New Phytologist

Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed

Paul V. Dunnette[1], Philip E. Higuera[1], Kendra K. McLauchlan[2], Kelly M. Derr[1], Christy E. Briles[3] and Margaret H. Keefe[1]

[1]College of Natural Resources, University of Idaho, PO Box 441133, Moscow, ID 83844-1133, USA; [2]Department of Geography, Kansas State University, Manhattan, KS 66506, USA; [3]Department of Geography, University of Colorado at Denver, Denver, CO 80217-3364, USA

Author for correspondence:
Philip E. Higuera
Tel: +1 208 649 6034
Email: phiguera@uidaho.edu

Received: *31 January 2014*
Accepted: *31 March 2014*

New Phytologist (2014) **203:** 900–912
doi: 10.1111/nph.12828

Key words: biogeochemistry, disturbance, fire severity, nitrogen isotopes, paleoecology, *Pinus contorta*, Rocky Mountain National Park, subalpine forests.

Summary

- Wildfires can significantly alter forest carbon (C) storage and nitrogen (N) availability, but the long-term biogeochemical legacy of wildfires is poorly understood.
- We obtained a lake-sediment record of fire and biogeochemistry from a subalpine forest in Colorado, USA, to examine the nature, magnitude, and duration of decadal-scale, fire-induced ecosystem change over the past *c.* 4250 yr. The high-resolution record contained 34 fires, including 13 high-severity events within the watershed.
- High-severity fires were followed by increased sedimentary N stable isotope ratios ($\delta^{15}N$) and bulk density, and decreased C and N concentrations – reflecting forest floor destruction, terrestrial C and N losses, and erosion. Sustained low sediment C : N *c.* 20–50 yr post-fire indicates reduced terrestrial organic matter subsidies to the lake. Low sedimentary $\delta^{15}N$ *c.* 50–70 yr post-fire, coincident with C and N recovery, suggests diminishing terrestrial N availability during stand development. The magnitude of post-fire changes generally scaled directly with inferred fire severity.
- Our results support modern studies of forest successional C and N accumulation and indicate pronounced, long-lasting biogeochemical impacts of wildfires in subalpine forests. However, even repeated high-severity fires over millennia probably did not deplete C or N stocks, because centuries between high-severity fires allowed for sufficient biomass recovery.

Introduction

Predicted increases in fire activity under warmer and drier conditions (Pechony & Shindell, 2010; Westerling *et al.*, 2011) have raised concerns about interactions among climate, fire, and key ecosystem processes (Lavorel *et al.*, 2006). Fires release CO_2 to the atmosphere, affect carbon (C) storage, and reduce nitrogen (N) stocks (Amiro *et al.*, 2001; Nave *et al.*, 2011; Kashian *et al.*, 2013), which limit net primary productivity and C accumulation in forests world-wide (Lebauer & Treseder, 2008). Thus, understanding the implications of modern fires and anticipating changes in ecosystem C storage and N cycling under climate change require knowledge about the long-term biogeochemical consequences of fire.

Quantifying the biogeochemical impacts of disturbance, particularly over multiple disturbance intervals, has been challenging for ecologists. Current knowledge of the long-term C and N biogeochemistry of fire-prone forests comes largely from chronosequences (Smithwick *et al.*, 2009), which hinge on the assumption that conditions differed little among study sites or over time. However, the biogeochemical effects of disturbance are diverse, as a consequence of ecosystem heterogeneity over space and time (White & Jentsch, 2001). The nature of the disturbance and the response may vary over decades to millennia with climate-induced changes in vegetation, ecosystem processes, and disturbance regimes (Lenihan *et al.*, 2003; Marlon *et al.*, 2009). For example, fires could build or diminish forest N stocks and availability as climate changes, depending on variability in fire frequency or severity and rates of N mineralization and symbiotic N fixation (Rustad *et al.*, 2001; Giesen *et al.*, 2008; Yelenik *et al.*, 2013). Paleoecological analysis of lake-sediment records can complement chronosequences and long-term ecological research by quantifying past disturbance patterns and biogeochemical changes over decades to thousands of years, helping to contextualize modern disturbances and to anticipate ecosystem response to climate change (McLauchlan *et al.*, 2014). Moreover, in ecosystems with high-severity fire regimes, high-resolution analysis of lake-sediment records may be the only way to capture site-specific post-fire biogeochemical changes over successional and longer time-scales (i.e. decades to centuries).

In high-elevation forested catchments, where surface water C and N biogeochemistry is strongly regulated by terrestrial inputs (Baron *et al.*, 1991; Bunting *et al.*, 2010), forest disturbance and succession may have profound effects on lakes – and thus lake sediment composition – reflecting changes in terrestrial biogeochemical cycling and the magnitude and duration of perturbance and recovery (Likens & Bormann, 1974; McLauchlan *et al.*, 2007; Schindler, 2009). Recent research suggests that disturbance-induced shifts in terrestrial N cycling may be recorded in the natural abundance N stable isotope composition (standardized ratio of $^{15}N:^{14}N$ ($\delta^{15}N$)) of bulk lake-sediment organic matter (Hu *et al.*, 2001; McLauchlan *et al.*, 2007). When terrestrial N availability is high, soil and vegetation $\delta^{15}N$ tend to increase as N is lost from the system via hydrologic and gaseous pathways, because the processes that regulate and govern N export discriminate against ^{15}N (e.g. nitrification and denitrification; Högberg, 1997; Robinson, 2001; Craine *et al.*, 2009). Conversely, strong biotic N retention under low N availability tends to depress organic matter $\delta^{15}N$ by minimizing these losses (Martinelli *et al.*, 1999; Craine *et al.*, 2009).

Forest disturbances disrupt this biotic control over N by reducing plant biomass, resulting in elevated N availability, N losses, and organic matter $\delta^{15}N$ (Pardo *et al.*, 2002). Fires thus temporarily increase terrestrial N availability, but most N losses to these events occur via volatilization (Johnson *et al.*, 1998; Nave *et al.*, 2011) – a process shown to preferentially release ^{14}N to the atmosphere (Turekian *et al.*, 1998; Saito *et al.*, 2007). Recent work suggests that fires can increase soil and vegetation $\delta^{15}N$ by causing losses of ^{15}N-depleted gaseous N, nitrate, and organic matter (Grogan *et al.*, 2000; Boeckx *et al.*, 2005), and that higher severity burns may cause greater isotopic enrichment (Stephan, 2007; LeDuc *et al.*, 2013). Modern ecological studies of the impacts of fire on N cycling are complicated by the spatial and temporal heterogeneity of processes affecting N pools throughout forested landscapes (Turner *et al.*, 2011; LeDuc *et al.*, 2013). Because lake-sediment $\delta^{15}N$ integrates N cycle processes over space and time, this paleoecological proxy has the potential to overcome these challenges at the watershed scale.

To help advance understanding of the biogeochemical impacts of disturbance over decadal to millennial time-scales, we obtained a new *c.* 4250-yr high-resolution (*c.* 4 yr per sample) lake-sediment record from a lodgepole pine forest in Rocky Mountain National Park, Colorado, USA – an ecosystem characterized by low N availability (Fahey & Knight, 1986) and strong biotic conservation of N after disturbance (Turner *et al.*, 2007). To assess fire-induced ecosystem change, we analyzed bulk sedimentary $\delta^{15}N$ (which integrates N cycling changes caused by terrestrial and aquatic processes) as well as supporting proxies of biogeochemical, physical, and biological change (e.g. %C, %N, C : N, biogenic silica, and pollen) which are also indicators of resource flux and availability. We used macroscopic charcoal accumulation rates (CHARs) and magnetic susceptibility (MS, a proxy for soil erosion; Millspaugh & Whitlock, 1995) to define two types of fire events: 'local' fires occurring within *c.* 1 km of the lake were defined by statistically significant CHAR peaks (Higuera *et al.*, 2010), whereas high-severity fires specifically within the lake catchment (i.e. 'high-severity catchment fires') were defined by CHAR peaks coincident with significant MS peaks. We then quantified the average biogeochemical response to high-severity catchment fires and a subset of the other fires using superposed epoch analysis (SEA; also known as data compositing). We hypothesized that: (1) lake-sediment $\delta^{15}N$ would increase and C and N concentrations would decrease in the years immediately following high-severity catchment fires, reflecting organic matter and N losses to fire; (2) declining terrestrial N availability several decades after high-severity catchment fires would lower sediment $\delta^{15}N$ as organic matter recovered, as a result of strong nutrient demand from an aggrading forest; and (3) the degree of post-fire change in $\delta^{15}N$ and supporting proxies of biogeochemical, physical, and biological processes would scale directly with the location and/or severity of fire events, inferred from the combination of MS data and charcoal peak magnitude.

Materials and Methods

Study site and regional setting

Chickaree Lake (40.334249°N, 105.847270°W, 2796 m above sea level (asl)) is a small, deep lake in Rocky Mountain National Park, Colorado, USA (*c.* 1.5 ha surface area; 7.9 m maximum depth; Fig. 1). No perennial streams feed or drain the lake, but it has an ephemeral inlet and outlet. The *c.* 31-ha watershed has gentle to moderate topography and well-drained sandy loam soils derived from granite, gneiss, and schist overlain by a layer of decomposing litter (US Department of Agriculture, 2007). The lake is surrounded by an even-aged stand of lodgepole pine (*Pinus contorta* Douglas ex Loudon) dating to a 1782 Common Era (CE) stand-replacing fire (Sibold *et al.*, 2007). A surface fire that burned a portion of the watershed in 1872 CE notably had little impact on stand structure or composition (Sibold *et al.*, 2007). The subdominant forest species are Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), with a variety of shrub taxa (e.g. *Artemisia* and *Rosa*) in the understory. The fire regime is characterized by infrequent, high-severity crown fires (*c.* 100–300-yr mean return intervals) associated with severe seasonal drought (Sibold *et al.*, 2006).

