# BIOGEOCHEMICAL IMPACTS OF FIRE OVER FOUR MILLENNIA IN A ROCKY MOUNTAIN SUBALPINE WATERSHED

A Thesis
Presented in Partial Fulfillment of Requirements for the
Degree of Master of Science
with a
Major in Natural Resources
in the
College of Graduate Studies
University of Idaho

by
Paul V. Dunnette

December 2013

Major Professor: Philip E. Higuera, Ph.D.

# AUTHORIZATION TO SUBMIT THESIS

This thesis of Paul V. Dunnette, submitted for the degree of Master of Science and titled "Biogeochemical Impacts of Fire over Four Millennia in a Rocky Mountain Subalpine Watershed," has been reviewed in final form. Permission, as indicated by the signatures and dates given below, is now granted to submit final copies to the College of Graduate Studies for approval.

Major Professor: ________________________________ Date: __________________
Philip E. Higuera

Committee Members:
________________________________ Date: _________________
Kathleen L. Kavanagh

________________________________ Date: _________________
John D. Marshall

________________________________ Date: _________________
Kendra K. McLauchlan

________________________________ Date: _________________
Frank M. Wilhelm

Department
Administrator: ________________________________ Date: _________________
Anthony S. Davis

Discipline's
College Dean: _________________________________ Date: __________________
Kurt S. Pregitzer

Final Approval and Acceptance by the College of Graduate Studies:

_________________________________ Date: __________________
Jie Chen

# ABSTRACT

Wildfires have the potential to dramatically alter forest carbon (C) storage and nitrogen (N) availability, but the long-term biogeochemical legacy of these events is poorly understood. I used a high-resolution lake-sediment record of fire occurrence and biogeochemical change from a subalpine watershed in Colorado, USA, to examine the nature, magnitude, and duration of fire-induced ecosystem impacts over the last ~4250 yr. Superposed Epoch Analysis (SEA) revealed pronounced biogeochemical responses to multiple high-severity fires, inferred from statistically significant peaks in charcoal accumulation and magnetic susceptibility (an indicator of erosion). On average, fires were followed closely by significant increases in bulk sediment N isotopic composition ($\delta^{15}N$) and bulk density, and declines in %C and %N – likely reflecting destruction of the forest floor, terrestrial C and N losses, and erosion. Anomalously low sediment C:N ~20-50 yr after fires suggests a long-lived reduction in terrestrial organic matter subsidies to the lake. The magnitude of post-fire change was well-correlated with charcoal peak magnitude, indicating that the extent of disturbance impacts scaled directly with inferred fire size and/or severity. Trends ~30-75 yr following fire, including a significant decline in $\delta^{15}N$, were consistent with patterns observed in chronosequences of forest C and N accumulation, suggesting that terrestrial successional processes were reflected in the sediments. The results of this study, the first to systematically test the utility of lake-sediment $\delta^{15}N$ as an indicator of fire-induced N cycle change, indicate that high-resolution analysis of sediment records may offer a unique and powerful tool for elucidating the effects of fire on ecosystem biogeochemistry over decades to millennia.

# ACKNOWLEDGMENTS

I would like to thank my major advisor, Philip Higuera, for financial support and guidance; my committee members, John Marshall, Kathleen Kavanagh, Frank Wilhelm, and Kendra McLauchlan, for their feedback and advice; and current and former members of the University of Idaho Paleoecology and Fire Ecology Lab for their friendship and assistance. And, most importantly, I would like to thank my partner, Joan Rutkowski, for her unconditional love and support during this difficult project.

Thanks to the National Park Service and Dave McWethy for logistical support and field assistance, and to Kelly Derr, Maggie Keefe, Ryan Moran, Justin Ziegler, Shannon Pauli, and Christy Briles for laboratory assistance. This research was supported by a National Parks Ecological Research Fellowship and the WildFIRE PIRE project, funded at the University of Idaho through NSF grant OISE-0966472 to Philip Higuera, and by a C.R. Stillinger Forest Science Research Fellowship from the University of Idaho, awarded to the author.

# TABLE OF CONTENTS

# INTRODUCTION

Predicted increases in global fire activity under warmer and drier conditions (e.g., Pechony and Shindell 2010, Moritz et al. 2012) have raised concerns about interactions among climate, fire, and key ecosystem processes (e.g., Lavorel et al. 2006, Bonan 2008). Fires release $CO_2$ to the atmosphere, affect carbon (C) storage, and reduce nitrogen (N) stocks (e.g., Amiro et al. 2001, Kashian et al. 2006, Nave et al. 2011) – which limit net primary productivity and C accumulation in forests worldwide (Lebauer and 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 relationship between climate and the rate and 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 (e.g., Zackrisson et al. 2004, Smithwick et al. 2009), which hinge on the assumption that conditions differed little among study sites or over time (Johnson and Miyanishi 2008). However, the biogeochemical effects of disturbance are diverse, owing to ecosystem heterogeneity over space and time (White and 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 (e.g., Lenihan et al. 2003, Marlon et al. 2009, Kreyling et al. 2011). For example, fires could build or diminish forest N stocks and availability as temperatures increase, depending on changes in fire severity or frequency and the rates of N mineralization and symbiotic N fixation (Rustad et al. 2001, Thornley and Cannell 2004, 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 environmental changes over decades to thousands of years, helping to contextualize modern disturbance (e.g., Whitlock et al. 2011) and informing predictions of ecosystem response under climate change. Moreover, high-resolution analysis of lake-sediment records may be the only way to capture post-fire biogeochemical changes over successional and longer time scales (i.e., several decades to centuries) at a single site.

In high-elevation forested catchments, where allochthonous inputs strongly regulate surface water C and N biogeochemistry (e.g., Richey and Wissmar 1979, Baron et al. 1991, Hood et al. 2005, Bunting et al. 2010) forest disturbance and succession may have profound effects on lakes – and thus lake sediment composition – that reflect changes in terrestrial biogeochemical cycling and the magnitude and duration of the perturbation and recovery (Likens and Bormann 1974, McEachern et al. 2000, 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 $^{15}N$ / $^{14}N$; denoted $\delta^{15}N$) of bulk lake-sediment organic matter (Hu et al. 2001, O'Reilly et al. 2005, McLauchlan et al. 2007). When terrestrial N availability is high, soil and vegetation $\delta^{15}N$ tend to rise as N is lost from the system via hydrologic and gaseous pathways because the processes responsible for N export discriminate against $^{15}N$ (e.g., nitrification, denitrification; Hogberg 1997, Robinson 2001, Dijkstra et al. 2008, Craine et al. 2009). Conversely, strong biotic N retention under low N availability tends to depress soil and vegetation $\delta^{15}N$ by minimizing these losses (Martinelli et al. 1999, Craine et al. 2009). Forest disturbances disrupt this biotic control over N by reducing biomass – leading to increased N availability, N losses, and organic matter $\delta^{15}N$ (e.g., Pardo et al. 2002, Boeckx et al. 2005, Smaill et al. 2009). Fires temporarily raise terrestrial N availability, but most N losses to these events occur via volatilization (Johnson et al. 1998, Nave et al. 2011) – a process that appears to preferentially release $^{14}N$ to the atmosphere (Turekian et al. 1998, Saito et al. 2007). Recent work suggests that fires tend to increase soil and vegetation $\delta^{15}N$ by causing losses of $^{15}N$-depleted gaseous N, organic matter, and nitrate (e.g., Grogan et al. 2000, Boeckx et al. 2005, Stephan 2007, Thiffault et al. 2008, LeDuc et al. 2013) and that higher-severity events may cause greater isotopic enrichment (e.g., Stephan 2007, LeDuc et al. 2013). Modern studies of fire's impacts on N cycling are complicated by the spatial and temporal heterogeneity of processes affecting N pools throughout forested landscapes (e.g., Turner et al. 2011, LeDuc et al. 2013). Because lake-sediment $\delta^{15}N$ integrates N cycle processes over space and time (Robinson 2001, Dijkstra et al. 2008, McLauchlan 2008), 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, I tested the utility of lake-sediment $\delta^{15}N$ as an indicator of fire-induced ecosystem change. I analyzed sediments from a lake within a Rocky Mountain subalpine lodgepole pine forest – an ecosystem characterized by low N availability and cycling rates (Fahey and Knight 1986). Lake-sediment $\delta^{15}N$ is a product of both terrestrial and aquatic processes, so my interpretations are constrained by supporting proxies of biogeochemical and physical change (e.g., %C, %N, C:N) – themselves invaluable indicators of resource flux and availability. I used a high-resolution (~4 yr/sample) lake-sediment record of macroscopic charcoal accumulation rate (CHAR; # pieces $cm^{-2}$ $yr^{-1}$) and magnetic susceptibility (MS, a proxy for soil erosion; e.g., Millspaugh and Whitlock 1995) spanning the past ~4250 years to define two types of fire events. Statistically significant CHAR peaks were defined as "local" fires occurring within ~1 km of the lake (Gavin et al. 2003, Higuera et al. 2007), and CHAR peaks coincident with significant MS peaks were identified as local fires that were likely high-severity events within the catchment. I then quantified the average biogeochemical response to these within-watershed fires and a subset of the other fires using Superposed Epoch Analysis (SEA; aka data compositing). I hypothesized that (a) lake-sediment $\delta^{15}N$ would increase and C and N content would decrease in the years following within-watershed events, reflecting organic matter and N losses to fire; (b) the degree of post-fire change would scale with the magnitude of disturbance, inferred from charcoal peak magnitude (Whitlock et al. 2006); and (c) declining terrestrial N availability due to strong nutrient demand from an aggrading forest would lower sediment $\delta^{15}N$ several decades after fires.

# METHODS

## Study Site and Regional Setting

Chickaree Lake (40.334249°N, 105.847270°W, 2796 m a.s.l.) is a small, deep lake in Rocky Mountain National Park, Colorado, USA (1.6 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 ~28 ha Chickaree Lake watershed (Fig. 1) has gentle to moderate topography and well-drained sandy loam soils derived from granite, gneiss, and schist overlain by a layer of decomposing litter (U.S. Department of Agriculture 2007).

