and shortly after the fire followed by a crash when the carbon and nutrients from ash are depleted, which can occur in as little as 1 year (Hanan *et al.* 2016*a*). Elevated microbial biomass may explain why soils in locations that burned at moderate severity had consistently lower rates of net N cycling than those observed in control locations and those that burned at low severity. Elevated microbial biomass may have immobilised NH_4^+, thereby preventing increases in nitrification that could have otherwise resulted from elevated pH (Hanan *et al.* 2016*b*). These results are corroborated by studies that have identified strong microbial controls on N availability in fire-dominated coniferous forests (Vitousek and Melillo 1979; Turner *et al.* 2007).

Soil pH

Soil pH frequently increases following fire (Certini 2005; Alcañiz *et al.* 2018), which we observed in the low and moderate severity sampling locations (Fig. 3). This increase likely occurred because fires consume organic acids in the soil and deposit base-forming cations with ash residues (Certini 2005). We found that the pH increases in soils that burned at low severity occurred very quickly; values increased immediately after fire but levelled off by 1.5 months and remained elevated, approximately 0.5 pH units above pre-fire values, through 6 months post-fire (Fig. 3). Not all studies have found a pH change in mineral soil after low severity fires (Murphy *et al.* 2006; Knicker 2007; Alcañiz *et al.* 2018); however, in some cases this could have occurred because these studies sampled soils weeks to months after fire – because soil can act as a strong pH buffer, longer-term studies may sometimes miss immediate pH changes.

In soils that burned at moderate severity, pH increased over a longer period of time (through 1.5 months post-fire) and rose higher than in soils that burned at low severity (Fig. 3), perhaps because fire deposited more ash and char. However, this effect was still relatively short-lived: by 6 months post-fire, pH in moderate severity locations dropped below the values observed in locations that burned at low severity. Similarly, other studies have observed an increased magnitude of pH change with increasing burn severity (Certini 2005; Alcañiz *et al.* 2018).

Post-fire changes in pH play an important role in N cycling because pH regulates the conversion of NH_4^+ to ammonia (NH_3^-). Over the typical range of soil pH values, a one-unit increase in pH leads to a ten-fold increase in the NH_3^- to NH_4^+ ratio (De Boer and Kowalchuk 2001; Hanan *et al.* 2016b). Different nitrifiers are active at different pH levels (Prosser and Nicol 2012), but NH_3 is the preferred substrate for most nitrifying bacteria (Watson *et al.* 1989; Prosser 1990). Therefore, we would expect to see higher net nitrification rates when soil pH is elevated, even if the NH_4^+ availability does not change. We did not observe this pattern: although pH varied across burn severity and time post-fire, net nitrification rates remained steady within each severity group and incubation type (Figs 3, 6). The apparent lack of pH control suggests that the microbial controls discussed above may be strong enough to outstrip any pH-driven increases in net nitrification.

Soil moisture

Soils from the control sampling locations demonstrated almost no N cycling response to increased water availability in the laboratory incubations. This was surprising because, short of anoxic conditions that occur under saturated conditions, soils with higher water content typically exhibit increased net nitrification rates (Stark and Firestone 1995). These findings further suggest that N cycling is tight in mature stands in this system, which is consistent with rates observed in other conifer forests (Vitousek *et al.* 1979; Turner *et al.* 2007). N cycling was less consistent in wetted incubations for the burned locations. We observed consistent increases in net mineralisation following water addition in soil samples that burned at low severity and a non-monotonic response to water addition in samples that burned at moderate severity (increases in mineralisation rates after 1 week, decreases after 3 weeks; Fig. 5). These findings illustrate how complex the interactions among burn severity, precipitation, and N mineralisation can be. It is not surprising that greater levels of disturbance led to a larger change in N mineralisation rates; however, the direction of change varied with time and severity. Thus, understanding the processes controlling these responses requires further research.