The modern regional climate is continental, with cold, dry winters and warm, wet summers. In nearby Grand Lake (*c.* 8 km from the lake, 2664 m asl), the monthly mean temperature is −8.5°C in January and 14°C in July. Average total annual precipitation is 483 mm, and average annual snowfall is 3503 mm (Western Regional Climate Center 1940–2013 observations).

Sediment collection and chronology

Two parallel, overlapping sediment cores (*c.* 6.5 m length; 5.0 and 7.6 cm diameter) were collected at 7.9 m water depth in August 2010 with a modified Livingstone piston corer (Wright *et al.*, 1984). The sediment–water interface was retrieved using a polycarbonate tube fitted with a piston in September 2007, and the top *c.* 12 cm was subsampled at 0.5-cm intervals in the field. Cores were stored at *c.* 4°C at the University of Idaho Paleoecology and Fire Ecology Laboratory, where they were split lengthwise, correlated visually and using stratigraphic patterns in

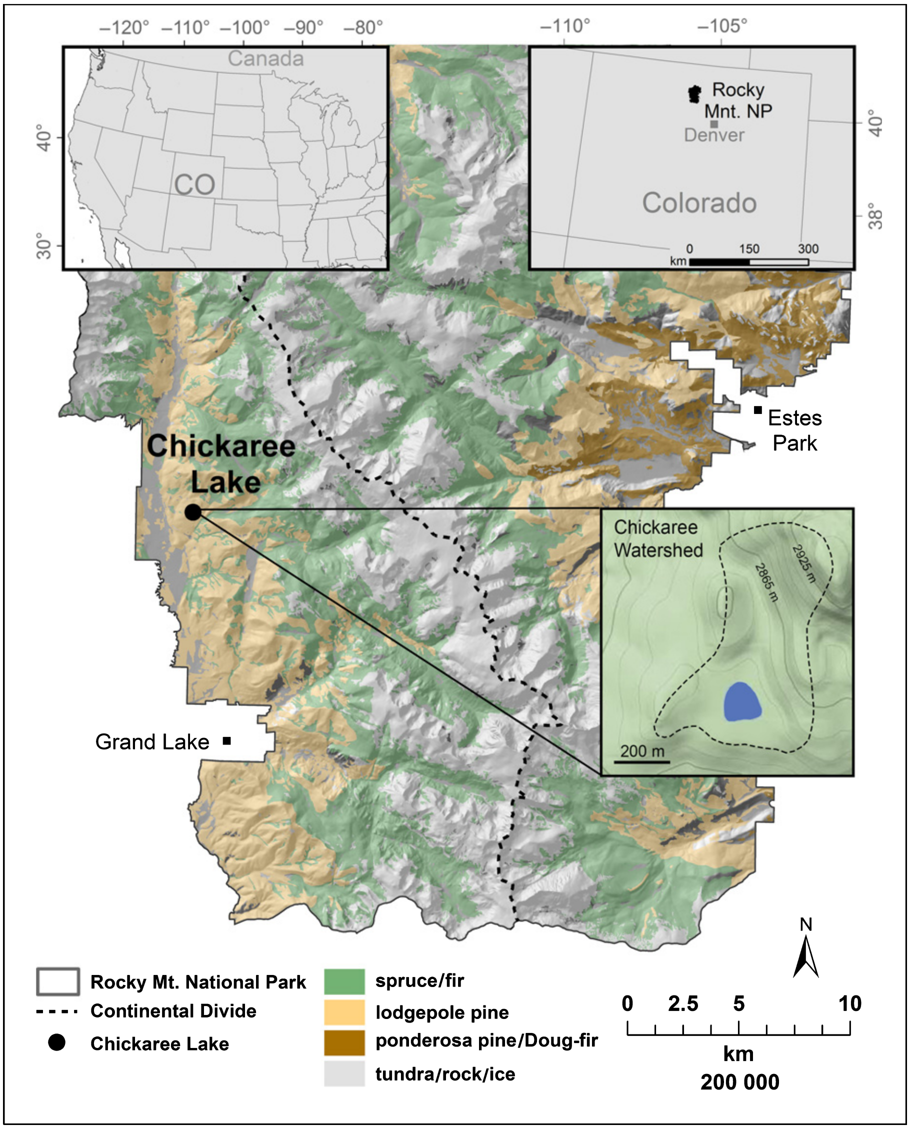

Fig. 1 Location of the study site. Chickaree Lake lies within a subalpine forest on the west side of Rocky Mountain National Park (CO, USA). The *c.* 1.5-ha lake has a *c.* 31-ha watershed (map data source: Rocky Mountain National Park; inset data source: Google Maps).

MS and charcoal concentration, and sectioned continuously at 0.5-cm intervals.

The sediment chronology is based on ^{210}Pb activity in 13 samples from the upper 20 cm, and 25 accelerator mass spectrometry ^{14}C dates from terrestrial macrofossils, concentrated charcoal, and bulk gyttja from deeper sediments (Supporting Information Table S1). Dating of bulk gyttja was justified based on a lack of carbonates in the watershed and sediments (US Department of Agriculture, 2007; see Sediment biogeochemistry section), and statistically similar calibrated ages from nearly paired samples of gyttja and concentrated charcoal ($n=4$; Table S1; Fig. 2).

Measurements of ^{210}Pb were performed by Flett Research Ltd (Winnipeg, MB, Canada) and the ^{210}Pb chronology was developed using the constant rate of supply model adapted from Binford (1990). Radiocarbon measurements were performed at Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectrometry. Radiocarbon ages were calibrated to 1950 CE (hereafter 'cal yr BP') using the program CALIB 6.0 (Stuiver & Reimer, 1993) and the IntCal09 data set (Reimer *et al.*, 2009). The age–depth model used a weighted cubic smoothing spline derived from 1000 bootstrapped samples from the calibrated age distributions using the program MCAGEDEPTH (Higuera *et al.*, 2009).

The Chickaree Lake sediment record spans *c.* 6300 yr, but here we report on the record from *c.* 4250 cal yr BP to present, when sedimentation rates ranged from 0.08 to 0.41 cm yr^{-1}, and averaged 0.15 cm yr^{-1} (4 yr per sample; Fig. 2). The only clear evidence of instantaneous sedimentation was a *c.* 1.5-cm section of charcoal at *c.* 3720 cal yr BP (535.0–536.5 cm), probably representing rapid delivery of charred material to the lake after a high-severity fire close to the lake. This section was removed from the chronology, and all data were averaged over the three 0.5-cm samples.

Sediment biogeochemistry

Bulk sediment C and N concentrations (% by mass) and isotopic composition (delta notation (δ^{13}C and δ^{15}N); ‰) were

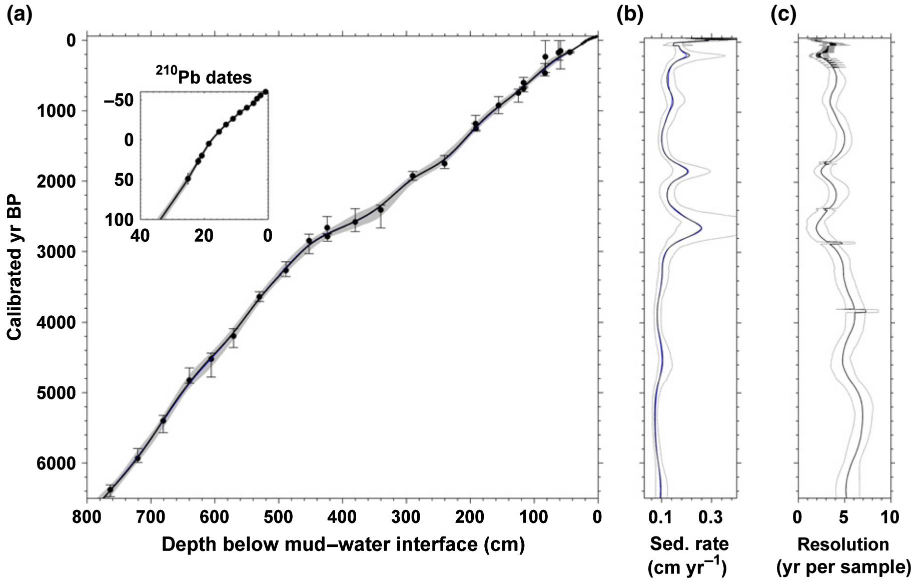

Fig. 2 Chickaree Lake age–depth model. (a–c) Radiometric ages (^{210}Pb and ^{14}C; closed circles) and the cubic spline fit (solid line) (a), sedimentation rate (b), and sample resolution (c), all with 95% confidence intervals (CIs). CIs were based on Monte Carlo resampling of 1000 chronologies. The mean and median for the period of analysis was 4 yr per sample. In the original age–depth model, the tree-ring dated stand-replacing fire in 1782 CE (168 calibrated yr BP) fell within the 95% CI of the corresponding charcoal peak. To further constrain the final age–depth model, the modified age was ascribed to this peak.

measured at a median interval of 0.5 cm (n = 618). Sediment subsamples (1 cm^3) were dried at 65°C for 24 h, then ground to a fine powder and homogenized before analysis in a continuous flow isotope ratio mass spectrometer at the Idaho Stable Isotopes Laboratory, University of Idaho (UI; n = 470), or the Stable Isotope Core Laboratory, Washington State University (WSU; n = 148). Analysis of 20 subsamples at both facilities revealed nearly identical results across the full range of $\delta^{13}C$ (r^2 = 0. 99) and $\delta^{15}N$ (r^2 = 0.97) values. Analytical error was estimated with standard deviations from replicate analysis of lake sediment and laboratory standards. Error (1 SD) was < 0.23‰ for $\delta^{15}N$ and < 0.10‰ for $\delta^{13}C$ (Notes S1).