The lake is surrounded by an even-aged stand of lodgepole pine (*Pinus contorta*) dating to a 1782 Common Era (CE) stand-replacing fire (Sibold et al. 2007). The subdominant forest species are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), with a variety of shrub taxa (e.g., *Artemisia*, *Rosa*) in the understory. The fire regime is characterized by infrequent, high-severity crown fires (~100-300 yr mean return intervals) associated with severe seasonal drought (Buechling 2004, Sibold et al. 2006). The modern regional climate is continental, with cold, dry winters and warm, wet summers. In nearby Grand Lake (~8 km from the lake, 2664 m a.s.l.), 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 (~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 ~12 cm were subsampled at 0.5 cm intervals in the field. Cores were stored at ~4$^{o}$C at the University of Idaho Paleoecology and Fire Ecology Laboratory, where they were split lengthwise, correlated visually and using stratigraphic patterns in magnetic susceptibility and charcoal concentration, and sectioned continuously at 0.5 cm intervals.

The sediment chronology is based on 13 $^{210}$Pb dates for the upper 20 cm and 25 $^{14}$C dates from deeper sediments (Table B1). Measurements of $^{210}$Pb were performed by Flett Research Ltd. (Manitoba, Canada) and the $^{210}$Pb chronology was developed using the constant rate of supply model with old age correction adapted from Binford (1990). Bulk sediments, concentrated charcoal, and terrestrial macrofossils were treated with an acid-base-acid procedure (Oswald et al. 2005) prior to submission to Lawrence Livermore National Laboratory Center for Accelerator Mass Spectrometry (CAMS; Livermore, CA) for radiocarbon analysis. Radiocarbon ages were calibrated to years before Common Era (CE) 1950 (hereafter "cal yr BP") using the program CALIB 6.0 (Stuiver and Reimer 1993) and the IntCal09 dataset (Reimer et al. 2009). The final age-depth model was developed with a weighted cubic smoothing spline derived from 1000 bootstrapped samples from the calibrated age distributions using the program MCAgeDepth (Higuera et al. 2009).

## Sediment Biogeochemistry

Bulk sediment C and N content (% by mass) and isotopic composition (delta notation [$\delta^{13}C$, $\delta^{15}N$] , ‰) were measured at a median interval of 0.5 cm (n = 618). Sediment subsamples (1 $cm^3$) were dried at $65^oC$ for 24 hr, then ground to a fine powder and homogenized. Approximately 2-4 mg from each subsample was combusted in an elemental analyzer and analyzed 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 primarily via within-run and between-run standard deviations (stdev.) from replicate analysis of a lake-sediment standard. Error (one stdev.) was < 0.23‰ for $\delta^{15}N$ and < 0.10‰ for $\delta^{13}C$. Measurement accuracy and variability associated with subsampling were also evaluated (Appendix A). Additionally, organic matter samples collected from the forest around the lake as modern reference material were prepared and analyzed for biogeochemistry as described above (Table B2).

Bulk density (dry g/wet $cm^3$) was measured on all sediment samples analyzed for biogeochemistry. Organic matter and inorganic C content were estimated in subsamples composed of sediments from two consecutive 0.5 cm samples at a median interval of 5 cm ($n = 121$) via sequential loss on ignition of 1 $cm^3$ subsamples at $550^oC$ (4 hr; $LOI_{550}$) and $1000^oC$ (2 hr; $LOI_{1000}$), respectively. A strong positive correlation between %C and $LOI_{550}$ ($r = 0.97$, $p < 0.01$; Fig. 4) and low estimated inorganic C content (~6% of total C) indicated that sediment C was dominated by organic C, with little carbonate (Dean 1974, Heiri et al. 2001, Santisteban et al. 2004). Thus, I interpreted C as total organic carbon. Strong positive correlations between %N and both %C ($r = 0.91$, $p < 0.01$; Fig. 4) and $LOI_{550}$ ($r = 0.93$, $p < 0.01$) indicated that N was also largely organic. I 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 and 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 (~ 4-10; Meyers and Lallier-Verges 1999).

Sediment biogenic silica content (BSi; % by mass) was measured in subsamples composed of sediments from multiple consecutive samples (spanning ~2-3 cm) 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 (e.g., Hu et al. 2003). To help infer factors controlling sediment biogeochemistry, relationships among variables were evaluated using Spearman ($r_s$) 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 and Matalas (1964). Correlations were deemed significant if p was less than or equal to (≤) 0.05, using the adjusted sample size.

## Fire and Vegetation History

Theoretical (Higuera et al. 2007) and empirical (Gavin et al. 2003, Higuera et al. 2011) evidence suggest that distinct peaks in lake-sediment charcoal accumulation represent fires occurring within ~1 km of small lakes, particularly in ecosystems with high-severity fire regimes. Given the small Chickaree Lake watershed (~28 ha; Fig. 1), some charcoal peaks likely reflect charcoal deposition resulting from events that occurred within 1 km of the lake but outside the drainage basin – meaning their biogeochemical effects would not be recorded in the lake sediments.

To identify fires that occurred within the watershed, I relied upon a supporting paleoecological proxy of disturbance: lake-sediment magnetic susceptibility (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 and King 2003). Because these inputs are positively correlated with lake-sediment MS (Thompson et al. 1975), a significant increase in MS coincident with or closely following a charcoal peak strongly suggests erosion after a high-severity fire within the watershed (e.g., Millspaugh and Whitlock 1995, Colombaroli and Gavin 2010).

I inferred fires and erosion events from statistically significant peaks in macroscopic (> 125 µm) charcoal accumulation rate (CHAR; # 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 days to facilitate disaggregation, wet-sieved through a 125 µm mesh, and soaked in a 2% sodium hypochlorite solution for 24 hours to remove or lighten the non-charcoal organic content. Charcoal particles were identified based on texture, color, and morphology and counted with the aid of a Nikon SMZ800 microscope at 40x magnification. I calculated CHAR by multiplying sediment accumulation rates (cm/yr) by charcoal concentrations (# 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 (Higuera et al. 2009; Appendix A; available online at http://www.charanalysis.googlepages.com). In short, I used a locally defined (500 yr) threshold and the 99.9th percentile of the peak component of each time series to define fire and erosion events. Background CHAR and MS were modeled with a 500 yr locally weighted regression and subtracted from the interpolated time series to isolate their peak components. Significant CHAR peaks (fires) preceding significant MS peaks (erosion events) by $\leq$ 20 yr (1-2 interpolated samples) or following erosion events by 10 yr (1 sample) were identified as probable high-severity fires within the Chickaree Lake watershed, hereafter “high-severity catchment fires.” I interpreted other CHAR-inferred fires as either lower-severity events or fires occurring outside the watershed, hereafter “lower-severity/extra local fires.” A signal-to-noise index (SNI) based on the statistical separation of CHAR values attributed to fires (i.e., “signal”) and high-frequency CHAR values resulting from other factors (i.e., “noise”) was used to evaluate whether the charcoal record was suitable for peak detection (Kelly et al. 2011).

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 ~175 cm and a median interval of 25 cm below ~175 cm. Samples were prepared using standard digestion methods (Faegri and Iversen 1975). Pollen was examined at 400 -1000 x magnification with the aid of a Nikon Eclipse C*i* microscope and identified using taxonomic keys and on-line reference materials**.** Results are reported as percentages relative to the terrestrial pollen sum.

## Quantifying Biogeochemical Response to Fire

I assessed the biogeochemical effects of fire via Superposed Epoch Analysis (SEA), a nonparametric method used to evaluate the average response to multiple events in a time series (e.g., Prager and Hoenig 1989, 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. Response variables ($\delta^{15}N$, $\delta^{13}C$, %N, %C, $C_{acc}$, C:N, bulk density) were sampled every 0.5 cm for ~5 cm before and after each fire event. Outside of this window, subsamples composed of sediments from two consecutive 0.5 cm samples were analyzed at ~1 cm intervals. The high-resolution sampling window represents ~50 to 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; e.g., Pearson et al. 1987). Prior to SEA, samples were interpolated to the median sample resolution 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, I subtracted the low-frequency trends from the interpolated time series to obtain a residual series. The 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. Because many samples ~50-75 yr post-fire were not included in high-resolution sampling, composite patterns during this period may be more muted than if they were sampled at higher resolution.

To assess statistical significance of response series values, confidence intervals were generated with a Monte Carlo randomization method. For each response variable, 10,000 time series were created by randomly shuffling samples in 5-sample blocks to account for 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% confidence intervals.

As a complementary analysis to the SEA, I used correlation analysis to evaluate if the degree of biogeochemical response to fire varied with the magnitude of the events, measured via charcoal peak magnitude (# particles/cm$^2$), an assumed metric of fire severity, size, and/or proximity to the lake (e.g., Whitlock et al. 2006). Specifically, I determined the Pearson correlation coefficient ($r_p$) between log-transformed peak magnitude and response variable residuals averaged over two post-fire temporal windows (0-20 yr; 20-50 yr) corresponding to significant responses to high-severity catchment fires revealed by the SEA. The correlation analysis was performed for both types of fire events.

# RESULTS

## Sediment Chronology, Fire History, and Vegetation History

The entire Chickaree Lake sediment record spans ~6300 yr, but here I report on the record from ~4250 cal yr BP to present, when sedimentation rates ranged from 0.08 to 0.41 cm/yr, and averaged 0.15 cm/yr (4 yr/sample; Fig. 2). The only clear evidence of instantaneous sedimentation was a ~1.5 cm section of charcoal at ca. 3720 cal yr BP (535.0-536.5 cm), likely 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.

Charcoal and magnetic susceptibility (MS) peak analysis revealed 34 fires and 20 erosion events. Thirteen fires coincided with erosion events, meeting my definition for high-severity catchment fires, while other fires were defined as lower-severity/extra local fires (Fig. 3). Two high-severity catchment fires (ca. 4176 and 3313 cal yr BP) were excluded from the analysis of biogeochemical response because they were followed too closely (< 75 yr) by other high-severity catchment fires. Including these events in the SEA would have resulted in overlapping and thus distorted composite records.

The CHAR record median signal-to-noise index (SNI; 19.1) far exceeded the minimum median SNI of 3 suggested for charcoal peak analysis (Appendix A; Kelly et al. 2011) – providing strong evidence that significant CHAR peaks represent fires. A surface fire identified in a tree ring fire history reconstruction near the lake (ca. 1872 CE; Sibold et al.