High severity

The challenges in interpreting the data from the high severity locations reinforce the utility of sampling designs that incorporate immediate pre-fire sampling. The high severity samples had the most extreme values for post-fire pH and estimated microbial biomass in our study (e.g. pH of 7.4 and microbial respiration of 9.3 μg C g^{-1} dry soil h^{-1} at 6 months post-fire; Figs 3, 4, Supplementary Table S5). Further, N cycling rates were much more variable in sites that burned at high severity than in those that burned at lower severity (Figs 5, 6). Had we been able to sample these locations pre-fire, we would have baseline conditions to compare the post-fire values against. Without those samples, the extreme values and variability are intriguing but robust interpretation of changes and trends is impossible. Although we do have a set of control locations (plot C3) approximately 1.5 km away from H1, there is risk in assuming that because the locations are close together, they had similar pre-fire soil characteristics – this is a problematic assumption inherent in space-for-time studies. Without location specific pre-fire data, we cannot quantify the extent to which observed values were due to fire. Our results suggest that high severity fire may have far more dramatic effects on soil characteristics than low or moderate severity fires, which is important for understanding the effects of large fires with heterogeneous burn severity. We hope that future studies will be able to increase sampling in high severity areas and incorporate pre-fire samples to gain additional insight and clarity.

Even within high severity burns there can be a lot of heterogeneity due to fine-scale differences in fuel distribution, soil moisture, and fire residence time (Neary *et al.* 2005; Alcañiz *et al.* 2018). Estimates of severity are based primarily on visible changes to an area post-fire, a method not well suited to distinguishing differences in mineral soil heating, given that mineral soils themselves do not combust (Brady *et al.* 2022). The chance of grouping together soils that experienced different heating regimes increases with increasing burn severity – once the forest floor has combusted, there is little remaining organic matter to visually identify whether soils experienced more or less heat. Accordingly, the sampling locations in H1 may not have experienced the fire in the same manner, leading to the highly variable soil characteristics we observed. One way to circumvent the limitations associated with burn severity metrics would be to measure soil temperatures during fires and use those temperatures to create more meaningful categories. Recent research has developed methods to make soil temperature data easier to collect and model (Robichaud and Brown 2019; Brady *et al.* 2022).

Conclusion

Climate change is increasing the size and severity of fires across western North America (Westerling *et al.* 2006; van Mantgem *et al.* 2013; Hanan *et al.* 2021; Ren *et al.* 2022) and altering winter snowpack and precipitation (Howat and Tulaczyk 2005; Gergel *et al.* 2017; Hatchett *et al.* 2017). Thus, examining how fire and water availability influence post-fire N cycling is critical for understanding forest health and resilience in these systems. Although importance of rain in driving post-fire N cycling has long been established in the literature (Neary *et al.* 1999; Grogan *et al.* 2000; Certini 2005), in our study system, N cycling appears to be tight. In other words, we did not observe net N mineralisation or nitrification without recent fire. This does not necessarily mean that N is not cycling, but any N that is made available is rapidly taken up by plants and soil microbes. Because fire may have a stronger effect on N cycling than atmospheric deposition and leaching in semiarid systems (Johnson *et al.* 1998, 2009), it likely plays an important role in ecosystem N budgets.

While studies that look years-to-decades after fire offer valuable information about long-term recovery, this study provides a method for examining short-term responses, which are particularly important for low severity burns that can shape biogeochemical cycling of forest systems (Pellegrini *et al.* 2021). We found that fire and soil moisture interacted to generate pulses of N mineralisation that varied non-monotonically with increasing burn severity. These changes were particularly noteworthy juxtaposed against the control sampling locations, which exhibited minimal changes through time for any soil characteristic other than soil moisture, which changed with the weather and seasons. Although not all soil characteristics could be assessed before the fire, the consistency through time in the control sites and minimal pre-fire differences among sampling locations together support the finding that fire and soil moisture play a key role in N cycling in the early stages of ecosystem recovery.

Supplementary material

Supplementary material is available online.

References

Alcañiz M, Outeiro L, Francos M, Úbeda X (2018) Effects of prescribed fires on soil properties: a review. *Science of The Total Environment* **613–614**, 944–957. doi:10.1016/j.scitotenv.2017.09.144

Aoyama M, Nozawa T (1993) Microbial biomass nitrogen and mineralization-immobilization processes of nitrogen in soils incubated with various organic materials. *Soil Science and Plant Nutrition* **39**, 23–32. doi:10.1080/00380768.1993.10416971

Bailey VL, Peacock AD, Smith JL, Bolton H (2002) Relationships between soil microbial biomass determined by chloroform fumigation–extraction, substrate-induced respiration, and phospholipid fatty acid analysis. *Soil Biology and Biochemistry* **34**, 1385–1389. doi:10.1016/S0038-0717(02)00070-6