Sediment bulk density (dry g wet cm^{-3}) was measured on all samples analyzed for biogeochemistry. Organic matter and inorganic C content were estimated in 1-cm^3 subsamples of homogenized sediments from two consecutive 0.5-cm samples, taken at a median interval of 5 cm (n = 121) via sequential loss on ignition at 550°C (4 h; LOI_{550}) and 1000°C (2 h; LOI_{1000}), respectively. A strong positive correlation between %C and LOI_{550} (r = 0.97; P < 0.01; Fig. S1) and low inorganic C content (*c.* 6% of total C) indicated that sediment C was dominated by organic C, with little carbonate (Dean, 1974; Santisteban *et al.*, 2004). Thus, we interpret C concentration as total organic carbon. Strong positive correlations between %N and both %C (r = 0.91; P < 0.01; Fig. S1) and LOI_{550} (r = 0.93; P < 0.01) indicated that N was also largely organic. We converted %C to C accumulation rates (C_{acc}; g C cm^{-2} yr^{-1}), considered a better measure of C delivery to the sediments because dilution by clastic material strongly influences %C (Meyers & Lallier-Verges, 1999). The ratio of organic C to total N (C : N), a robust proxy for the provenance of lake organic matter, is expressed as an atomic mass ratio. The C : N of cellulose-rich, protein-poor terrestrial organic matter (> 20) is significantly higher than the C : N of algal biomass (*c.* 4–10; Meyers & Lallier-Verges, 1999).

Sediment biogenic silica concentration (BSi; % by mass) was measured in *c.* 2–3-cm consecutive subsamples, spaced at a median interval of 14 cm (n = 40), at the Limnological Research Center, University of Minnesota, Minneapolis, using a time-series wet chemical extraction method and molybdate blue spectrophotometry (DeMaster, 1979). Biogenic silica, a product of diatom frustule (i.e. skeleton) deposition, is a widely used proxy for aquatic productivity (Hu *et al.*, 2003). To help infer factors controlling sediment biogeochemistry, relationships among variables were evaluated using Spearman correlation coefficients. The probability of Type I error (P) for these analyses was adjusted to account for temporal autocorrelation by reducing the original sample size to an effective sample size, calculated according to Dawdy & Matalas (1964).

Fire and vegetation history

Theoretical and empirical evidence suggests that distinct peaks in high-resolution macroscopic charcoal records represent fires occurring within *c.* 1 km of small lakes, particularly in ecosystems with high-severity fire regimes (see Higuera *et al.*, 2010 and references therein). Given the small Chickaree Lake watershed (*c.* 31 ha; Fig. 1), some charcoal peaks probably reflect charcoal deposition from events that occurred within 1 km of the lake but outside the drainage basin – implying that the biogeochemical effects would not be recorded in the lake sediments.

To identify fires that occurred within the watershed, we used lake-sediment MS, an indicator of mineral soil erosion. High-severity fires promote erosion and delivery of terrestrial sediments to surface waters by exposing mineral soils, diminishing soil stability, and increasing surface runoff (Wondzell & King, 2003). Because these inputs are positively correlated with lake-sediment MS, a significant increase in MS coincident with or closely following a charcoal peak strongly suggests erosion after a high-severity fire within the watershed (Millspaugh & Whitlock, 1995; Colombaroli & Gavin, 2010). In this study, we inferred fires and erosion events from statistically significant peaks in macroscopic (> 125 μm) charcoal accumulation rate (CHAR; no. pieces cm^{-2} yr^{-1}) and sediment MS (SI units), respectively. Sample-specific MS was measured on the whole core at 0.5-cm intervals using a Bartington MS3 Meter and MS2E Core Logging Sensor (Bartington Instruments, Oxford, UK). For charcoal analysis, contiguous sediment subsamples (1.5–3 cm^3) from the same 0.5-cm intervals were soaked in a 5% sodium metaphosphate solution for 5–7 d to facilitate disaggregation, wet-sieved through a 125-μm mesh, and soaked in a 2% sodium hypochlorite solution for 24 h to remove or lighten the noncharcoal organic content.

Charcoal particles were identified based on texture, color, and morphology and counted at ×40 magnification. We calculated CHAR by multiplying sediment accumulation rates (cm yr^{-1}) by charcoal concentrations (no. pieces cm^{-3}). Significant CHAR and MS peaks were identified by decomposing interpolated (10-yr) time series into low-frequency (background) and high-frequency (peak) components using CharAnalysis version 1.1 (Appendix A, Higuera *et al.*, 2009; available online at http://www.charanalysis.googlepages.com). Before peak analysis, MS data were transformed by adding the minimum observed value to all measurements. Background CHAR and MS were estimated within 500-yr windows using a locally weighted regression robust to outliers. Residual CHAR and MS were calculated by subtracting background values from interpolated values to create CHAR and MS peak series, each composed of two populations: distinct peaks caused by local fires or erosion events, and variability (i.e. 'noise') associated with other factors (with a mean near zero). Within overlapping 500-yr sections, peak MS samples exceeding the 99.9th percentile of the local noise distribution estimated using a Gaussian mixture model were identified as erosion events. Charcoal peaks exceeding a similarly defined threshold were interpreted as fires if their maximum values had a < 5% probability of originating from the same Poisson distribution as the minimum charcoal count from the preceding 75 yr (Higuera *et al.*, 2010). Significant CHAR peaks (fires) within 20 yr before or 10 yr after significant MS peaks (erosion events) were identified as high-severity fires within the Chickaree Lake watershed, hereafter 'high-severity catchment fires.' We interpreted other CHAR-inferred fires as either lower severity events or fires occurring outside the watershed (but within *c.* 1 km of the lake; Fig. 1), hereafter 'lower severity/extra local fires.'

Local vegetation composition was reconstructed using fossil pollen from sediment subsamples (1 cm^3) taken at a median interval of 7.5 cm in the upper *c.* 175 cm of the core and a median interval of 25 cm below *c.* 175 cm. Samples were prepared using standard digestion methods (Faegri & Iversen, 1975), and pollen was identified at ×400 or ×1000 magnification and reported as percentages relative to the terrestrial pollen sum.

Statistical analyses

We assessed the biogeochemical impacts of fire using superposed epoch analysis (SEA), a nonparametric method used to evaluate the average response to multiple events in a time series (Adams *et al.*, 2003). The analysis was conducted on high-severity catchment fires ($n = 11$) and a subset of lower severity/extra local fires ($n = 9$) using custom scripts written in Matlab (avaliable online at http://dx.doi.org/10.6084/m9.figshare.988687). Response variables ($\delta^{15}N$, %C, %N, C_{acc}, C : N, and bulk density) were sampled every 0.5 cm for *c.* 5 cm before and after each fire event. Outside of this window, subsamples from two consecutive 0.5-cm samples were analyzed at *c.* 1-cm intervals. The high-resolution sampling window represents *c.* 50–125 yr (depending on local sediment accumulation rates). The SEA was performed specifically on samples from 50 yr pre-fire to 75 yr post-fire (a span selected based on trends during lodgepole pine stand development; Pearson *et al.*, 1987). Because many samples *c.* 50–75 yr post-fire were not included in high-resolution sampling, composite patterns over this span may be more muted than if they were sampled at higher resolution.

Before SEA, samples were interpolated to the median sample resolution (for biogeochemical samples) of 5 yr, and low-frequency trends were summarized with a 500-yr locally weighted regression robust to outliers. To minimize bias arising from long-term changes in response variables, we subtracted the low-frequency trends from the interpolated time series to obtain residual series. Residuals were averaged across events to produce composite time series (hereafter 'response series') showing each variable's mean response to fire events, in 5-yr bins.

To assess the statistical significance of the response series, confidence intervals (CIs) were generated with a Monte Carlo randomization method. For each response variable, 10 000 time series were created by randomly shuffling samples in five-sample blocks to account for temporal autocorrelation. Each random time series was sampled via the same method used to generate the observed response series, producing random composites. The 0.5th, 2.5th, 97.5th, and 99.5th percentiles from the 10 000 random composites were used to construct 95% and 99% CIs.

As a complementary analysis to the SEA, we used correlation analysis to evaluate if the degree of biogeochemical response to fire varied with the magnitude of fire events, measured via charcoal peak magnitude (no. pieces cm^{-2}), an assumed metric of fire severity, size, and/or proximity to the lake (Whitlock *et al.*, 2006). Specifically, for both types of fire event, we determined Pearson correlation coefficients between log-transformed peak magnitude and response variables, averaged over two post-fire time periods (0–20 and 20–50 yr) corresponding to significant responses to high-severity catchment fires revealed by the SEA.

Results

Fire and vegetation history

We reconstructed 34 fires and 20 erosion events with charcoal and magnetic susceptibility peak analysis. Thirteen fires coincided with erosion events, meeting our definition for high-severity catchment fires, while the other 21 fires were defined as lower severity/extra local fires (Fig. 3). Two high-severity catchment fires were excluded from the SEA because they were followed too closely (< 75 yr) by other high-severity fires. The CHAR record median signal-to-noise index was 19.1, providing strong evidence that CHAR peaks represent stand-replacing fires (Kelly *et al.*, 2011). Additionally, the 1782 CE stand-replacing fire corresponded well with the most recent high-severity catchment fire identified in the charcoal record (Fig. 3). By contrast, the 1872 CE surface fire did not yield any discernible charcoal accumulation in the sediments, suggesting similar events did not leave charcoal signatures.