2007) – which had little ecological impact – caused no discernible sediment charcoal accumulation, suggesting that similar events did not leave charcoal signatures. In contrast, the 1782 CE tree ring-dated stand-initiating fire corresponded well with the most recent high-severity catchment fire in the charcoal record (Fig. 3), indicating that large, high-severity events were recorded in the sediments. In the original age-depth model, the 1782 fire fell within the 95% confidence interval of the date of this charcoal peak (to further constrain the final age model, a date of 1782 was ascribed to this peak). Given the small catchment area (~28 ha), many of the lower-severity/extra local fires could have occurred beyond the watershed boundary (but still within ~1 km of the lake).

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

Pollen percentages indicate that lodgepole pine dominated the forest around the lake for the entire record (Fig. B1). *Pinus* pollen accounted for 70% (mean) of total terrestrial pollen (range, 46-88%). I assume that *Pinus* pollen primarily represents lodgepole rather than limber pine (*Pinus flexilis*) based on abundance of the *Pinus* subgenus *Pinus* type pollen (e.g., Minckley et al. 2012). *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*, *Ceanothus*, *Shepherdia* spp.), were nearly absent from the pollen record, never accounting for more than ~1% of the pollen in any single sample.

## Sediment Biogeochemistry

### *Provenance and Preservation of Organic Matter*

Abundant organic C (mean, 16.2%, stdev., 4.4%; Fig. 4), 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 about fire-induced forest and lake ecosystem change. High organic matter content, the strong correlation between %C and %N, an absence of persistent down-core trends, and the infrequency of unexplained strong correlations between isotopic composition and %C, %N, or C:N (Fig. 4, Fig. B2, Table B3) suggest that sediment organic matter was relatively well-preserved and subject to minimal systematic diagenetic degradation of labile material, possibly due to rapid burial under anoxic conditions (Hodell and Schelske 1998, Meyers and Lallier-Verges 1999, Lehmann et al. 2002, Galman et al. 2008, Galman et al. 2009). A weak correlation between %C and %N could indicate preferential degradation of N-enriched organic matter, and a strong positive correlation between C:N and $\delta^{15}N$ may be caused by preferential losses of $^{14}N$ under oxic conditions (Lehmann et al. 2002) – but these relationships were not evident in the Chickaree record (Fig. 4). Thus, I conclude that diagenetic changes likely did not obscure biogeochemical signals of organic matter source or fire impacts.

Sediment $\delta^{15}N$ values lower than those typical of algae (which take up $^{15}N$-enriched dissolved inorganic N [DIN] ), and a weak negative correlation between $\delta^{15}N$ and %N (Fig.

4), are consistent with regulation of sediment isotopic composition by dissolved organic N (DON) derived from the isotopically depleted forest floor (Hogberg 1997, Meyers and Lallier-Verges 1999, Michalzik et al. 2001, Bunting et al. 2010). DON accounts for most hydrologic N losses from many undisturbed temperate forests (e.g., Perakis and Hedin 2002, Vanderbilt et al. 2002). Work by Bunting et al. (2010) demonstrated that terrestrial DON inputs strongly influenced N cycling and sediment $\delta^{15}N$ in a series of subalpine lakes in the Canadian Rockies. Mean Chickaree Lake $\delta^{15}N$ (0.96‰, stdev., 0.49‰,) was similar to sediment $\delta^{15}N$ values of Canadian Rockies lakes where DON accounted for > 75% of lake N (mean, 0.97‰, stdev., 1.5‰,). Mean Chickaree Lake sediment C:N (14.9, stdev., 1.8; Fig. 4) was considerably higher than the C:N of algal organic matter (~ 4-10; Meyers and Lallier-Verges 1999) and similar to the sediment C:N of subalpine lakes receiving significant terrestrial organic matter inputs (14.8; 14.1; Wissmar et al. 1977, Bunting et al. 2010). However, high terrestrial organic matter C:N values in Rocky Mountain subalpine forests (~25-70; Fahey et al. 1985, Baron et al. 2000; Table B2) suggest that allochthonous inputs did not dominate Chickaree Lake sediment organic matter. Rather, sediment composition was also heavily influenced by algal productivity, further evidenced by high BSi content (mean, 26%, stdev., 4.3%) and correlations among proxies (Fig. 4, Table B3). For example, negative correlations between BSi and both C:N and %C (Fig. 4, Table B3) indicate that algal organic matter tended to reduce C:N while diatom remains diluted organic matter derived from non-siliceous algae and/or terrestrial sources.

The imprint of algal productivity was also apparent in sediment isotopic composition. Algal discrimination against $^{15}N$ and $^{13}C$ tends to subside as DIN and dissolved inorganic C (DIC) stocks are depleted during periods of high aquatic productivity, leading to isotopic enrichment of algal biomass (e.g., Hollander and McKenzie 1991, Hodell and Schelske 1998, Teranes and Bernasconi 2000). In the Chickaree Lake record, a positive correlation between BSi and $\delta^{15}$N (Fig. 4) suggests that elevated algal productivity periodically led to isotopic enrichment of sediment organic matter. Productivity-induced $^{13}$C enrichment was most evident between ~1300 cal yr BP and present, when $\delta^{13}$C was positively correlated with BSi and negatively related to C:N and %C (Table B3). Positive correlations between $\delta^{13}$C and C:N in other sections of the core (e.g., ~2800 to 1300 cal yr BP; Table B3) indicate periods when within-lake C respiration likely depressed DIC $\delta^{13}$C, resulting in autochthonous organic matter that was isotopically depleted relative to terrestrial plants (Rau 1978, LaZerte 1983). All $\delta^{13}$C values fall within the range characteristic of both algal organic matter and temperate forest vegetation (Fig. B2; Meyers and Lallier-Verges 1999).

### *Biogeochemical Response to Fire*

Superposed Epoch Analysis (SEA) revealed pronounced and statistically significant biogeochemical and physical changes following high-severity catchment fires (Fig. 5, Fig. 6). The events were followed closely (~0-20 yr) by significant increases in lake-sediment $\delta^{15}$N and bulk density and decreases in %C and %N. Within ~25 yr post-fire, $\delta^{15}$N and bulk density returned to non-significant values, while %C and %N were anomalously low until ~35-40 yr after fire. C:N and $C_{acc}$ were significantly high immediately after fire, then dropped sharply ~15-20 yr post-fire to anomalously low values. C:N remained low ~20-50 yr post-fire, while $C_{acc}$ anomalies occurred between ~15 and 35 yr after events. Recovery of %C, %N, C:N, and $C_{acc}$ toward average levels ~30-50 yr after fire coincided with a monotonic decrease in $\delta^{15}$N to significantly low values ~55-70 yr post-fire. Sediment $\delta^{15}$N, bulk density, %C, and %N all returned to near-pre-fire levels by ~75 yr after events. Unlike other variables, composite $\delta^{13}C$ did not differ from random before or after fire events; however, examination of patterns after individual high-severity catchment fires revealed several pronounced responses that varied in direction, resulting in a neutral composite post-fire record (Fig. 5). In contrast to the marked responses to high-severity catchment fires, the SEA showed little response variable change following 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. 7). Peak magnitude was significantly correlated with mean residual $\delta^{15}N$ ($r_p = 0.75$), bulk density ($r_p = 0.79$), %C ($r_p = -0.62$), and %N ($r_p = -0.74$) ~0-20 yr after fires ($p \leq 0.05$; Fig. 7) – the period of anomalously high $\delta^{15}N$ revealed by the SEA (Fig. 6). Between 20 and 50 yr post-fire, the period marked by significantly low composite C:N (Fig. 6), peak magnitude was significantly correlated with mean residual bulk density ($r_p = 0.75$), %C ($r_p = -0.81$), %N ($r_p = -0.80$), and C:N ($r_p = -0.66$), but was uncorrelated with $\delta^{15}N$ ($r_p = 0.11$, $p = 0.75$; Fig. 7). Peak magnitude of lower-severity/extra local fires was uncorrelated with all response variables within both post-fire temporal windows (Fig. B3).

## DISCUSSION

### Biogeochemical Response to Fire

This analysis revealed significant biogeochemical changes following high-severity catchment fires that likely reflect terrestrial C and N losses to combustion/volatilization, 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. The significant composite responses indicate that ecosystem impacts and recovery were relatively consistent over the past ~4250 yr, a period characterized by marked climatic change in the Colorado Rockies (Shuman et al. 2009, Anderson 2011), though examination of trends over multi-centennial-and-longer time scales is beyond the scope of this study.

Consistent with my hypotheses, the fires were followed closely by statistically significant increases in sediment $\delta^{15}N$ and declines in %C and %N, and responses were more pronounced after events that were higher-severity, larger, or closer to the lake (inferred from charcoal peak magnitude). As predicted, $\delta^{15}N$ declined significantly as sediment organic matter recovered over decades, suggesting diminishing terrestrial N availability during forest aggradation. These multi-decadal post-fire biogeochemical trends, similar to patterns from forest chronosequences, highlight a long-lived coupling between the forest and lake following severe disturbance and suggest that successional terrestrial processes were recorded in the sediments.

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. The results reveal a clear link between lake-sediment $\delta^{15}N$ and fire that has not been explicit in lower-resolution and broader-temporal-scale paleoecological reconstructions (e.g., Gillson and Ekblom 2009, Jeffers et al. 2012). Detecting the biogeochemical impacts of fire hinged on several factors. First, the analysis isolated fires that clearly occurred within the catchment, excluding events outside the basin that could not have affected the composition of terrestrial exports to the lake. Second, high-resolution sampling around fires allowed me to capture high-magnitude changes that may have been erased or blunted at coarser resolution. And finally, the SEA highlighted signals of fire amidst other high-frequency variability caused by processes operating over similar and longer time scales.