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**, 1–48. doi:10.18637/jss.v067.i01

Beare MH, Neely CL, Coleman DC, Hargrove WL (1990) A substrate-induced respiration (SIR) method for measurement of fungal and bacterial biomass on plant residues. *Soil Biology and Biochemistry* **22**, 585–594. doi:10.1016/0038-0717(90)90002-H

Brady MK, Dickinson MB, Miesel JR, Wonkka CL, Kavanagh KL, Lodge AG, Rogers WE, Starns HD, Tolleson DR, Treadwell ML, Twidwell D, Hanan EJ (2022) Soil Heating in Fire (SheFire): a model and measurement method for estimating soil heating and effects during wildland fires. *Ecological Applications* e2627. doi:10.1002/eap.2627

Campbell JB (1978) Spatial variation of sand content and pH within single contiguous delineations of two soil mapping units. *Soil Science Society of America Journal* **42**, 460–464. doi:10.2136/sssaj1978.03615995004200030017x

Certini G (2005) Effects of fire on properties of forest soils: a review. *Oecologia* **143**, 1–10. doi:10.1007/s00442-004-1788-8

De Boer W, Kowalchuk GA (2001) Nitrification in acid soils: micro-organisms and mechanisms. *Soil Biology and Biochemistry* **33**, 853–866. doi:10.1016/S0038-0717(00)00247-9

DeLuca TH, MacKenzie MD, Gundale MJ, Holben WE (2006) Wildfire-produced charcoal directly influences nitrogen cycling in Ponderosa Pine Forests. *Soil Science Society of America Journal* **70**, 448–453. doi:10.2136/sssaj2005.0096

Dickinson M, Loncar L, Reiner A, Dailey S, Bednarczyk J, Drake C, Gordon J, Heckel M, Kleckler B, Miesel J, Wade L (2019) 2019 Walker Fire, Plumas National Forest, Fire Behavior Assessment Team (FBAT) Report. US Forest Service 34.

Fierer N (2003) 'Stress Ecology and the Dynamics of Microbial Communities and Processes in Soil.' (University of California: Santa Barbara, CA, USA)

Fox J, Weisberg S (2018) 'An R Companion to Applied Regression', 3rd edn. (Sage Publications: Thousand Oaks, CA, USA)

Gallardo A, Schlesinger WH (1995) Factors determining soil microbial biomass and nutrient immobilization in desert soils. *Biogeochemistry* **28**, 55–68. doi:10.1007/BF02178061

Gergel DR, Nijssen B, Abatzoglou JT, Lettenmaier DP, Stumbaugh MR (2017) Effects of climate change on snowpack and fire potential in the western USA. *Climatic Change* **141**, 287–299. doi:10.1007/s10584-017-1899-y