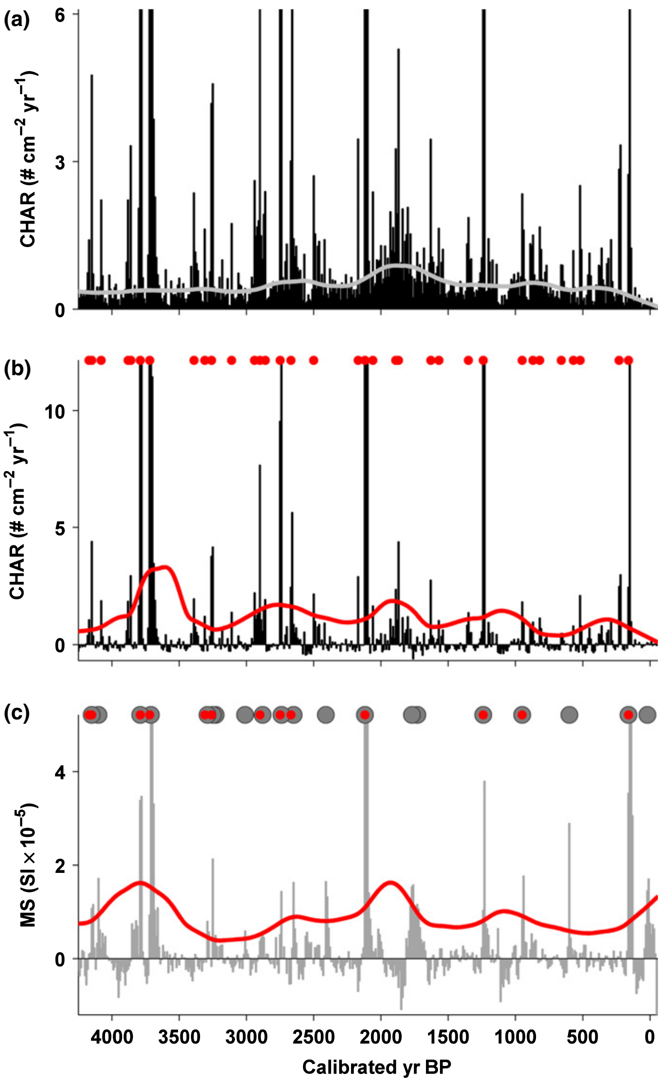

Fig. 3 Sediment charcoal and magnetic susceptibility (MS) records. (a) Charcoal accumulation rate (CHAR; black line), interpolated to 10-yr intervals, and the 500-yr trend (gray line), representing 'background' CHAR. (b) Residual CHAR values (black line), the threshold used to identify potential fire events (red line), and CHAR values exceeding this threshold and thus identified as local fire events (red dots). (c) Residual MS values (gray line), the threshold used to identify MS peaks (red line), and MS values exceeding the threshold and thus identified as MS peaks (gray circles), with coincident CHAR and MS peaks identified as high-severity catchment fires (gray circles with red dots).

Individual fire return intervals (FRIs) for all fires varied from 20 to 330 yr, with a series-wide mean of 122 yr (95% CI = 91–152). Mean FRIs (summarized over 1000-yr intervals) did not differ significantly through time, indicating an absence of millennial-scale changes in fire frequency. However, FRIs for high-severity catchment fires (FRI_{hs}) were higher early in the record; 10 events occurred between *c.* 4250 and 2000 cal yr BP (mean FRI_{hs} = 225 yr), while only three occurred over the last two millennia (mean FRI_{hs} = 667 yr; Fig. 3c).

Pollen percentages indicate that lodgepole pine dominated the forest around the lake for the entire record (Fig. S2). *Pinus* pollen accounted for 70% (mean) of total terrestrial pollen (range 46–88%). Sixty-three per cent of the *Pinus* grains were preserved well enough to separate into subgenera, and, of these, 98% were identified to subgenus *Pinus* and 2% to subgenus *Strobus*. We therefore assume that *Pinus* pollen primarily represents lodgepole pine (*Pinus contorta*, subgenus *Pinus*) rather than limber pine (*Pinus flexilis* James, subgenus *Strobus*). *Picea* was a minor component of the pollen spectra, with percentages ranging from < 1% to 13% (mean 5%), and *Abies* was usually present but rare (< 2%). Known N-fixing taxa (e.g. *Alnus*, *Lupinus*, and *Shepherdia*) were absent or rare in the pollen record, never accounting for more than *c.* 1% in any single sample.

Provenance and preservation of organic matter

Abundant organic C (mean 16.2%; SD 4.4%; Fig. S3), high sedimentation rates (Fig. 2), and several other lines of evidence suggest that rapid accumulation of allochthonous (terrestrial) and autochthonous (originating within the lake) organic matter preserved biogeochemical signals of terrestrial processes and algal productivity, permitting inferences regarding post-fire forest and lake ecosystem change. Proxy trends (Fig. 4) and correlations indicate that diagenetic degradation probably did not significantly alter primary biogeochemical signals (Notes S2, Figs S1, S3).

Sediment biogeochemistry suggests a mix of organic matter derived from terrestrial and aquatic primary productivity, typical of subalpine lakes. Sediment C : N (mean 14.9; SD 1.8) and $\delta^{15}N$ (mean 0.96‰; SD 0.49; Fig. S3), and a weak negative correlation between $\delta^{15}N$ and %N ($r = -0.26$; $P < 0.01$; Fig. S1), are consistent with values from lakes receiving significant terrestrial organic matter subsidies (Notes S2, Fig. S1). The influence of algal productivity on sediment composition was evident in high BSi content (mean 26%; SD 4.3%), negative correlations between BSi and both C : N ($r = -0.42$; $P < 0.01$) and %C ($r = -0.59$; $P < 0.01$), and positive correlations between BSi and both $\delta^{15}N$ ($r = 0.34$; $P = 0.04$) and $\delta^{13}C$ ($r = 0.36$; $P = 0.03$) (Table S2, Fig. S1, Notes S2).

Biogeochemical response to fire

High-severity catchment fires were followed by pronounced physical and biogeochemical changes, as shown by SEA (Figs 4, 5). The relative timing of these changes is robust, because all

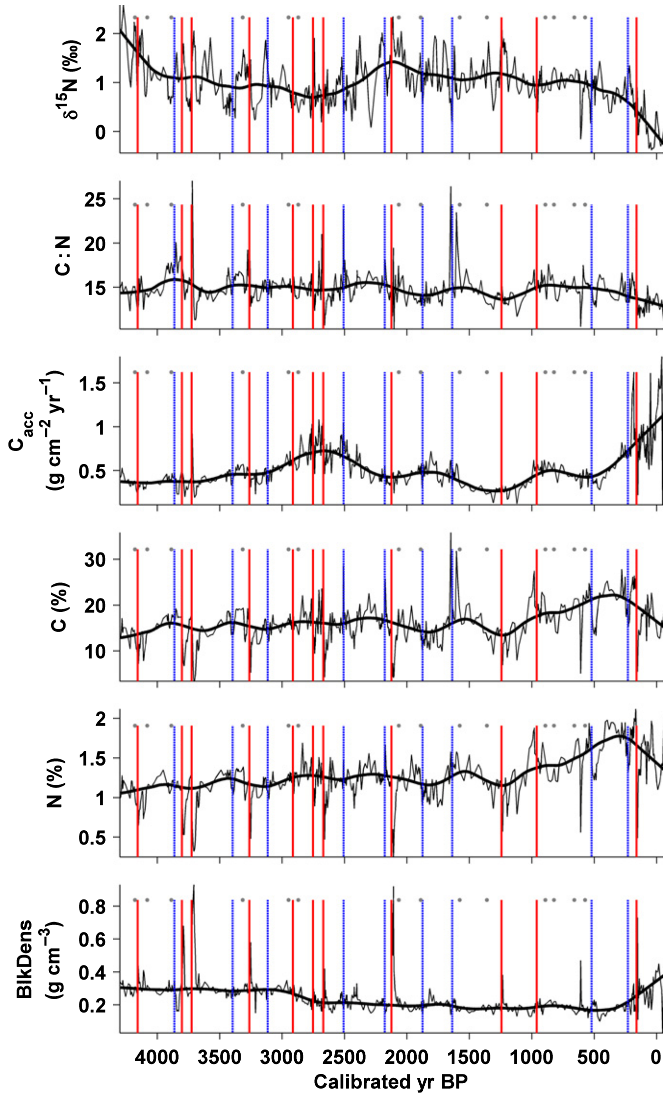

Fig. 4 Time series of sediment biogeochemistry and bulk density. Raw and smoothed (500-yr trend; bold line) time series are shown, with vertical solid red lines denoting high-severity catchment fires ($n = 11$) and vertical dashed blue lines denoting lower severity/extra local fires ($n = 9$) used in superposed epoch analysis (SEA). Gray dots represent lower severity/extra local fires not included in the SEA (see the Materials and Methods section). BlkDens, bulk density.