### *Short-Term Response (~0-20 yr post-fire)*

The significant increase in lake-sediment $\delta^{15}N$ following high-severity catchment fires is consistent with isotopic enrichment caused by terrestrial N loss (Fig. 6). Several mechanisms may share responsibility for the response, including preferential volatilization of $^{14}N$ (Turekian et al. 1998, Saito et al. 2007), combustion of isotopically light organic matter pools (Hogberg 1997, LeDuc et al. 2013), and elevated nitrification followed by losses of $^{15}N$-depleted nitrate and gaseous N (Pardo et al. 2002, Boeckx et al. 2005, Pörtl et al. 2007, LeDuc et al. 2013). While it is possible that climatic conditions at the time of fire or an influx of soil nutrients to the lake after fire promoted aquatic processes that contributed to the $\delta^{15}N$ signal (i.e., algal productivity, denitrification; Teranes and Bernasconi 2000, Veraart et al. 2011), the coincident significant declines in %C and %N and increase in bulk density (Fig. 5, Fig. 6) indicate that the $\delta^{15}N$ anomaly was driven by a marked shift in the physical and biogeochemical composition of forest inputs to the lake. Algal biomass $\delta^{15}N$ tends to reflect the isotopic composition of source N (e.g., Kaushal et al. 2006), so an increase in terrestrial $\delta^{15}N$ following fire may be recorded in autochthonous, as well as allochthonous, sediment organic matter as isotopically enriched material enters a lake.

The magnitude of post-fire change was well-correlated with charcoal peak magnitude, while proxy response to lower-severity/extra local fires was comparatively muted or non-existent and uncorrelated with peak magnitude (Fig. 7, Fig. B3). These results suggest that larger or more severe fires caused greater organic matter losses, erosion, and isotopic enrichment (e.g., Stephan 2007) – indicating that this suite of lake-sediment proxies can help infer the severity and/or extent of past fires. The results also provide some of the strongest support for previous interpretations of charcoal peak magnitude as an indicator of fire severity (e.g., Whitlock et al. 2006, Higuera et al. 2009).

I propose that combustion of the $^{15}$N-depleted forest floor (Hogberg 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 dissolved and particulate organic matter to the lake – all raising sediment $\delta^{15}$N. Destruction of the forest floor removed the chief pre-fire source of allochthonous C (Baron et al. 1991, Brooks et al. 1999, Michalzik et al. 2001) and the resulting influx of soil-derived mineral material increased bulk density and reduced % organic matter (i.e., %C, %N) in the sediments. High C:N and $C_{acc}$ immediately after fire suggest a short-lived surge of terrestrial material to the lake (Fig. 6).

High-severity fires may cause wholesale losses of litter and organic soil (e.g., Turner et al. 2007, Bormann et al. 2008), which typically hold about one-third of temperate forest soil N (Nave et al. 2011). Because soil $\delta^{15}$N increases with soil depth (e.g., Natelhoffer and Fry 1988), these losses expose more isotopically enriched horizons to erosion, likely raise the $\delta^{15}$N of soil leachates, and may result in elevated foliage and litter $\delta^{15}$N during early succession as plants take up isotopically heavier N (Hogberg 1997, Grogan et al. 2000, Stephan 2007, LeDuc et al. 2013). Thus, the isotopic signal in the Chickaree Lake sediments may be a product of both N loss to fire and increased contributions from a more $^{15}$N-enriched N pool. The proxy responses, and their strong relationships with charcoal peak magnitude, suggest that post-fire $^{15}N$ enrichment may reflect the extent of ($^{15}N$-depleted ) forest floor combustion – identified as a strong indicator of fire severity in Colorado Front Range forests (Lewis et al. 2006).

The correlation between charcoal peak magnitude and sediment $\delta^{15}N$ (Fig. 7) also suggests that the charcoal itself may have contributed to isotopic enrichment. Charred material isolated from the sediments had $\delta^{15}N$ values (mean, 1.88‰, n = 4) similar to the charcoal-rich bulk sediment sample from which it came (1.51‰) and markedly higher than values observed in vegetation and forest floor detritus from the Chickaree watershed and other lodgepole pine forests (e.g., Table B2, Choi et al. 2005). Laboratory experiments have shown fire-induced enrichment in burned material (e.g., + 2.5‰ ; Turekian et al. 1998). These observations suggest that fires preferentially volatilized $^{14}N$, leaving a signal of N loss in charred material, and that deposition of the material in the lake contributed to the post-fire $\delta^{15}N$ peak. However, given my dataset, I cannot determine the degree to which the signal reflects the extent of N volatilization vs. the charcoal content of the sediment.

Although volatilization is likely the main mechanism of N depletion in lodgepole pine forests (Fahey et al. 1985, Johnson et al. 1998), elevated nitrification and nitrate losses also could have contributed to post-fire isotopic enrichment (Hogberg 1997, Pardo et al. 2002, Boeckx et al. 2005, Pörtl et al. 2007, LeDuc et al. 2013), as stand-replacing fires reduce plant N demand, mineralize organic N, and foster soil conditions that favor nitrification (Vitousek and Melillo 1979, Certini 2005, Smithwick et al. 2005). Nitrification yields isotopically enriched ammonium and mobile, $^{15}N$-depleted nitrate that may be lost from a system via leaching and denitrification – progressively enriching soils in $^{15}N$ (Hogberg 1997, Pörtl et al. 2007).

Elevated nitrate outflow has been observed after disturbance in lodgepole pine forests (e.g., Knight et al. 1991, Bladon et al. 2008), but post-disturbance nitrate losses in N-poor forests are typically minor relative to the large losses seen after deforestation in more N-enriched forests in the Northeastern United States (e.g., Likens et al. 1970) – likely owing to microbial N immobilization favored by high organic matter C:N ratios (e.g., Vitousek and Melillo 1979, Vitousek and Matson 1985, Turner et al. 2007, Koyama et al. 2010). For example, Turner et al. (2007) concluded that a microbial N sink strongly conserved mineralized N during early succession (1-4 yr post-fire) after high-severity fires in Greater Yellowstone Ecosystem lodgepole pine forests. Early successional re-vegetation also may strongly limit N availability and losses after stand-replacing events in these forests (Turner et al. 2011). These studies suggest that any isotopic enrichment due to post-fire changes in N availability/nitrate loss rates would be minor and short-lived in the Chickaree Lake watershed.

### *Long-Term Response (~20-50 yr post-fire)*

Although lake-sediment signatures immediately following high-severity catchment fires were dramatic, proxy anomalies several decades after the events may be more ecologically significant. Most notably, the fires appear to have caused long-lived changes in the provenance of lake organic matter, evidenced by significantly low sediment C:N between ~20 and 50 yr after events (Fig. 5, Fig. 6). The change could have resulted from 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 material (Meyers and Lallier-Verges 1999).

Previous research, largely in boreal watersheds, has revealed little fire-induced change in terrestrial C inputs to lakes (e.g., Carignan et al. 2000, Marchand et al. 2009). Marked decreases in terrestrial dissolved organic C (DOC) export were observed after severe boreal forest fires (Schindler et al. 1996), but the change was attributed to drought. Increases in aquatic primary productivity have been linked to nutrient pulses to lakes after fires in upper montane (Kelly et al. 2006) and boreal (Planas et al. 2000) watersheds, though this effect is believed to be short-lived (e.g., weeks to ~5 yr; Ranalli 2004, Schindler 2009).

Based on the duration of the response (~30 yr) and patterns in other proxies, I believe that the C:N decline in the Chickaree Lake sediment record was driven primarily by reduced inputs of terrestrial organic matter after fire and perhaps secondarily by the indirect effects of this change on algal productivity. Colored DOC, derived largely from the forest floor, suppresses benthic productivity in small, nutrient-poor lakes by inhibiting light penetration (Carpenter et al. 1998, Karlsson et al. 2009). Thus, a reduction in allochthonous DOC inputs in the decades following fire could promote algal productivity, contributing to lower sediment C:N. A marked decline in terrestrial organic matter subsidies also could significantly impact lake food webs and biogeochemical cycling (e.g., Cole et al. 2002, Sobek et al. 2003, Carpenter et al. 2005, Bunting et al. 2010).

My conclusion that the C:N anomaly was driven mainly by a decline in allochthonous subsidies to the lake, rather than by autochthonous processes, is supported by several lines of evidence. First, significantly low sediment $C_{acc}$ and %C values between ~20 and 35 yr after fire (Fig. 5, Fig. 6) are consistent with reduced organic matter inputs and long-term elevated erosion resulting from combustion of the forest floor (again, the primary source of allochthonous C) and lower litter production by mature trees. Although sediment %C may be greatly influenced by inputs of clastic material, such as soil mineral matter or diatom remains (i.e., BSi; Fig. 4), the significant decline in the rate of sediment organic matter accumulation ($C_{acc}$) coincident with low %C and C:N (Fig. 6) suggests that the changes resulted largely from reduced terrestrial inputs rather than increased organic matter contributions from aquatic primary producers.

Second, the strong correlations between response variables and charcoal peak magnitude (Fig. 7) indicate that the trends ~20-50 yr post-fire were closely linked to organic matter combustion and more pronounced after events that were higher-severity, larger, and/or closer to the lake. And finally, while post-fire nutrient subsidies could be recycled within the lake for a few years (e.g., Axler et al. 1981, Sondergaard et al. 2003), fueling algal productivity, the sediment record evolves over a multi-decadal time scale that seems more consistent with organic matter losses and gains associated with fire and forest C accumulation. High $C_{acc}$, %C, and C:N in the decades preceding high-severity catchment fires (Fig. 6), suggesting elevated organic matter delivery from the forest to the lake late in stand development, provide further support for this interpretation.

Although the SEA revealed no $\delta^{13}C$ response, changes in sediment $\delta^{13}C$ following multiple high-severity catchment fires also appear to be consistent with a shift in the provenance of lake organic matter. Sediment $\delta^{13}C$ declined sharply after some fires (e.g., 2670, 2752 cal yr BP; Fig. 5) that occurred during periods when lower $\delta^{13}C$ was likely associated with algal organic matter (e.g., ~2800-1300 cal yr BP; Table B3). Thus, multi-decadal changes in $C_{acc}$, %C, C:N, and $\delta^{13}C$ may reflect the extent of terrestrial organic matter losses to fire, successional organic matter accumulation, and fire impacts on lake C cycling and productivity.