González-Pérez JA, González-Vila FJ, Almendros G, Knicker H (2004) The effect of fire on soil organic matter – a review. *Environment International* **30**, 855–870. doi:10.1016/j.envint.2004.02.003
Goodridge BM, Hanan EJ, Aguilera R, Wetherley EB, Chen Y-J, D'Antonio CM, Melack JM (2018) Retention of nitrogen following wildfire in a chaparral ecosystem. *Ecosystems* **21**, 1608–1622. doi:10.1007/s10021-018-0243-3
Grogan P, Burns TD, Chapin III FS (2000) Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* **122**, 537–544. doi:10.1007/s004420050977
Gustine RN, Hanan EJ, Robichaud PR, Elliot WJ (2022) From burned slopes to streams: how wildfire affects nitrogen cycling and retention in forests and fire-prone watersheds. *Biogeochemistry* **157**, 51–68. doi:10.1007/s10533-021-00861-0
Hanan EJ, D'Antonio CM, Roberts DA, Schimel JP (2016*a*) Factors regulating nitrogen retention during the early stages of recovery from fire in coastal Chaparral ecosystems. *Ecosystems* **19**, 910–926. doi:10.1007/s10021-016-9975-0
Hanan EJ, Schimel JP, Dowdy K, D'Antonio CM (2016*b*) Effects of substrate supply, pH, and char on net nitrogen mineralization and nitrification along a wildfire-structured age gradient in chaparral. *Soil Biology and Biochemistry* **95**, 87–99. doi:10.1016/j.soilbio.2015.12.017
Hanan EJ, Ren J, Tague CL, Kolden CA, Abatzoglou JT, Bart RR, Kennedy MC, Liu M, Adam JC (2021) How climate change and fire exclusion drive wildfire regimes at actionable scales. *Environmental Research Letters* **16**, 024051. doi:10.1088/1748-9326/abd78e
Hatchett BJ, Daudert B, Garner CB, Oakley NS, Putnam AE, White AB (2017) Winter snow level rise in the northern Sierra Nevada from 2008 to 2017. *Water* **9**, 899. doi:10.3390/w9110899
Homann PS, Bormann BT, Darbyshire RL, Morrissette BA (2011) Forest soil carbon and nitrogen losses associated with wildfire and prescribed fire. *Soil Science Society of America Journal* **75**, 1926–1934. doi:10.2136/sssaj2010-0429
Hood-Nowotny R, Umana NH-N, Inselbacher E, Oswald-Lachouani P, Wanek W (2010) Alternative methods for measuring inorganic, organic, and total dissolved nitrogen in soil. *Soil Science Society of America Journal* **74**, 1018–1027. doi:10.2136/sssaj2009.0389
Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* **50**, 346–363. doi:10.1002/bimj.200810425
Howat IM, Tulaczyk S (2005) Climate sensitivity of spring snowpack in the Sierra Nevada. *Journal of Geophysical Research: Earth Surface* **110**, F04021. doi:10.1029/2005JF000356
Hudak AT, Morgan P, Bobbitt MJ, Smith AMS, Lewis SA, Lentile LB, Robichaud PR, Clark JT, McKinley RA (2007) The relationship of multispectral satellite imagery to immediate fire effects. *Fire Ecology* **3**, 64–90. doi:10.4996/fireecology.0301064
Johnson DW, Susfalk RB, Dahlgren RA, Klopatek JM (1998) Fire is more important than water for nitrogen fluxes in semi-arid forests. *Environmental Science & Policy* **1**, 79–86. doi:10.1016/S1462-9011(98)00008-2
Johnson DW, Miller WW, Susfalk RB, Murphy JD, Dahlgren RA, Glass DW (2009) Biogeochemical cycling in forest soils of the eastern Sierra Nevada Mountains, USA. *Forest Ecology and Management* **258**, 2249–2260. doi:10.1016/j.foreco.2009.01.018
Keeley JE (2009) Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* **18**, 116–126. doi:10.1071/WF07049
Knelman JE, Graham EB, Trahan NA, Schmidt SK, Nemergut DR (2015) Fire severity shapes plant colonization effects on bacterial community structure, microbial biomass, and soil enzyme activity in secondary succession of a burned forest. *Soil Biology and Biochemistry* **90**, 161–168. doi:10.1016/j.soilbio.2015.08.004
Knicker H (2007) How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry* **85**, 91–118. doi:10.1007/s10533-007-9104-4
Kranz C, Whitman T (2019) Short communication: surface charring from prescribed burning has minimal effects on soil bacterial community composition two weeks post-fire in jack pine barrens. *Applied Soil Ecology* **144**, 134–138. doi:10.1016/j.apsoil.2019.07.004