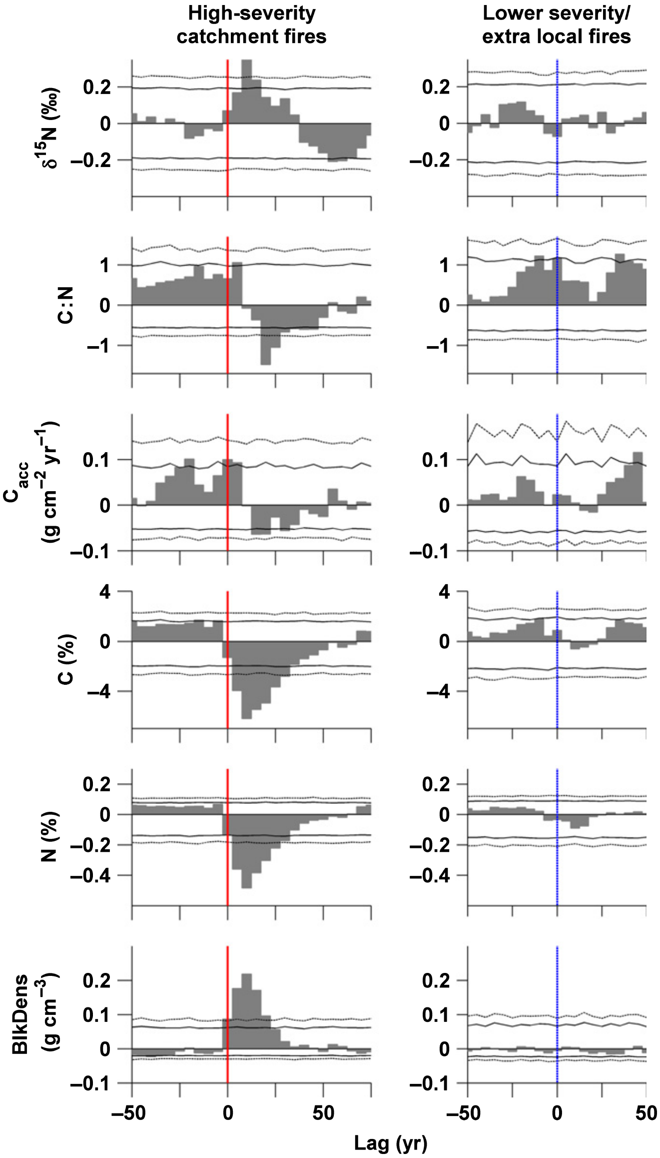

Fig. 5 Results of superposed epoch analysis (SEA). Composite residual response values (*y*-axis) before and after high-severity catchment fires (solid red lines, left column) and lower severity/extra local fires (dashed blue lines, right column) are shown. The horizontal dashed and solid lines represent Monte Carlo-derived 99% and 95% confidence intervals, respectively. BlkDens, bulk density.

proxies were measured from the same, continuously sampled sediments. The absolute timing of these changes, however, is limited by the precision of the age–depth model; the well-constrained chronology, relatively constant sediment accumulation rate (Fig. 2), and lack of evidence suggesting rapid sedimentation events (as observed after fires in watersheds with more extreme topography; Colombaroli & Gavin, 2010) all lend confidence to the timing and duration of post-fire trends in our record.

During the two decades following high-severity catchment fires, $\delta^{15}N$ and bulk density increased significantly, and %C and %N decreased significantly. The composite pattern in bulk density was nearly identical to the pattern in MS (used to define high-severity catchment fires; data not shown), and the series-wide trends in these two proxies were correlated ($r = 0.66$; $P < 0.01$). The composite patterns in %C and %N, however, differed slightly from bulk density (and MS). Within *c.* 25 yr post-fire, $\delta^{15}N$ and bulk density returned to near-average values, while %C and %N remained anomalously low until *c.* 35–40 yr after fire. C : N and C_{acc} were significantly high immediately after fire and then dropped sharply to anomalously low values *c.* 15–20 yr post-fire. C : N remained significantly low *c.* 20–50 yr following fire, while low C_{acc} anomalies occurred *c.* 15–35 yr after events. The recovery of %C, %N, C : N, and C_{acc} toward average levels *c.* 30–60 yr after fire coincided with a monotonic decrease in $\delta^{15}N$ to significantly low values *c.* 55–70 yr post-fire. Sediment $\delta^{15}N$, bulk density, %C, and %N all returned to near-pre-fire levels by *c.* 75 yr after events. In contrast to the marked responses following high-severity catchment fires, the SEA revealed little change after lower severity/extra local fires (Fig. 5).

Biogeochemical and physical responses to high-severity catchment fires were more pronounced following events with greater charcoal peak magnitudes (Fig. 6). Peak magnitude was significantly correlated ($P < 0.05$) with mean $\delta^{15}N$ ($r = 0.75$), %C ($r = -0.63$), %N ($r = -0.74$), and bulk density ($r = 0.79$) *c.* 0–20 yr after fires (Fig. 6) – the period of anomalously high $\delta^{15}N$ revealed by the SEA (Fig. 5). Between 20 and 50 yr post-fire, the period marked by significantly low composite C : N, peak magnitude was significantly correlated with C : N ($r = -0.66$), %C ($r = -0.81$), %N ($r = -0.80$), and bulk density ($r = 0.74$) but was uncorrelated with $\delta^{15}N$ ($r = 0.11$; $P = 0.75$; Fig. 6). Peak magnitude of lower severity/extra local fires was uncorrelated with all response variables within both post-fire temporal windows (Fig. S4).

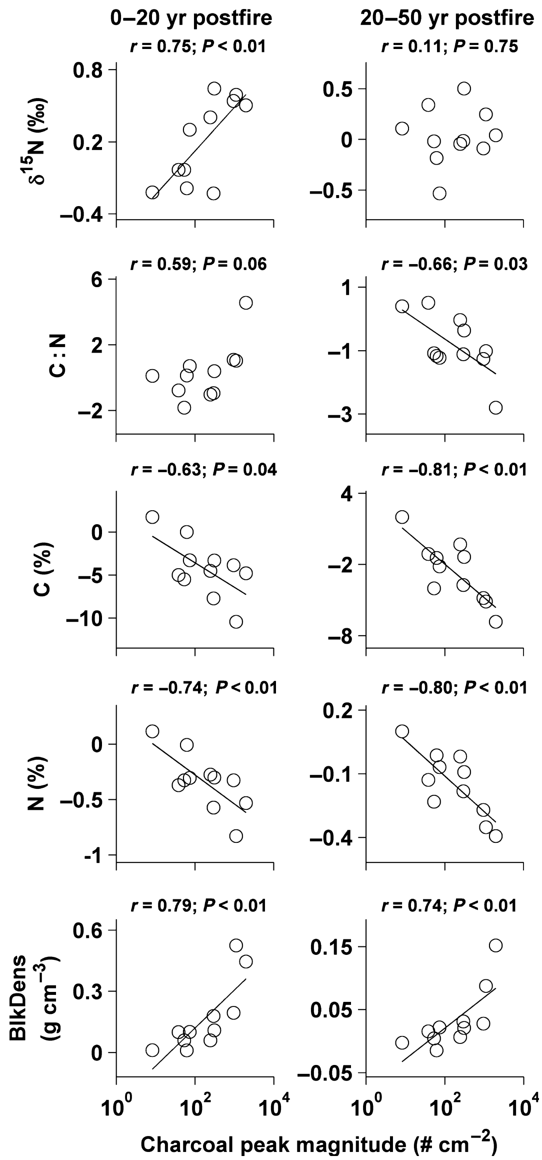

Fig. 6 Relationships between charcoal peak magnitude and the proxy responses following high-severity catchment fires. Pearson correlation coefficients (*r*) were calculated using the log-transformed peak magnitude of each fire event and mean residual response variable values *c.* 0–20 yr (left column) and *c.* 20–50 yr (right column) after each event. BlkDens, bulk density.

Discussion

Our analysis revealed significant biogeochemical changes following high-severity fires, reflecting processes operating from instantaneous to near-centennial time-scales: combustion, increased mineral soil inputs to the lake, marked shifts in the provenance of lake organic matter, and C and N accumulation in forest biomass during stand recovery. This high-resolution analysis – the first to systematically test the utility of bulk lake-sediment $\delta^{15}N$ as an indicator of fire-induced N cycle change – suggests that lake-sediment $\delta^{15}N$ can provide insights into N loss and availability in ecosystems shaped by stand-replacing fires. Detecting the biogeochemical impacts of fire in this sedimentary record hinged on several factors. First, the analysis isolated fires that occurred within the catchment, excluding events that could not have affected the composition of terrestrial exports to the lake. Secondly, high-resolution sampling allowed us to capture high-magnitude changes that may have been blunted at coarser resolution. Finally, the SEA highlighted signals of fire amidst other high-frequency variability caused by processes operating over similar and longer time-scales.

Studies of lodgepole pine forest recovery following high-severity fire have revealed strong early successional biotic N retention (Turner *et al.*, 2007, 2011) and relatively rapid (*c.* 100 yr) recovery of N stocks (Smithwick *et al.*, 2009) – indicating N cycle resilience to single disturbances under modern climatic conditions. Our results suggest that high rates of N accumulation in organic matter during mid-successional lodgepole forest aggradation also play a key role in N conservation and ecosystem resilience, consistent with biogeochemical theory (Vitousek & Reiners, 1975). More importantly, our paleoecological approach allowed for a multi-millennial assessment of the biogeochemical impacts of wildfires. The significant composite changes in $\delta^{15}N$ and other proxies observed after fires were products of multiple responses similar in timing and direction, indicating that ecosystem response and recovery were relatively consistent over the past *c.* 4250 yr. This suggests terrestrial biogeochemical resilience to infrequent, severe disturbance over thousands of years marked by significant climatic change (Shuman *et al.*, 2009). Post-fire trends indicate that FRIs greater than *c.* 100 yr allowed for sufficient biomass recovery and N accumulation between events such that even high-severity fires did not deplete C or N stocks over millennia.

Immediate impacts of high-severity fires (years to decades)

Consistent with our first hypothesis, high-severity catchment fires were followed closely by statistically significant increases in lake-sediment $\delta^{15}N$, suggesting isotopic enrichment of forest N pools resulting from organic matter combustion and N losses to fire. Several mechanisms may share responsibility for the increase in $\delta^{15}N$ (Fig. 5), including preferential volatilization of ^{14}N, combustion of isotopically light organic matter pools, and elevated nitrification and nitrate losses.