### *Ecosystem Recovery*

Trends > 40-50 yr after fire suggest recovery of terrestrial organic matter inputs to the lake and tightening of the N cycle during forest aggradation, providing perhaps the strongest evidence in the record that forest ecosystem processes were reflected in lake-sediment biogeochemistry. As indicators of allochthonous organic matter accumulation ($C_{acc}$, %C, C:N) increased, $\delta^{15}N$ declined to anomalously low values (Fig. 5, Fig. 6), consistent with theory and modern ecological research indicating that terrestrial N availability and thus plant and soil $\delta^{15}N$ may drop as N is sequestered in growing biomass and forest floor detritus (Vitousek and Reiners 1975, Fahey 1983, Chang and Handley 2000, Compton et al. 2007, Craine et al. 2009, Garten et al. 2011, LeDuc et al. 2013). Diminishing N availability during terrestrial C accumulation has been previously inferred from declines in lake-sediment $\delta^{15}N$ over multi-millennial global (McLauchlan et al. 2013) and multi-decadal catchment (McLauchlan et al. 2007) scales.

Research in forests shaped by stand-replacing fires has shown conflicting and complex patterns in terrestrial N availability in the decades following disturbance (e.g., Smithwick et al. 2005, Smithwick et al. 2009). Nevertheless, the negative excursion in Chickaree Lake sediment $\delta^{15}N$ (~55-70 yr post-fire; Fig. 5, Fig. 6) and recovery of organic matter content occurred during the period when lodgepole pine forest N demand and net primary productivity are expected to peak (forest age of 40-70 yr; e.g., Pearson et al. 1987, Olsson et al. 1998, Kashian et al. 2013), suggesting a pattern of declining terrestrial N availability during stand development on a landscape with diminished N stocks. This tightening of the N cycle as the forest matures may lower ecosystem $\delta^{15}N$ by minimizing N losses and diminish 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 and Handley 2000, Hobbie and Colpaert 2003, Compton et al. 2007, Högberg et al. 2011, Hyodo et al. 2012, Mayor et al. 2012, LeDuc et al. 2013). Ectomycorrhizal fungi (common in lodgepole forests; e.g., Douglas et al. 2005) retain $^{15}$N-enriched N and deliver $^{15}$N-depleted N to vegetation, contributing to declining $\delta^{15}$N in foliage and the forest floor and increasing $\delta^{15}$N in deeper mineral soils (Billings and Richter 2006, Compton et al. 2007, Hobbie and Högberg 2012).

I considered the possibility that organic matter inputs derived from symbiotic N-fixing vegetation drove the $\delta^{15}$N anomaly, as increasing incorporation of atmospheric N ($\delta^{15}$N ~0 ‰) in the plant-soil system has been implicated in ecosystem $\delta^{15}$N declines (e.g., Compton et al. 2007, Perakis et al. 2011) and N-fixation may be high after fire in some forests (Johnson et al. 1998, Smithwick et al. 2005). However, the litter of N-fixing taxa tends to be more isotopically enriched than the litter of other lodgepole forest plants (Miller 2011), likely owing to the latter's reliance on isotopically depleted N transferred by mycorrhizae. Moreover, the pollen record shows little evidence of N-fixing taxa, even in the decades following fire (potential N-fixers accounted for only ~0.5% of terrestrial pollen in sediments deposited between 10 and 80 yr after four high-severity catchment fires). Thus, elevated symbiotic N-fixation seems an unlikely driver of the significant $\delta^{15}$N decline ~40-70 yr after fire (Fig. 6).

I also considered autochthonous explanations for the $\delta^{15}$N trough, but even the strongest candidates (e.g., increased algal discrimination against $^{15}$N due to high DIN availability) seemed implausible given the composite nature of the record, the fact that the feature coincided with the period of peak forest N demand, and the lack of supporting evidence from other proxies. Rather, the proxies appear to support my interpretation – that the $\delta^{15}N$ trend was driven by terrestrial successional processes. Composite %C and %N had largely returned to pre-fire levels by ~75-80 yr after high-severity catchment fires (Fig. 5, Fig. 6), broadly consistent with chronosequences of C and N accumulation during stand development. In Rocky Mountain lodgepole pine forests, 80% of C was regained within 50 yr of stand-replacing fire and 90% within 100 yr (Kashian et al. 2013), and all pre-fire N was recovered within 100 yr (Smithwick et al. 2009).

To my knowledge, no other studies have examined lake-sediment $\delta^{15}N$ response to individual fires, but links between the proxy and other terrestrial disturbances have been tested. My results are similar to those of McLauchlan et al. (2007), who observed significant changes in $\delta^{15}N$ values of sediments deposited during deforestation and forest recovery within a New England watershed. They attributed a marked, multi-decadal increase in sediment $\delta^{15}N$ during disturbance to elevated terrestrial N availability and an influx of $^{15}N$-enriched N and organic matter to the lake. Sediment $\delta^{15}N$ dropped over decades as the forest recovered, in concert with declines in stream nitrate concentrations and tree ring $\delta^{15}N$. In contrast, Morris et al. (2013) found no relationship between lake-sediment $\delta^{15}N$ and severe spruce beetle outbreaks in Utah. The contrasting results are likely a product of differences in regional N cycling and the nature and duration of the disturbance. The New England disturbance was longer-lived, caused larger changes in biomass, likely resulted in greater soil erosion, and occurred on a more N-enriched landscape with greater potential for nitrate losses. Decadal-scale beetle outbreaks leave live understory vegetation and beetle-resistant trees that may prevent erosion and strongly retain N following disturbance in N-limited conifer forests (Rhoades et al. 2013). While strong biotic N retention may have similarly minimized isotopic enrichment via nitrification and nitrate losses immediately after fires around Chickaree Lake, combustion/volatilization of $^{15}$N-depleted N and organic matter during fires may have been significant, possibly driving the $\delta^{15}$N signal.

## Conclusions

My results suggest that analysis of lake-sediment charcoal records in concert with $\delta^{15}$N and other proxies can provide a unique and powerful tool for illuminating decadal- to-centennial-scale biogeochemical change following fire, over thousands of years. The post-fire trends appear to reflect terrestrial impacts, fire size and/or severity, and forest recovery over time scales relevant to modern forest ecology and management. Moreover, because this paleoecological approach permits repeated evaluation of disturbance response over many disturbance intervals spanning diverse climates, it has the potential to provide insights into biogeochemical response to fire under anticipated climatic change.

Interpretation of sediment biogeochemical change is inherently complex and indirect, requiring multiple proxies to untangle the myriad terrestrial and aquatic processes that may influence a record. While this work is no exception, the statistically significant composite signals of disturbance were products of multiple responses to fires similar in timing and direction, providing unusually strong paleoecological evidence of cause and effect. Although much work is needed to inform inferences about the mechanisms responsible for change – including modern calibration studies that directly link terrestrial processes to lake sediment patterns under a variety of climatic conditions – this research helps build an interpretive framework for similar studies at broader scales and in other ecosystems shaped by stand-replacing fires.

# REFERENCES

Adams, J. B., M. E. Mann, and C. M. Ammann. 2003. Proxy evidence for El Nino-like response to volcanic forcing. Nature **426**:274-278.

Amiro, B. D., J. B. Todd, B. M. Wotton, K. A. Logan, M. D. Flannigan, B. J. Stocks, J. A. Mason, D. L. Martell, and K. G. Hirsch. 2001. Direct carbon emissions from Canadian forest fires, 1959-1999. Canadian Journal of Forest Research **31**:512-525.

Anderson, L. 2011. Holocene record of precipitation seasonality from lake calcite δ18O in the central Rocky Mountains, United States. Geology **39**:211-214.

Axler, R. P., G. W. Redfield, and C. R. Goldman. 1981. The importance of regenerated nitrogen to phytoplankton productivity in a subalpine lake. Ecology **62**:345-354.

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

Baron, J. S., H. M. Rueth, A. M. Wolfe, K. R. Nydick, E. J. Allstott, J. T. Minear, and B. Moraska. 2000. Ecosystem Responses to Nitrogen Deposition in the Colorado Front Range. Ecosystems **3**:352-368.

Billings, S. A. and D. D. Richter. 2006. Changes in stable isotopic signatures of soil nitrogen and carbon during 40 years of forest development. Oecologia **148**:325-333.

Binford, M. W. 1990. Calculation and uncertainty analysis of 210Pb dates for PIRLA project lake sediment cores. Journal of Paleolimnology **3**:253-267.

Bladon, K. D., U. Silins, M. J. Wagner, M. Stone, M. B. Emelko, C. A. Mendoza, K. J. Devito, and S. Boon. 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., L. Paulino, C. Oyarzún, O. V. Cleemput, and R. Godoy. 2005. Soil δ15N patterns in old-growth forests of southern Chile as integrator for N-cycling. Isotopes in Environmental and Health Studies **41**:249-259.

Bonan, G. B. 2008. Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests. Science **320**:1444-1449.

Bormann, B. T., P. S. Homann, R. L. Darbyshire, and B. A. Morrissette. 2008. Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Canadian Journal of Forest Research **38**:2771-2783.

Brooks, P. D., D. M. McKnight, and K. E. Bencala. 1999. The relationship between soil heterotrophic activity, soil dissolved organic carbon (DOC) leachate, and catchment-scale DOC export in headwater catchments. Water Resources Research **35**:1895-1902.

Buechling, A., Baker, William, L. 2004. A fire history from tree rings in a high-elevation forest of Rocky Mountain National Park. Canadian Journal of Forest Research **34**:1259-1273.

Bunting, L., P. R. Leavitt, R. P. Weidman, and R. D. Vinebrooke. 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., P. D'Arcy, and S. Lamontagne. 2000. Comparative impacts of fire and forest harvesting on water quality in Boreal Shield lakes. Canadian Journal of Fisheries and Aquatic Sciences **57 (suppl. 2)**:105-117.

Carpenter, S. R., J. J. Cole, J. F. Kitchell, and M. L. Pace. 1998. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. Limnology and Oceanography **43**:73-80.

Carpenter, S. R., J. J. Cole, M. L. Pace, M. Van de Bogert, D. L. Bade, D. Bastviken, C. M. Gille, J. R. Hodgson, J. F. Kitchell, and E. S. Kritzberg. 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from 13C 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, S. X. and L. L. Handley. 2000. Site history affects soil and plant 15N natural abundances (δ15N) in forests of northern Vancouver Island, British Columbia. Functional Ecology **14**:273-280.