MacDonald NW, Zak DR, Pregitzer KS (1995) Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. *Soil Science Society of America Journal* **59**, 233–240. doi:10.2136/sssaj1995.03615995005900010036x
Morgan P, Keane RE, Dillon GK, Jain TB, Hudak AT, Karau EC, Sikkink PG, Holden ZA, Strand EK (2014) Challenges of assessing fire and burn severity using field measures, remote sensing and modelling. *International Journal of Wildland Fire* **23**, 1045–1060. doi:10.1071/WF13058
Murphy JD, Johnson DW, Miller WW, Walker RF, Blank RR (2006) Prescribed fire effects on forest floor and soil nutrients in a Sierra Nevada Forest. *Soil Science* **171**, 181–199. doi:10.1097/01.ss.0000193886.35336.d8
Neary DG, Klopatek CC, DeBano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. *Forest Ecology and Management* **122**, 51–71. doi:10.1016/S0378-1127(99)00032-8
Neary DG, Ryan KC, DeBano LF (2005) Wildland fire in ecosystems: effects of fire on soils and water. Gen Tech Rep RMRS-GTR-42-Vol4. Vol. 42, p. 262. (US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Ogden, UT) doi:10.2737/RMRS-GTR-42-V4
NRCS, UC Davis (2020) 'Web Soil Survey.' (California Soil Resources Lab)
Parson A, Robichaud PR, Lewis SA, Napper C, Clark JT (2010) Field guide for mapping post-fire soil burn severity. General Technical Report of the Rocky Mountain Research Station GTR-243. (US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Ft. Collins, CO, USA) doi:10.2737/RMRS-GTR-243
Pellegrini AFA, Caprio AC, Georgiou K, Finnegan C, Hobbie SE, Hatten JA, Jackson RB (2021) Low-intensity frequent fires in coniferous forests transform soil organic matter in ways that may offset ecosystem carbon losses. *Global Change Biology* **27**, 3810–3823. doi:10.1111/gcb.15648
Pingree MRA, Homann PS, Morrissette B, Darbyshire R (2012) Long and short-term effects of fire on soil charcoal of a conifer forest in southwest Oregon. *Forests* **3**, 353–369. doi:10.3390/f3020353
Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) nlme: linear and nonlinear mixed effects models. Available at https://CRAN.R-project.org/package=nlme
Prosser JI (1990) Autotrophic nitrification in bacteria. In 'Advances in Microbial Physiology'. (Eds AH Rose, DW Tempest) pp. 125–181. (Academic Press: New York, NY, USA) doi:10.1016/S0065-2911(08)60112-5
Prosser JI, Nicol GW (2012) Archaeal and bacterial ammonia-oxidisers in soil: the quest for niche specialisation and differentiation. *Trends in Microbiology* **20**, 523–531. doi:10.1016/j.tim.2012.08.001
R Core Team (2020) 'R: A Language and Environment for Statistical Computing.' (R Foundation for Statistical Computing: Vienna, Austria) Available at https://www.R-project.org/
Ren G, He M, Li G, Anandkumar A, Dai Z, Zou CB, Hu Z, Ran Q, Du D (2020) Effects of *Solidago canadensis* invasion and climate warming on soil net N mineralization. *Polish Journal of Environmental Studies* **29**, 3285–3294. doi:10.15244/pjoes/114237
Ren J, Hanan EJ, Abatzoglou JT, Kolden CA, Tague C(N)L, Kennedy MC, Liu M, Adam JC (2022) Projecting future fire regimes in a semiarid watershed of the inland northwestern United States: interactions among climate change, vegetation productivity, and fuel dynamics. *Earth's Future* **10**, e2021EF002518. doi:10.1029/2021EF002518
Robichaud P, Brown RE (2019) High temperature soil probe. Available at https://patents.google.com/patent/US20190072434A1/en
Santos F, Wymore AS, Jackson BK, Sullivan SMP, McDowell WH, Berhe AA (2019) Fire severity, time since fire, and site-level characteristics influence streamwater chemistry at baseflow conditions in catchments of the Sierra Nevada, California, USA. *Fire Ecology* **15**, 3. doi:10.1186/s42408-018-0022-8
Scheipl F, Greven S, Kuechenhoff H (2008) Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Computational Statistics & Data Analysis* **52**, 3283–3299. doi:10.1016/j.csda.2007.10.022
Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. *Ecology* **85**, 591–602. doi:10.1890/03-8002
Sierra J (1997) Temperature and soil moisture dependence of N mineralization in intact soil cores. *Soil Biology and Biochemistry* **29**, 1557–1563. doi:10.1016/S0038-0717(96)00288-X