We propose that combustion of the ^{15}N-depleted forest floor (Högberg, 1997; Grogan *et al.*, 2000; LeDuc *et al.*, 2013) and preferential volatilization of ^{14}N from vegetation and soils (Turekian *et al.*, 1998; Saito *et al.*, 2007) led to an influx of isotopically enriched mineral soil, charred material, and organic matter to the lake – all increasing sediment $\delta^{15}N$. Destruction of the forest floor removed the largest pre-fire source of terrestrial C (Baron *et al.*, 1991; Michalzik *et al.*, 2001), and the resulting influx of terrestrial mineral material significantly increased bulk density and reduced the proportion of organic matter in the sediments (i.e. %C and %N; Fig. 5). Such wholesale losses of litter and organic soil to high-severity fires (Turner *et al.*, 2007) should raise the $\delta^{15}N$ of soil leachates and may result in elevated foliage and litter $\delta^{15}N$ as recovering vegetation takes up isotopically heavier N (Högberg, 1997; Grogan *et al.*, 2000; Stephan, 2007; LeDuc *et al.*, 2013).

We also considered elevated nitrification and nitrate losses as potential mechanisms contributing to post-fire isotopic enrichment. Stand-replacing fires reduce plant N demand, mineralize organic N, and foster soil conditions that favor nitrification (Certini, 2005; Smithwick *et al.*, 2005) – which yields ^{15}N-enriched ammonium and leads to losses of ^{15}N-depleted nitrate and gaseous N (Högberg, 1997; Pardo *et al.*, 2002; Boeckx *et al.*, 2005; LeDuc *et al.*, 2013). However, while elevated nitrate leaching and outflow have been observed after disturbance in lodgepole forests (Knight *et al.*, 1991; Bladon *et al.*, 2008), retention of N in microbial biomass is thought to strongly conserve mineralized N after high-severity fires in these ecosystems (Turner *et al.*, 2007). Vegetation re-growth also serves as a strong early successional N sink (Turner *et al.*, 2011). Thus, any isotopic enrichment resulting from post-fire changes in N availability/nitrate loss rates would probably be minor and short-lived in the Chickaree Lake watershed.

In agreement with our third hypothesis, the magnitude of post-fire changes was well correlated with charcoal peak magnitude (Fig. 6), while proxy response to lower severity/extra local fires was weak and uncorrelated with peak magnitude (Fig. S4). These relationships, in concert with the SEA results, further support our interpretation that post-fire increases in $\delta^{15}N$ and bulk density and declines in %C and %N reflect the extent of combustion of the isotopically depleted forest floor – identified as a strong indicator of fire severity in Colorado Front Range forests (Lewis *et al.*, 2006). Thus, consistent with modern studies, our results indicate that more severe or larger fires caused greater organic matter losses (Certini, 2005), erosion (Wondzell & King, 2003), and isotopic enrichment (Stephan, 2007) – suggesting that this suite of proxies can help infer fire severity and/or extent and providing strong support for previous interpretations of peak magnitude as a proxy of fire severity (Whitlock *et al.*, 2006; Higuera *et al.*, 2009).

Multi-decadal scale impacts of high-severity fires

The Chickaree Lake sediment record further reveals biogeochemical impacts of high-severity fires lasting several decades. Most notably, high-severity catchment fires appear to have caused long-lived changes in the provenance of lake organic matter, evidenced by significantly lower than average sedimentary C : N between *c.* 20 and 50 yr after events (Fig. 5). These changes could reflect declines in terrestrial organic matter subsidies to the lake, and/or increases in aquatic primary productivity, as the C : N of algal biomass is significantly lower than that of forest organic matter (Meyers & Lallier-Verges, 1999). Previous limnological (Carignan *et al.*, 2000; Marchand *et al.*, 2009) and paleolimnological (Paterson *et al.*, 1998; Philibert *et al.*, 2003b) research, largely in boreal watersheds, has revealed little post-fire change in terrestrial C inputs to lakes. By contrast, increased aquatic primary productivity has been linked to post-fire nutrient pulses to lakes in forested watersheds (Kelly *et al.*, 2006), although this effect is believed to be short-lived (weeks to *c.* 5 yr; Philibert *et al.*, 2003a; Ranalli, 2004; Schindler, 2009).

We propose that the C : N decline in the Chickaree Lake sediment record was driven primarily by reduced inputs of terrestrial organic matter after fire – a change that could significantly impact lake food webs and biogeochemical cycling (Carpenter *et al.*, 2005; Bunting *et al.*, 2010). The significant drop in the rate of sediment organic matter accumulation (C_{acc}) coincident with low %C and C : N (Fig. 5) *c.* 20–50 yr after fire suggests that the changes resulted largely from reduced terrestrial inputs rather than increased organic matter contributions from aquatic primary producers. Moreover, the strong correlations between response variables and charcoal peak magnitude (Fig. 6) indicate that the trends *c.* 20–50 yr post-fire were closely linked to inferred fire severity. Finally, while post-fire nutrient subsidies could be recycled within the lake for a few years, the sediment record changes over a multi-decadal time-scale that is more consistent with organic matter losses and gains associated with fire and successional C accumulation during ecosystem recovery.

Ecosystem recovery

As predicted by our second hypothesis, $\delta^{15}N$ declined significantly several decades after fire, suggesting diminishing terrestrial N availability during forest development. The decrease in $\delta^{15}N$ occurred as proxies of terrestrial organic matter accumulation (C_{acc}, %C, and C : N) increased (Fig. 5), consistent with theory and modern ecological research indicating that N availability and thus plant and soil $\delta^{15}N$ should drop as N is sequestered in growing biomass and forest floor detritus (Vitousek & Reiners, 1975; Chang & Handley, 2000; Compton *et al.*, 2007; Garten *et al.*, 2011; LeDuc *et al.*, 2013). Together, these trends provide perhaps the strongest evidence that forest ecosystem processes were reflected in lake-sediment biogeochemistry.

The longevity of and mechanisms responsible for declining N availability during secondary succession have been debated. At Chickaree Lake, the timing of the negative excursions in sediment $\delta^{15}N$ is consistent with the successional period when lodgepole forest N demand and net primary productivity are expected to peak (forest age of 40–70 yr; Pearson *et al.*, 1987; Olsson *et al.*, 1998; Kashian *et al.*, 2013). Declining N availability associated with strong N demand may lower ecosystem $\delta^{15}N$ by minimizing

N losses, and decrease foliage and litter $\delta^{15}N$ by increasing vegetation reliance on isotopically depleted N derived from organic soil horizons and/or transferred to host plants by mycorrhizal fungi (Chang & Handley, 2000; Garten *et al.*, 2011; Hyodo *et al.*, 2012; LeDuc *et al.*, 2013). Diminishing N availability during terrestrial C accumulation has previously been inferred from declines in lake-sediment $\delta^{15}N$ at multi-decadal, catchment scales (McLauchlan *et al.*, 2007).

We considered the possibility that the $\delta^{15}N$ anomaly was driven by increasing incorporation of atmospheric N ($\delta^{15}N$ *c.* 0‰) in the plant–soil system via post-fire symbiotic N fixation (Smithwick *et al.*, 2005; Perakis *et al.*, 2011). However, litter of N-fixing taxa tends to be more isotopically enriched than that of other lodgepole forest plants (Miller, 2011), probably as a result of the latter's reliance on isotopically depleted N transferred by mycorrhizal fungi. Moreover, the pollen record showed little evidence of N-fixing taxa, even in the decades following fire (Fig. S2). We also considered possible autochthonous (within-lake) mechanisms for the negative $\delta^{15}N$ anomaly, but they seemed implausible given the composite nature of the record and the lack of supporting evidence from other proxies. Rather, the proxies support a terrestrial explanation. The monotonic increase in %C and %N *c.* 20–50 yr post-fire and the return of %C, %N, C_{acc}, and C : N to average levels *c.* 75 yr after fire (Fig. 5) probably reflect recovery of the forest floor and an attendant decline in mineral soil erosion during forest organic matter accumulation. This pattern of recovery is broadly consistent with chronosequences of C and N accumulation during stand development. In Rocky Mountain lodgepole forests, 80% of C was regained within 50 yr of stand-replacing fire and 90% within *c.* 100 yr (Kashian *et al.*, 2013), and all pre-fire N was recovered within 100 yr (Smithwick *et al.*, 2009). At Chickaree Lake, the charcoal record indicates that return intervals between high-severity fires were typically longer than the *c.* 100 yr biogeochemical recovery time estimated from post-fire chronosequences (i.e. mean (median) return interval = 334 (325) yr; Fig. 3c). These dynamics would therefore probably allow sufficient recovery time to maintain C and N stocks over millennia, despite multiple high-severity fires.

Predicting the long-term trajectory of ecosystem C and N stocks requires information on diverse processes over multiple time-scales, including millennial-scale disturbance regimes, and the nature and duration of biogeochemical impacts of individual disturbances (McLauchlan *et al.*, 2014). To our knowledge, this is the first study to examine lake-sediment $\delta^{15}N$ response to individual fires. Comparing this work to other paleoecological reconstructions helps build a more nuanced understanding of disturbances by considering differences in event magnitude, the duration of response, and the degree of disturbance-induced change. For example, anthropogenic deforestation in a New England hardwood forest watershed during the early 20th Century increased terrestrial N availability, leading to an influx of ^{15}N-enriched N and organic matter that elevated lake-sediment $\delta^{15}N$ for several decades (McLauchlan *et al.*, 2007). By contrast, Morris *et al.* (2013) found no relationship between lake-sediment $\delta^{15}N$ and spruce beetle outbreaks in Utah subalpine forests. The New England disturbance was longer-lived, caused larger changes in biomass, probably resulted in greater soil erosion, and occurred on a more N-enriched landscape with greater potential for nitrate losses. Decadal-scale beetle outbreaks are fundamentally different from deforestation, leaving live understory vegetation and beetle-resistant trees that may prevent erosion and strongly retain N following disturbance (Rhoades *et al.*, 2013). Strong early successional biotic N retention may similarly minimize N losses after high-severity fires in N-limited subalpine forests. However, our work shows that widespread vegetation mortality coupled with organic matter and N losses during these near-instantaneous events can yield strong sediment signatures reflecting sudden restructuring of the forest ecosystem and biogeochemical and physical legacies that may persist for up to *c.* 75 yr.