Choi, W., S. X. Chang, M. P. Curran, H. Ro, M. Kamaluddin, and J. J. Zwiazek. 2005. Foliar δ13C and δ15N response of lodgepole pine and Douglas-fir seedlings to soil compaction and forest floor removal. Forest Science **51**:546-555.

Cleveland, S. 1979. Robust locally weighted regression and smoothing scatterplots. Journal of the American Statistical Association **74**:829-836.

Cole, J. J., S. R. Carpenter, J. Kitchell, and M. L. Pace. 2002. Pathways of organic carbon utilization in small lakes: results from a whole-lake 13C addition and coupled model. Limnology and Oceanography **47**:1664-1675.

Colombaroli, D. and D. G. Gavin. 2010. Highly episodic fire and erosion regime over the past 2,000 y in the Siskiyou Mountains, Oregon. Proceedings of the National Academy of Sciences **107**:18909-18914.

Compton, J. E., T. D. Hooker, and S. S. Perakis. 2007. Ecosystem N Distribution and δ15N during a Century of Forest Regrowth after Agricultural Abandonment. Ecosystems **10**:1197-1208.

Craine, J. M., A. J. Elmore, M. P. M. Aidar, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, M. C. Mack, K. K. McLauchlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, J. Peñuelas, P. B. Reich, E. A. G. Schuur, W. D. Stock, P. H. Templer, R. A. Virginia, J. M. Welker, and I. J. Wright. 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, D. R. and N. C. Matalas. 1964. Statistical and probability analysis of hydrologic data, part III: analysis of variance, covariance, and time series. In: Handbook of Applied Hydrology, a Compendium of Water Resources Technology (ed. Chow VT). McGraw-Hill Book Company, New York.

Dean, W. E., 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, D. J. 1979. The marine budgets of silica and 31Si. PhD Dissertation. Yale University, New Haven.

Dijkstra, P., C. M. LaViolette, J. S. Coyle, R. R. Doucett, E. Schwartz, S. C. Hart, and B. A. Hungate. 2008. 15N enrichment as an integrator of the effects of C and N on microbial metabolism and ecosystem function. Ecology Letters **11**:389-397.

Douglas, R. B., V. T. Parker, and K. W. Cullings. 2005. Belowground ectomycorrhizal community structure of mature lodgepole pine and mixed conifer stands in Yellowstone National Park. Forest Ecology and Management **208**:303-317.

Faegri, K. and J. Iversen. 1975. Text book of pollen analysis. Third edition. Hafner, New York, New York, USA.

Fahey, T. J. 1983. Nutrient dynamics of aboveground detritus in lodgepole pine (pinus contorta ssp. latifolia) ecosystems, southeastern Wyoming. Ecological Monographs **53**:51-72.

Fahey, T. J. and D. H. Knight. 1986. Lodgepole pine ecosystems. Bioscience **36**:610-617.

Fahey, T. J., J. B. Yavitt, J. A. Pearson, and D. H. Knight. 1985. The nitrogen cycle in lodgepole pine forests, southeastern Wyoming. Biogeochemistry **1**:257-275.

Galman, V., J. Rydberg, and C. Bigler. 2009. Decadal diagenetic effects on δ13C and δ15N studied in varved lake sediment. Limnology and Oceanography **54**:917-924.

Galman, V., J. Rydberg, S. S. de-Luna, R. Bindler, and I. Renberg. 2008. Carbon and nitrogen loss rates during aging of lake sediment: Changes over 27 years studied in varved lake sediment. Limnology and Oceanography **53**:1076-1082.

Garten, C. T., C. M. Iversen, and R. J. Norby. 2011. Litterfall 15N abundance indicates declining soil nitrogen availability in a free-air CO2 enrichment experiment. Ecology **92**:133-139.

Gavin, D. G., L. B. Brubaker, and K. P. Lertzman. 2003. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. Canadian Journal of Forest Research **33**:573-586.

Giesen, T. W., S. S. Perakis, and K. Cromack. 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.

Gillson, L. and A. Ekblom. 2009. Resilience and thresholds in savannas: Nitrogen and fire as drivers and responders of vegetation transition. Ecosystems **12**:1189-1203.

Grogan, P., T. D. Bruns, and F. S. Chapin, III. 2000. Fire effects on ecosystem nitrogen cycling in a Californian bishop pine forest. Oecologia **122**:537-544.

Heiri, O., A. F. Lotter, and G. Lemcke. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology **25**:101-110.

Higuera, P., M. Peters, L. Brubaker, and D. Gavin. 2007. Understanding the origin and analysis of sediment-charcoal records with a simulation model. Quaternary Science Reviews **26**:1790-1809.

Higuera, P. E., L. B. Brubaker, P. M. Anderson, F. S. Hu, and T. A. Brown. 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, P. E., D. G. Gavin, P. J. Bartlein, and D. J. Hallet. 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.

Higuera, P. E., C. Whitlock, and J. A. Gage. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in subalpine forests of Yellowstone National Park, USA. The Holocene **21**:327-341.

Hobbie, E. A. and J. V. Colpaert. 2003. Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. New Phytologist **157**:115-126.

Hobbie, E. A. and P. Högberg. 2012. Nitrogen isotopes link mycorrhizal fungi and plants to nitrogen dynamics. New Phytologist **196**:367-382.

Hodell, D. A. and C. L. Schelske. 1998. Production, sedimentation, and isotopic composition of organic matter in Lake Ontario. Limnology and Oceanography **43**:200-214.

Hogberg, P. 1997. 15N natural abundance in soil-plant systems. New Phytologist **137**:179-203.

Högberg, P., C. Johannisson, S. Yarwood, I. Callesen, T. Näsholm, D. D. Myrold, and M. N. Högberg. 2011. Recovery of ectomycorrhiza after 'nitrogen saturation' of a conifer forest. New Phytologist **189**:515-525.

Hollander, D. J. and J. A. McKenzie. 1991. CO2 control on carbon-isotope fractionation during aqueous photosynthesis: A paleo-pCO2 barometer. Geology **19**:929-932.

Hood, E., M. W. Williams, and D. M. McKnight. 2005. Sources of dissolved organic matter (DOM) in a Rocky Mountain stream using chemical fractionation and stable isotopes. Biogeochemistry **74**:231-255.

Hu, F. S., B. P. Finney, and L. B. Brubaker. 2001. Effects of holocene Alnus expansion on aquatic productivity, nitrogen cycling, and soil development in southwestern Alaska. Ecosystems **4**:358-368.

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

Hyodo, F., S. Kusaka, D. A. Wardle, and M. Nilsson. 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.

Jeffers, E. S., M. B. Bonsall, J. E. Watson, and K. J. Willis. 2012. Climate change impacts on ecosystem functioning: evidence from an Empetrum heathland. New Phytologist **193**:150-164.

Johnson, D. W., R. B. Susfalk, R. A. Dahlgren, and J. M. Klopatek. 1998. Fire is more important than water for nitrogen fluxes in semi-arid forests. Environmental Science and Policy **1**:79-86.

Johnson, E. A. and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. Ecology Letters **11**:419-431.

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460**:506-509.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. Bioscience **56**:598-606.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2013. Postfire changes in forest carbon storage over a 300-year chronosequence of Pinus contorta-dominated forests. Ecological Monographs **83**:49-66.

Kaushal, S. S., W. M. Lewis, and J. H. McCutchan. 2006. Land use change and nitrogen enrichment of a Rocky Mountain watershed. Ecological Applications **16**:299-312.

Kelly, E. N., D. W. Schindler, V. L. St. Louis, D. B. Donald, and K. E. Vladicka. 2006. Forest fire increases mercury accumulation by fishes via food web restructuring and increased mercury inputs. Proceedings of the National Academy of Sciences **103**:19380-19385.

Kelly, R. F., P. E. Higuera, C. M. Barrett, and F. S. Hu. 2011. A signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quaternary Research **75**:11-17.

Knight, D. H., J. B. Yavitt, and G. D. Joyce. 1991. Water and nitrogen outflow from lodgepole pine forest after two levels of tree mortality. Forest Ecology and Management **46**:215-225.

Koyama, A., K. L. Kavanagh, and K. Stephan. 2010. Wildfire Effects on Soil Gross Nitrogen Transformation Rates in Coniferous Forests of Central Idaho, USA. Ecosystems **13**:1112-1126.

Kreyling, J., A. Jentsch, and C. Beierkuhnlein. 2011. Stochastic trajectories of succession initiated by extreme climatic events. Ecology Letters **14**:758-764.

Lavorel, S., M. D. Flannigan, E. F. Lambin, and M. C. Scholes. 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.

LaZerte, B. D. 1983. Stable carbon isotope ratios: Implications for the source of sediment carbon and for phytoplankton carbon assimilation in Lake Memphremagog, Quebec. Canadian Journal of Fisheries and Aquatic Sciences **40**:1658-1666.

Lebauer, D. S. and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology **89**:371-379.

LeDuc, S. D., D. E. Rothstein, Z. Yermakov, and S. E. Spaulding. 2013. Jack pine foliar δ15N indicates shifts in plant nitrogen acquisition after severe wildfire and through forest stand development. Plant and Soil **373**:955-965.

Lehmann, M. F., S. M. Bernasconi, A. Barbieri, and J. A. McKenzie. 2002. Preservation of organic matter and alteration of its carbon and nitrogen isotope composition during simulated and in situ early sedimentary diagenesis. Geochimica et Cosmochimica Acta **66**:3573-3584.

Lenihan, J. M., R. Drapek, D. Bachelet, and R. P. Neilson. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications **13**:1667-1681.

Lewis, S. A., J. Q. Wu, and P. R. Robichaud. 2006. Assessing burn severity and comparing soil water repellency, Hayman Fire, Colorado. Hydrological Processes **20**:1-16.

Likens, G. E. and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. Bioscience **24**:447-456.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed ecosystem. Ecological Monographs **40**:23-47.

Marchand, D., Y. T. Prairie, and P. A. del Giorgio. 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, J. R., P. J. Bartlein, M. K. Walsh, S. P. Harrison, K. J. Brown, M. E. Edwards, P. E. Higuera, M. J. Power, R. S. Anderson, C. Briles, A. Brunelle, C. Carcaillet, M. Daniels, F. S. Hu, M. Lavoie, C. Long, T. Minckley, P. J. H. Richard, A. C. Scott, D.

