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

Paul V. Dunnette¹, Philip E. Higuera¹, Kendra K. McLauchlan², Kelly M. Derr¹, Christy E. Briles³ and Margaret H. Keefe¹

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

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 (δ¹⁵N) 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 sediment δ¹⁵N 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 CO₂ 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). Paleocological 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 perturbation and recovery (Likens & Bormann, 1974; McLaughlan 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; McLaughlan 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 (Martellini 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; Millsbaugh & 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 composting). 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 Paleoeology and Fire Ecology Laboratory, where they were split lengthwise, correlated visually and using stratigraphic patterns in...
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 ($\delta^{13}$C and $\delta^{15}$N); ‰) were
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 elastic 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 (Millsbaugh & 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 cm³) 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.charanalyses.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 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 cm³) 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 (available online at http://dx.doi.org/10.6084/m9.figshare.988687). Response variables (δ¹⁵N, %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 catch-
ment fires were excluded from the SEA because they were fol-
lowed 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 catch-
ment 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.

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 millen-
niage-scale changes in fire frequency. However, FRIs for high-
severity catchment fires (FRIhs) were higher early in the record;
10 events occurred between c. 4250 and 2000 cal yr BP (mean
FRIhs = 225 yr), while only three occurred over the last two
calendrical millennia (mean FRIhs = 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
even to separate into subgenera, and, of these, 98% were iden-
tified to subgenus Pinus and 2% to subgenus Strobus. We there-
fore 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 sedi-
mentation rates (Fig. 2), and several other lines of evidence suggest
that rapid accumulation of allochthonous (terrestrial) and autoch-
thonous (originating within the lake) organic matter preserved
biogeochemical signals of terrestrial processes and algal productiv-
ity, permitting inferences regarding post-fire forest and lake eco-
system 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
δ15N (mean 0.96‰; SD 0.49; Fig. S3), and a weak negative cor-
relation between δ13C and %N (r = −0.26; P < 0.01; Fig. S1),
are consistent with values from lakes receiving significant terres-
trial 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 δ13C (r = 0.34; P = 0.04) and δ15N (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
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, δ¹⁵N 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, δ¹⁵N 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 Cacc 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 Cacc anomalies occurred c. 15–35 yr after events. The recovery of %C, %N, C : N, and Cacc toward average levels c. 30–60 yr after fire coincided with a monotonic decrease in δ¹⁵N to significantly low values c. 55–70 yr post-fire. Sediment δ¹⁵N, bulk density, %C, and %N all returned to near-pre-fire levels by c. 75 yr
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 \(\delta^{15}N\) \(\left( r = 0.75 \right)\), %C \(\left( r = -0.63 \right)\), %N \(\left( r = -0.74 \right)\), and bulk density \(\left( r = 0.79 \right)\) 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 \(\left( r = -0.66 \right)\), %C \(\left( r = -0.81 \right)\), %N \(\left( r = -0.80 \right)\), and bulk density \(\left( r = 0.74 \right)\) but was uncorrelated with \(\delta^{15}N\) \(\left( r = 0.11; \ P = 0.75; \right.\) Fig. 6). Peak magnitude of lower severity/extra local fires was uncorrelated with all response variables within both post-fire temporal windows (Fig. S4).

### 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 \(^{14}N\),
We propose that combustion of the $^{15}$N-depleted forest floor (Högb erg, 1997; Grogan et al., 2000; LeDuc et al., 2013) and preferential volatilization of $^{14}$N from vegetation and soils (Tureckian 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 (Högb erg, 1997; Grogan et al., 2000; Stephan, 2007; LeDuc et al., 2013).

We also considered elevated nitrification and nitrate losses aspotential 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 (Högb erg, 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 paleoecological (Paterson et al., 1998; Philibert et al., 2003b) research, largely in boreal watersheds, has revealed subtle 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 ($C_{sec}$) 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 ($C_{sec}$, %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 of c. 0%) in the plant–soil system via post-fire symbiotic N fixation (Smithwick et al., 2005; Petakis 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, $C_{\text{acc}}$, 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 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.

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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 \((^{210}\text{Pb} \text{ and } ^{14}\text{C})\) dates for the Chickaree Lake chronology.

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

**Notes S1** Estimated measurement error for isotopic analysis.

**Notes S2** Additional results supporting interpretation of biogeochemical variables.

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