Conclusions

The biogeochemical impacts of wildfire vary widely depending on the nature of fire events, reflecting mechanisms operating over a range of time-scales, from instantaneous organic matter combustion through multi-decadal-scale forest development. The Chickaree Lake record revealed significant biogeochemical change after high-severity fires, largely consistent with patterns observed in post-fire forest chronosequence studies (Smithwick *et al.*, 2009; Kashian *et al.*, 2013; LeDuc *et al.*, 2013) and highlighting the importance of high-severity disturbance and subsequent forest development in shaping biogeochemical processes. In most cases, return intervals between high-severity fires were longer than the recovery time of *c.* 100 yr, estimated from the post-fire lodgepole pine chronosequences and consistent with our findings. Thus, while the biogeochemical impacts of high-severity fires were pronounced, the repeated pattern of recovery over four millennia implies an inherent ability for ecosystem recovery and biogeochemical resilience in this subalpine forested watershed. If predicted warmer and drier summers (Ray *et al.*, 2008) lead to increased disturbance severity or significantly shorter return intervals (Westerling *et al.*, 2011), this long-standing resilience may become compromised.

Acknowledgements

This research was supported by NSF grant IIA-0966472 and a National Park Ecological Research Fellowship (P.E.H.), and by a C. R. Stillinger Forest Science Research Fellowship from the University of Idaho (P.V.D.). We thank D. McWethy, G. Carter, and the National Park Service for logistical support and field assistance, and R. Moran, J. Ziegler, and S. Pauli for laboratory assistance. We thank J. Sibold for pointing out Chickaree Lake and sharing existing tree-ring and fire-history information from the site, and T. Brown for aiding in radiocarbon dating. This manuscript was improved by comments from K. Kavanagh, J. Marshall, and F. Wilhelm, and from B. Shuman and two anonymous reviewers. All data and code used in this manuscript are publicly available via figshare (doi: 10.6084/m9.figshare.988687) or upon request to the corresponding author.

References

Adams JB, Mann ME, Ammann CM. 2003. Proxy evidence for El Nino-like response to volcanic forcing. *Nature* **426**: 274–278.

Amiro BD, Todd JB, Wotton BM, Logan KA, Flannigan MD, Stocks BJ, Mason JA, Martell DL, Hirsch KG. 2001. Direct carbon emissions from Canadian forest fires, 1959–1999. *Canadian Journal of Forest Research* **31**: 512–525.

Baron J, McKnight D, Denning AS. 1991. Sources of dissolved and particulate organic material in Loch Vale Watershed, Rocky Mountain National Park, USA. *Biogeochemistry* **15**: 89–110.

Binford MW. 1990. Calculation and uncertainty analysis of ^{210}Pb dates for PIRLA project lake sediment cores. *Journal of Paleolimnology* **3**: 253–267.

Bladon KD, Silins U, Wagner MJ, Stone M, Emelko MB, Mendoza CA, Devito KJ, Boon S. 2008. Wildfire impacts on nitrogen concentration and production from headwater streams in southern Alberta's Rocky Mountains. *Canadian Journal of Forest Research* **38**: 2359–2371.

Boeckx P, Paulino L, Oyarzún C, Cleemput OV, Godoy R. 2005. Soil δ^{15}N patterns in old-growth forests of southern Chile as integrator for N-cycling. *Isotopes in Environmental and Health Studies* **41**: 249–259.

Bunting L, Leavitt PR, Weidman RP, Vinebrooke RD. 2010. Regulation of the nitrogen biogeochemistry of mountain lakes by subsidies of terrestrial dissolved organic matter and the implications for climate studies. *Limnology and Oceanography* **55**: 333–345.

Carignan R, D'Arcy P, Lamontagne S. 2000. Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 105–117.

Carpenter SR, Cole JJ, Pace ML, Van de Bogert M, Bade DL, Bastviken D, Gille CM, Hodgson JR, Kitchell JF, Kritzberg ES. 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from ^{13}C addition to contrasting lakes. *Ecology* **86**: 2737–2750.

Certini G. 2005. Effects of fire on properties of forest soils: a review. *Oecologia* **143**: 1–10.

Chang SX, Handley LL. 2000. Site history affects soil and plant ^{15}N natural abundances (δ^{15}N) in forests of northern Vancouver Island, British Columbia. *Functional Ecology* **14**: 273–280.

Colombaroli D, Gavin DG. 2010. Highly episodic fire and erosion regime over the past 2000 y in the Siskiyou Mountains, Oregon. *Proceedings of the National Academy of Sciences, USA* **107**: 18909–18914.

Compton JE, Hooker TD, Perakis SS. 2007. Ecosystem N Distribution and δ^{15}N during a Century of Forest Regrowth after Agricultural Abandonment. *Ecosystems* **10**: 1197–1208.

Craine JM, Elmore AJ, Aidar MPM, Bustamante M, Dawson TE, Hobbie EA, Kahmen A, Mack MC, McLauchlan KK, Michelsen A *et al.* 2009. Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. *New Phytologist* **183**: 980–992.

Dawdy DR, Matalas NC. 1964. Statistical and probability analysis of hydrologic data, part III: analysis of variance, covariance, and time series. In: Chow VT, ed. *Handbook of applied hydrology, a compendium of water-resources technology.* New York, NY, USA: McGraw-Hill Book Company, 8.69–8.90.

Dean WE Jr. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. *Journal of Sedimentary Petrology* **44**: 242–248.

DeMaster DJ. 1979. *The marine budgets of silica and ^{32}Si.* PhD thesis, Yale University, New Haven, CT, USA.

Faegri K, Iversen J. 1975. *Text book of pollen analysis, 3rd edn.* New York, NY, USA: Hafner.

Fahey TJ, Knight DH. 1986. Lodgepole pine ecosystems. *BioScience* **36**: 610–617.

Garten CT Jr, Iversen CM, Norby RJ. 2011. Litterfall ^{15}N abundance indicates declining soil nitrogen availability in a free-air CO_2 enrichment experiment. *Ecology* **92**: 133–139.

Giesen TW, Perakis SS, Cromack K Jr. 2008. Four centuries of soil carbon and nitrogen change after stand-replacing fire in a forest landscape in the western Cascade Range of Oregon. *Canadian Journal of Forest Research* **38**: 2455–2464.

Grogan P, Bruns TD, Chapin FS III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. *Oecologia* **122**: 537–544.

Higuera PE, Brubaker LB, Anderson PM, Hu FS, Brown TA. 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs* **79**: 201–219.

Higuera PE, Gavin DG, Bartlein PJ, Hallet DJ. 2010. Peak detection in sediment-charcoal records: impacts of alternative data analysis methods on fire-history interpretations. *International Journal of Wildland Fire* **19**: 996–1014.

Högberg P. 1997. ^{15}N natural abundance in soil-plant systems. *New Phytologist* **137**: 179–203.

Hu FS, Finney BP, Brubaker LB. 2001. Effects of Holocene *Alnus* expansion on aquatic productivity, nitrogen cycling, and soil development in southwestern Alaska. *Ecosystems* **4**: 358–368.

Hu FS, Kaufman D, Yoneji S, Nelson D, Shemesh A, Yongsong H, Tian J, Bond G, Clegg B, Brown T. 2003. Cyclic variation and solar forcing of Holocene climate in the Alaskan subarctic. *Science* **301**: 1890–1893.

Hyodo F, Kusaka S, Wardle DA, Nilsson M. 2012. Changes in stable nitrogen and carbon isotope ratios of plants and soil across a boreal forest fire chronosequence. *Plant and Soil* **364**: 315–323.

Johnson DW, Susfalk RB, Dahlgren RA, Klopatek JM. 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. *Environmental Science and Policy* **1**: 79–86.

Kashian DM, Romme WH, Tinker DB, Turner MG, Ryan MG. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of *Pinus contorta*-dominated forests. *Ecological Monographs* **83**: 49–66.

Kelly EN, Schindler DW, St Louis VL, Donald DB, Vladicka KE. 2006. Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. *Proceedings of the National Academy of Sciences, USA* **103**: 19380–19385.

Kelly RF, Higuera PE, Barrett CM, Hu FS. 2011. A signal-to-noise index to quantify the potential for peak detection in sediment-charcoal records. *Quaternary Research* **75**: 11–17.

Knight DH, Yavitt JB, Joyce GD. 1991. Water and nitrogen outflow from lodgepole pine forest after two levels of tree mortality. *Forest Ecology and Management* **46**: 215–225.

Lavorel S, Flannigan MD, Lambin EF, Scholes MC. 2006. Vulnerability of land systems to fire: Interactions among humans, climate, the atmosphere, and ecosystems. *Mitigation and Adaptation Strategies for Global Change* **12**: 33–53.

Lebauer DS, Treseder KK. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology* **89**: 371–379.

LeDuc SD, Rothstein DE, Yermakov Z, Spaulding SE. 2013. Jack pine foliar δ^{15}N indicates shifts in plant nitrogen acquisition after severe wildfire and through forest stand development. *Plant and Soil* **373**: 955–965.

Lenihan JM, Drapek R, Bachelet D, Neilson RP. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. *Ecological Applications* **13**: 1667–1681.