S. Shafer, W. Tinner, C. E. Umbanhowar, and C. Whitlock. 2009. Wildfire responses to abrupt climate change in North America. Proceedings of the National Academy of Sciences **106**:2519-2524.

Martinelli, L. A., M. C. Piccolo, A. R. Townsend, P. M. Vitousek, E. Cuevas, W. McDowell, G. P. Roberton, O. C. Santos, and K. Treseder. 1999. Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests. Biogeochemistry **46**:45-65.

Mayor, J. R., E. A. G. Schuur, M. C. Mack, T. N. Hollingsworth, and E. Bååth. 2012. Nitrogen Isotope Patterns in Alaskan Black Spruce Reflect Organic Nitrogen Sources and the Activity of Ectomycorrhizal Fungi. Ecosystems **15**:819-831.

McEachern, P., E. E. Prepas, J. J. Gibson, and W. P. Dinsmore. 2000. Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll a concentrations in boreal subarctic lakes of northern Alberta. Canadian Journal of Fisheries and Aquatic Sciences **57 (Suppl. 2)**:73-81.

McLauchlan, K. K. 2008. Reconstructing Nutrient and Energy Flows Through Terrestrial Ecosystems Of the Holocene. Palaios **23**:721-723.

McLauchlan, K. K., J. M. Craine, W. W. Oswald, P. R. Leavitt, and G. E. Likens. 2007. Changes in nitrogen cycling during the past century in a northern hardwood forest. Proceedings of the National Academy of Sciences **104**:7466-7470.

McLauchlan, K. K., J. J. Williams, J. M. Craine, and E. S. Jeffers. 2013. Changes in global nitrogen cycling during the Holocene epoch. Nature **495**:352-355.

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

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

Miller, Z. M. 2011. An investigation of nitrogen fixation by Russet buffaloberry in Colorado conifer forests. Master's Thesis. Colorado State University, Department of Forest and Rangeland Stewardship.

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

Minckley, T. A., R. K. Shriver, and B. Shuman. 2012. Resilience and regime change in a southern Rocky Mountain ecosystem during the past 17000 years. Ecological Monographs **82**:49-68.

Moritz, M. A., M. Parisien, E. Batllori, M. A. Krawchuk, J. Van Dorn, D. J. Ganz, and K. Hayhoe. 2012. Climate change and disruptions to global fire activity. Ecosphere **3**:art49.

Morris, J. L., P. C. le Roux, A. N. Macharia, A. Brunelle, E. G. Hebertson, and Z. J. Lundeen. 2013. Organic, elemental, and geochemical contributions to lake sediment deposits during severe spruce beetle (Dendroctonus rufipennis) disturbances. Forest Ecology and Management **289**:78-89.

Natelhoffer, K. J. and B. Fry. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. Soil Science Society of America Journal **52**:1633-1640.

Nave, L. E., E. D. Vance, C. W. Swantston, and P. S. Curtis. 2011. Fire effects on temperate forest soil C and N storage. Ecological Applications **21**:1189-1201.

O'Reilly, C. M., D. L. Dettman, and A. S. Cohen. 2005. Paleolimnological investigations of anthropogenic environmental change in Lake Tanganyika: VI. Geochemical indicators. Journal of Paleolimnology **34**:85-91.

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

Oswald, W. W., P. M. Anderson, T. A. Brown, L. B. Brubaker, F. S. Hu, A. V. Lozhkin, W. Tinner, and P. Kaltenrieder. 2005. Effects of sample mass and macrofossil type on radiocarbon dating of arctic and boreal sediments. The Holocene **15**:758-767.

Pardo, L. H., H. F. Hemond, J. P. Montoya, T. J. Fahey, and T. G. Siccama. 2002. Response of the natural abundance of15N in forest soils and foliage to high nitrate loss following clear-cutting. Canadian Journal of Forest Research **32**:1126-1136.

Pearson, J. A., D. H. Knight, and T. J. Fahey. 1987. Biomass and nutrient accumulation during stand development in Wyoming lodgepole pine forests. Ecology **68**:1966-1973.

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

Perakis, S. S. and L. O. Hedin. 2002. Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds. Nature **415**:416-419.

Perakis, S. S., E. R. Sinkhorn, and J. E. Compton. 2011. δ15N constraints on long-term nitrogen balances in temperate forests. Oecologia **167**:793-807.

Planas, D., M. Desrosiers, S. Grouix, S. Paquet, and R. Carignan. 2000. Pelagic and benthic algal responses in eastern Canadian Boreal Shield lakes following harvesting and wildfires. Canadian Journal of Fisheries and Aquatic Sciences **57 (Suppl. 2)**:136-145.

Pörtl, K., S. Zechmeister-Boltenstern, W. Wanek, P. Ambus, and T. W. Berger. 2007. Natural 15N abundance of soil N pools and N2O reflect the nitrogen dynamics of forest soils. Plant and Soil **295**:79-94.

Prager, M. H. and J. M. Hoenig. 1989. Superposed Epoch Analysis: A Randomization Test of Environmental Effects on Recruitment with Application to Chub Mackerel. Transactions of the American Fisheries Society **118**:608-618.

Ranalli, A. J. 2004. A summary of the scientific literature on the effects of fire on the concentration of nutrients in surface waters. No. USGS-2004-1296. U.S. Geological Survey, Reston VA.

Rau, G. 1978. Carbon-13 depletion in a subalpine lake: Carbon flow implications. Science **201**:901-902.

Reimer, P. J., M. G. L. Baillie, E. Bard, A. Bayliss, J. W. Beck, P. G. Blackwell, C. B. Ramsey, C. E. Buck, G. S. Burr, R. L. Edwards, M. Friedrich, P. M. Grootes, T. P. Guilderson, I. Hajdas, T. J. Heaton, A. G. Hogg, K. A. Hughen, K. F. Kaiser, B. Kromer, F. G. McCormac, S. W. Manning, R. W. Reimer, D. A. Richards, J. R. Southon, S. Talamo, C. S. M. Turney, J. van der Plicht, and C. E. Weyhenmeyer. 2009. INTCAL09 and Marine09 radiocarbon age calibration curves, 0-50,000 years cal BP. Radiocarbon **51**:1111-1150.

Rhoades, C. C., J. H. McCutchan, L. A. Cooper, D. Clow, T. M. Detmer, J. S. Briggs, J. D. Stednick, T. T. Veblen, R. M. Ertz, G. E. Likens, and W. M. Lewis. 2013.

Biogeochemistry of beetle-killed forests: Explaining a weak nitrate response. Proceedings of the National Academy of Sciences **110**:1756-1760.

Richey, J. E. and R. C. Wissmar. 1979. Sources and influences of allochthonous inputs on the productivity of a subalpine lake. Ecology **60**:318-329.

Robinson, D. 2001. δ15N as an integrator of the nitrogen cycle. Trends in Ecology and Evolution **16**:153-162.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, J. Gurevitch, and 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., W. W. Miller, D. W. Johnson, R. G. Qualls, L. Provencher, E. Carroll, and P. Szameitat. 2007. Fire Effects on Stable Isotopes in a Sierran Forested Watershed. Journal of Environment Quality **36**:91.

Santisteban, J. I., R. Mediavilla, E. Lopez-Pamo, C. J. Dabrio, M. Blanca Ruiz Zapata, M. Jose Gil Garcia, S. Castano, and P. E. Martinez-Alfaro. 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, D. W. 2009. Lakes as sentinels and integrators for the effects of climate change on watersheds, airsheds, and landscapes. Limnology and Oceanography **54**:2349-2358.

Schindler, D. W., S. E. Bayley, B. R. Parker, K. G. Beaty, D. R. Cruikshank, E. J. Fee, E. U. Schindler, and M. P. Stainton. 1996. The effects of climatic warming on the properties of boreal lakes and streams at the Experimental Lakes Area, northwestern Ontario. Limnology and Oceanography **41**:1004-1017.

Shuman, B., A. K. Henderson, S. M. Colman, J. R. Stone, S. C. Fritz, L. R. Stevens, M. J. Power, and C. Whitlock. 2009. Holocene lake-level trends in the Rocky Mountains, U.S.A. Quaternary Science Reviews **28**:1861-1879.

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

Sibold, J. S., T. T. Veblen, and M. E. Gonzalez. 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.

Smaill, S. J., P. W. Clinton, and R. B. Allen. 2009. Inter-specific variation in foliar nutritional responses to disturbance by small coupe harvesting varies with landscape position. Forest Ecology and Management **258**:2382-2387.

Smithwick, E. A. H., D. M. Kashian, M. G. Ryan, and M. G. Turner. 2009. Long-Term Nitrogen Storage and Soil Nitrogen Availability in Post-Fire Lodgepole Pine Ecosystems. Ecosystems **12**:792-806.

Smithwick, E. A. H., M. G. Turner, M. C. Mack, and F. S. Chapin. 2005. Postfire Soil N Cycling in Northern Conifer Forests Affected by Severe, Stand-Replacing Wildfires. Ecosystems **8**:163-181.

Sobek, S., G. Algesten, A. K. Bergstrom, M. Jansson, and L. J. Tranvik. 2003. The catchment and climate regulation of pCO2 in boreal lakes. Global Change Biology **9**:630-641.

Sondergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia **506-509**:135-145.

Stephan, K. 2007. Wildfire and prescribed burning effects on nitrogen dynamics in central idaho headwater ecosystems. Ph.D Dissertation. University of Idaho, College of Natural Resources.

Stuiver, M. and P. J. Reimer. 1993. Extended 14C database and revised CALIB radiocarbon calibration program. Radiocarbon **35**.

Teranes, J. L. and S. M. Bernasconi. 2000. The record of nitrate utilization and productivity limitation provided by δ15N values in lake organic matter--a study of sediment trap and core sediments from Baldeggersee, Switzerland. Limnology and Oceanography **45**:801-813.

Thiffault, E., K. D. Hannam, S. A. Quideau, D. Paré, N. Bélanger, S. W. Oh, and A. D. Munson. 2008. Chemical composition of forest floor and consequences for nutrient availability after wildfire and harvesting in the boreal forest. Plant and Soil **308**:37-53.