Stark JM, Firestone MK (1995) Mechanisms for soil moisture effects on activity of nitrifying bacteria. *Applied and Environmental Microbiology* **61**, 218–221. doi:10.1128/AEM.61.1.218-221.1995
Ste-Marie C, Paré D (1999) Soil, pH and N availability effects on net nitrification in the forest floors of a range of boreal forest stands. *Soil Biology and Biochemistry* **31**, 1579–1589. doi:10.1016/S0038-0717(99)00086-3
Stephens SL, Meixner T, Poth M, McGurk B, Payne D (2004) Prescribed fire, soils, and stream water chemistry in a watershed in the Lake Tahoe Basin, California. *International Journal of Wildland Fire* **13**, 27–35. doi:10.1071/WF03002
Turner MG, Hargrove WW, Gardner RH, Romme WH (1994) Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *Journal of Vegetation Science* **5**, 731–742. doi:10.2307/3235886
Turner MG, Smithwick EAH, Metzger KL, Tinker DB, Romme WH (2007) Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences* **104**, 4782–4789. doi:10.1073/pnas.0700180104
van Mantgem PJ, Nesmith JCB, Keifer M, Knapp EE, Flint A, Flint L (2013) Climatic stress increases forest fire severity across the western United States. *Ecology Letters* **16**, 1151–1156. doi:10.1111/ele.12151
van Wagtendonk JW, Fites-Kaufman JA, Safford HD, North MP, Collins B (2018) Sierra Nevada bioregion. In 'Fire in California's Ecosystems'. (Eds JW van Wagtendonk, NG Sugihara, SL Stephens, AE Thode, KE Shaffer, JA Fites-Kaufman) pp. 249–279. (University of California Press) Available at https://www.fs.usda.gov/treesearch/pubs/60811
Verma S, Jayakumar S (2012) Impact of forest fire on physical, chemical and biological properties of soil: A review. In 'Proceedings of the International Academy of Ecology and Environmental Sciences' Vol 2(3), (Eds WJ Zhang et al.) pp. 168–176. (International Academy of Ecology and Environmental Sciences) Available at http://www.iaees.org/publications/journals/piaees/articles/2012-2(3)/impact-of-forest-fire.pdf
Vitousek PM, Melillo JM (1979) Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Science* **25**, 605–619. doi:10.1093/forestscience/25.4.605
Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. *Science* **204**, 469–474. doi:10.1126/science.204.4392.469
Watson SW, Bock E, Harms H, Koops HP, Hooper AB (1989) Nitrifying bacteria. In 'Bergey's Manual of Systematic Bacteriology'. pp. 1808–1834. (The Williams and Wilkins Co.: Baltimore, MD, USA) Available at https://ci.nii.ac.jp/naid/10030102901/
Weber CF, Lockhart JS, Charaska E, Aho K, Lohse KA (2014) Bacterial composition of soils in ponderosa pine and mixed conifer forests exposed to different wildfire burn severity. *Soil Biology and Biochemistry* **69**, 242–250. doi:10.1016/j.soilbio.2013.11.010
West AW, Sparling GP (1986) Modifications to the substrate-induced respiration method to permit measurement of microbial biomass in soils of differing water contents. *Journal of Microbiological Methods* **5**, 177–189. doi:10.1016/0167-7012(86)90012-6
Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* **313**, 940–943. doi:10.1126/science.1128834
Whitman T, Whitman E, Woolet J, Flannigan MD, Thompson DK, Parisien M-A (2019) Soil bacterial and fungal response to wildfires in the Canadian boreal forest across a burn severity gradient. *Soil Biology and Biochemistry* **138**, 107571. doi:10.1016/j.soilbio.2019.107571
Wickham H (2016) 'ggplot2: Elegant Graphics for Data Analysis.' (Springer-Verlag: New York, NY, USA)

Data availability. The data are permanently archived and viewable at the following link: https://osf.io/pharg/?view_only=52b9c411639b44afb9225bd57913390b.

Conflicts of interest. The authors declare no conflicts of interest.

Declaration of funding. Funding for this research was provided in part by the National Science Foundation grant DEB-1916658 and the USDA National Institute of Food and Agriculture, Hatch project 1018368.

Acknowledgements. The Fire Behavior Assessment Team (https://www.frames.gov/fbat/home) collected the immediate pre- and post-fire data on the Walker Fire that made this paper possible. Team members included Matthew Dickinson, Lisa Loncar, Alicia Reiner, Scott Dailey, Jerry Bednarczyk, Cedar Drake, Jarred Gordon, Maryjane Heckel, Barry Kleckler, Jessica Miesel, and Laura Wade. Carol Ewell made sure equipment and transport were ready for the assignment. The FBAT thanks incident staff and others for their support (please see the Walker Fire report: Dickinson et al. 2019).

Author affiliations
[A]Department of Natural Resources and Environmental Science, University of Nevada - Reno, Reno, NV, USA.
[B]US Forest Service, Northern Research Station, Delaware, OH 43015, USA.
[C]Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing, MI, USA.
[D]Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI, USA.