Lewis SA, Wu JQ, Robichaud PR. 2006. Assessing burn severity and comparing soil water repellency, Hayman Fire, Colorado. *Hydrological Processes* **20**: 1–16.

Likens GE, Bormann FH. 1974. Linkages between terrestrial and aquatic ecosystems. *BioScience* **24**: 447–456.

Marchand D, Prairie YT, del Giorgio PA. 2009. Linking forest fires to lake metabolism and carbon dioxide emissions in the boreal region of Northern Quebec. *Global Change Biology* **15**: 2861–2873.

Marlon JR, Bartlein PJ, Walsh MK, Harrison SP, Brown KJ, Edwards ME, Higuera PE, Power MJ, Anderson RS, Briles C *et al.* 2009. Wildfire responses to abrupt climate change in North America. *Proceedings of the National Academy of Sciences, USA* **106**: 2519–2524.

Martinelli LA, Piccolo MC, Townsend AR, Vitousek PM, Cuevas E, McDowell W, Roberton GP, Santos OC, Treseder K. 1999. Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. *Biogeochemistry* **46**: 45–65.

McLauchlan K, Higuera PE, Gavin DG, Perakis SS, Mack MC, Alexander H, Battles J, Biondi F, Buma B, Colombaroli D *et al.* 2014. Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *BioScience* **64**: 105–116.

McLauchlan KK, Craine JM, Oswald WW, Leavitt PR, Likens GE. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. *Proceedings of the National Academy of Sciences, USA* **104**: 7466–7470.

Meyers PA, Lallier-Verges E. 1999. Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. *Journal of Paleolimnology* **21**: 345–372.

Michalzik B, Kalbitz K, Park JH, Solinger S, Matzner E. 2001. Fluxes and concentrations of dissolved organic carbon and nitrogen: a synthesis for temperate forests. *Biogeochemistry* **52**: 173–205.

Miller ZM. 2011. *An investigation of nitrogen fixation by Russet buffaloberry in Colorado conifer forests.* MS thesis, Colorado State University, Fort Collins, CO, USA.

Millspaugh SH, Whitlock C. 1995. A 750-year fire history based on lake sediment records in central Yellowstone National Park, USA. *The Holocene* **5**: 283–292.

Morris JL, le Roux PC, Macharia AN, Brunelle A, Hebertson EG, Lundeen ZJ. 2013. Organic, elemental, and geochemical contributions to lake sediment deposits during severe spruce beetle (*Dendroctonus rufipennis*) disturbances. *Forest Ecology and Management* **289**: 78–89.

Nave LE, Vance ED, Swantston CW, Curtis PS. 2011. Fire effects on temperate forest soil C and N storage. *Ecological Applications* **21**: 1189–1201.

Olsson U, Binkley D, Smith FW. 1998. Nitrogen supply, nitrogen use, and production in an age sequence of lodgepole pine. *Forest Science* **44**: 454–457.

Pardo LH, Hemond HF, Montoya JP, Fahey TJ, Siccama TG. 2002. Response of the natural abundance of ^{15}N in forest soils and foliage to high nitrate loss following clear-cutting. *Canadian Journal of Forest Research* **32**: 1126–1136.

Paterson AM, Cumming BF, Smol JP, Blais JM, France RL. 1998. Assessment of the effects of logging, forest fires and drought on lakes in northwestern Ontario: a 30-year paleolimnological perspective. *Canadian Journal of Forest Research* **28**: 1546–1556.

Pearson JA, Knight DH, Fahey TJ. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. *Ecology* **68**: 1966–1973.

Pechony O, Shindell DT. 2010. Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences, USA* **107**: 19167–19170.

Perakis SS, Sinkhorn ER, Compton JE. 2011. δ^{15}N constraints on long-term nitrogen balances in temperate forests. *Oecologia* **167**: 793–807.

Philibert A, Prairie YT, Campbell I, Laird L. 2003a. Effects of late Holocene wildfires on diatom assemblages in Christina Lake, Alberta, Canada. *Canadian Journal of Forest Research* **33**: 2405–2415.

Philibert A, Prairie YT, Carcaillet C. 2003b. 1200 years of fire impact on biogeochemistry as inferred from high resolution diatom analysis in a kettle lake from the *Picea mariana*-moss domain (Quebec, Canada). *Journal of Paleolimnology* **30**: 167–181.

Ranalli AJ. 2004. *A summary of the scientific literature on the effects of fire on the concentration of nutrients in surface waters.* Reston, VA, USA: Survey USG, No. USGS-2004-1296.

Ray AJ, Barsugli JJ, Averty KB, Wolter K, Hoerling M, Doesken N, Udall B, Webb RS. 2008. *Climate change in Colorado: a synthesis to support water resources management and adaptation.* Boulder, CO, USA: CU-NOAA WWA, Colorado Water Conservation Board: CU-Boulder University Communications, Marketing & Creative Services.

Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Burr GS, Edwards RL *et al.* 2009. INTCAL09 and Marine09 radiocarbon age calibration curves, 0–50 000 years cal BP. *Radiocarbon* **51**: 1111–1150.

Rhoades CC, McCutchan JH, Cooper LA, Clow D, Detmer TM, Briggs JS, Stednick JD, Veblen TT, Ertz RM, Likens GE *et al.* 2013. Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. *Proceedings of the National Academy of Sciences, USA* **110**: 1756–1760.

Robinson D. 2001. δ^{15}N as an integrator of the nitrogen cycle. *Trends in Ecology and Evolution* **16**: 153–162.

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**: 543–562.

Saito L, Miller WW, Johnson DW, Qualls RG, Provencher L, Carroll E, Szameitat P. 2007. Fire effects on stable isotopes in a Sierran forested watershed. *Journal of Environment Quality* **36**: 91.

Santisteban JI, Mediavilla R, Lopez-Pamo E, Dabrio CJ, Blanca Ruiz Zapata M, Jose Gil Garcia M, Castano S, Martinez-Alfaro PE. 2004. Loss on ignition: a qualitative or quantitative method for organic matter and carbonate mineral content in sediments? *Journal of Paleolimnology* **32**: 287–299.

Schindler DW. 2009. Lakes as sentinels and integrators for the effects of climate change on watersheds, airsheds, and landscapes. *Limnology and Oceanography* **54**: 2349–2358.

Shuman B, Henderson AK, Colman SM, Stone JR, Fritz SC, Stevens LR, Power MJ, Whitlock C. 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. *Quaternary Science Reviews* **28**: 1861–1879.

Sibold JS, Veblen TT, Chipko K, Lawson L, Mathis E, Scott J. 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. *Ecological Applications* **17**: 1638–1655.

Sibold JS, Veblen TT, Gonzalez ME. 2006. Spatial and temporal variation in historic fire regimes in subalpine forests across the Colorado Front Range in Rocky Mountain National Park, Colorado, USA. *Journal of Biogeography* **33**: 631–647.

Smithwick EAH, Kashian DM, Ryan MG, Turner MG. 2009. Long-term nitrogen storage and soil nitrogen availability in post-fire lodgepole pine ecosystems. *Ecosystems* **12**: 792–806.

Smithwick EAH, Turner MG, Mack MC, Chapin FS. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* **8**: 163–181.

Stephan K. 2007. *Wildfire and prescribed burning effects on nitrogen dynamics in central Idaho headwater ecosystems.* PhD thesis, University of Idaho, Moscow, ID, USA.

Stuiver M, Reimer PJ. 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C age calibration program. *Radiocarbon* **35**: 215–230.

Turekian VC, Macko S, Ballentine D, Swap RJ, Garstang M. 1998. Causes of bulk carbon and nitrogen isotopic fractionations in the products of vegetation burns: laboratory studies. *Chemical Geology* **152**: 181–192.

Turner MG, Romme WH, Smithwick EAH, Tinker DB, Zhu J. 2011. Variation in aboveground cover influences soil nitrogen availability at fine spatial scales following severe fire in subalpine conifer forests. *Ecosystems* **14**: 1081–1095.

Turner MG, Smithwick EAH, Metzger KL, Tinker DB, Romme WH. 2007. Inaugural article: Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proceedings of the National Academy of Sciences, USA* **104**: 4782–4789.

US Department of Agriculture NRCS, Soil Survey Staff. 2007. Soil survey of Rocky Mountain National Park, Colorado.

Vitousek PM, Reiners WA. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience* **25**: 376–381.

Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences, USA* **108**: 13165–13170.

White PS, Jentsch A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* **62**: 399–450.

Whitlock C, Bianchi MM, Bartlein PJ, Markgraf V, Marlon J, Walsh M, McCoy N. 2006. Postglacial vegetation, climate, and fire history along the east side of the Andes (lat 41–42.5°S), Argentina. *Quaternary Research* **66**: 187–201.

Wondzell SM, King JG. 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. *Forest Ecology and Management* **178**: 75–87.

Wright HE Jr, Mann DH, Glaser PH. 1984. Piston corers for peat and lake sediments. *Ecology* **65**: 657–659.

Yelenik S, Perakis S, Hibbs D. 2013. Regional constraints to biological nitrogen fixation in post-fire forest communities. *Ecology* **3**: 739–750.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Series-wide Spearman correlation coefficients (*r*) between selected biogeochemical variables from Chickaree Lake.

Fig. S2 Pollen diagram for Chickaree Lake.

Fig. S3 Biogeochemical time series for Chickaree Lake.

Fig. S4 Relationships between charcoal peak magnitude and proxy responses for lower severity/extra local fires.

Table S1 Radiometric (^{210}Pb and ^{14}C) dates for the Chickaree Lake chronology

Table S2 Spearman correlation coefficients for comparisons among $\delta^{13}C$, %C, C : N, and %BSi for three discrete time periods

Notes S1 Estimated measurement error for isotopic analysis.

Notes S2 Additional results supporting interpretation of biogeochemical variables.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.