Thompson, R., R. W. Battarbee, P. E. O'Sullivan, and F. Oldfield. 1975. Magnetic susceptibility of lake sediments. Limnology and Oceanography **20**:687-698.

Thornley, J. H. M. and M. G. R. Cannell. 2004. Long-term effects of fire frequency on carbon storage and productivity of boreal forests: a modeling study. Tree Physiology **24**:765-773.

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

Turner, M. G., W. H. Romme, E. A. H. Smithwick, D. B. Tinker, and J. Zhu. 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, M. G., E. A. H. Smithwick, K. L. Metzger, D. B. Tinker, and W. H. Romme. 2007. Inaugural Article: Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. Proceedings of the National Academy of Sciences **104**:4782-4789.

U.S. Department of Agriculture, N. R. C. S., Soil Survey Staff. 2007. Soil Survey of Rocky Mountain National Park, Colorado.

Vanderbilt, K. L., K. Lajtha, and F. J. Swanson. 2002. Biogeochemistry of unpolluted forested watersheds in the Oregon Cascades: Temporal patterns of precipitation and stream nitrogen fluxes. Biogeochemistry **62**:87-117.

Veraart, A. J., J. J. M. de Klein, and M. Scheffer. 2011. Warming can boost denitrification disproportionately due to altered oxygen dynamics. PLoS ONE **6**.

Vitousek, P. M. and P. A. Matson. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. Ecology **66**:1360-1376.

Vitousek, P. M. and J. M. Melillo. 1979. Nitrate losses from disturbed forests: Patterns and mechanisms. Forest Science **25**:605-619.

Vitousek, P. M. and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: A hypothesis. Bioscience **25**:376-381.

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

Whitlock, C., M. M. Bianchi, P. J. Bartlein, V. Markgraf, J. Marlon, M. Walsh, and N. McCoy. 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.

Whitlock, C., C. E. Briles, M. C. Fernandez, and J. Gage. 2011. Holocene vegetation, fire and climate history of the Sawtooth Range, central Idaho, USA. Quaternary Research **75**:114-124.

Wissmar, R. C., J. E. Richey, and D. E. Spyridakis. 1977. The importance of allochthonous particulate carbon pathways in a subalpine lake. Journal of the Fisheries Research Board of Canada **34**:1410-1418.

Wondzell, S. M. and J. G. King. 2003. Postfire erosional processes in the Pacific Northwest and Rocky Mountain regions. Forest Ecology and Management **178**:75-87.

Wright, H. E., Jr., D. H. Mann, and P. H. Glaser. 1984. Piston corers for peat and lake sediments. Ecology **65**:657-659.

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

Zackrisson, O., T. H. DeLuca, M. C. Nilsson, A. Sellstedt, and L. M. Berglund. 2004. Nitrogen fixation increases with successional age in boreal forests. Ecology **85**:3327-3334.

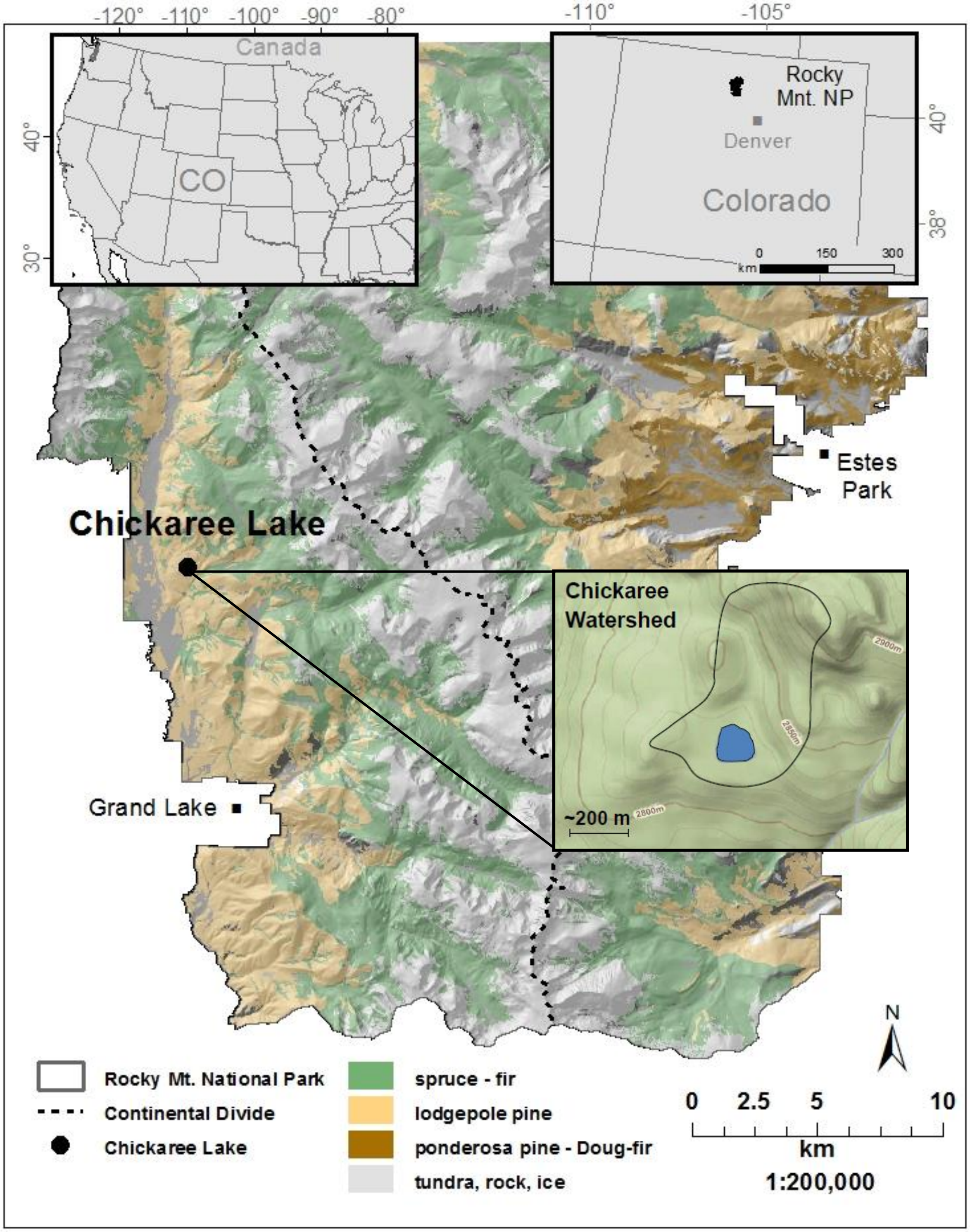

**Figure 1.** Map of study site. Chickaree Lake lies within a subalpine forest on the west side of Rocky Mountain National Park, CO. The ~1.6 ha lake has a ~28 ha watershed (Map data source: Rocky Mountain National Park; inset data source: Google Maps).

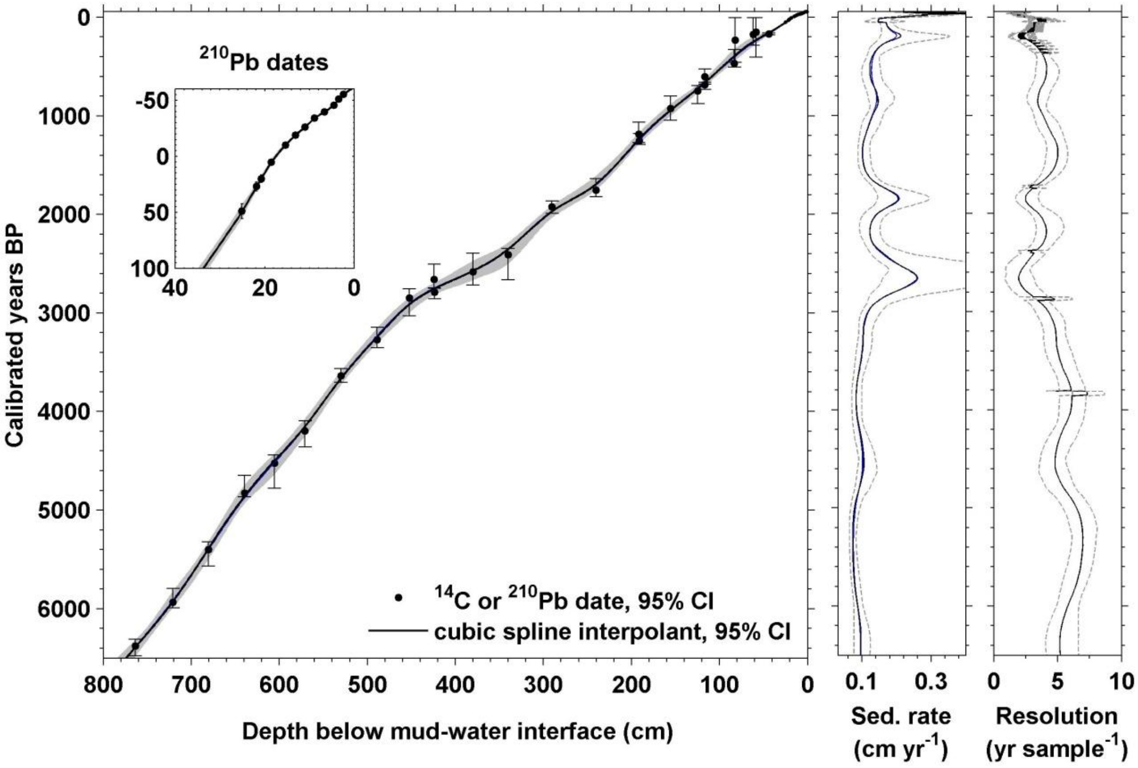

**Figure. 2.** Chickaree Lake age-depth model. Radiometric ages ($^{210}$Pb and $^{14}$C) and the cubic spline fit, sedimentation rate, and sample resolution, all with 95% confidence intervals. Confidence intervals were based on Monte Carlo resampling of 1000 chronologies. Sample resolution was ~4 yr/sample. Only the last ~4250 yr of the record were used in this study.

.

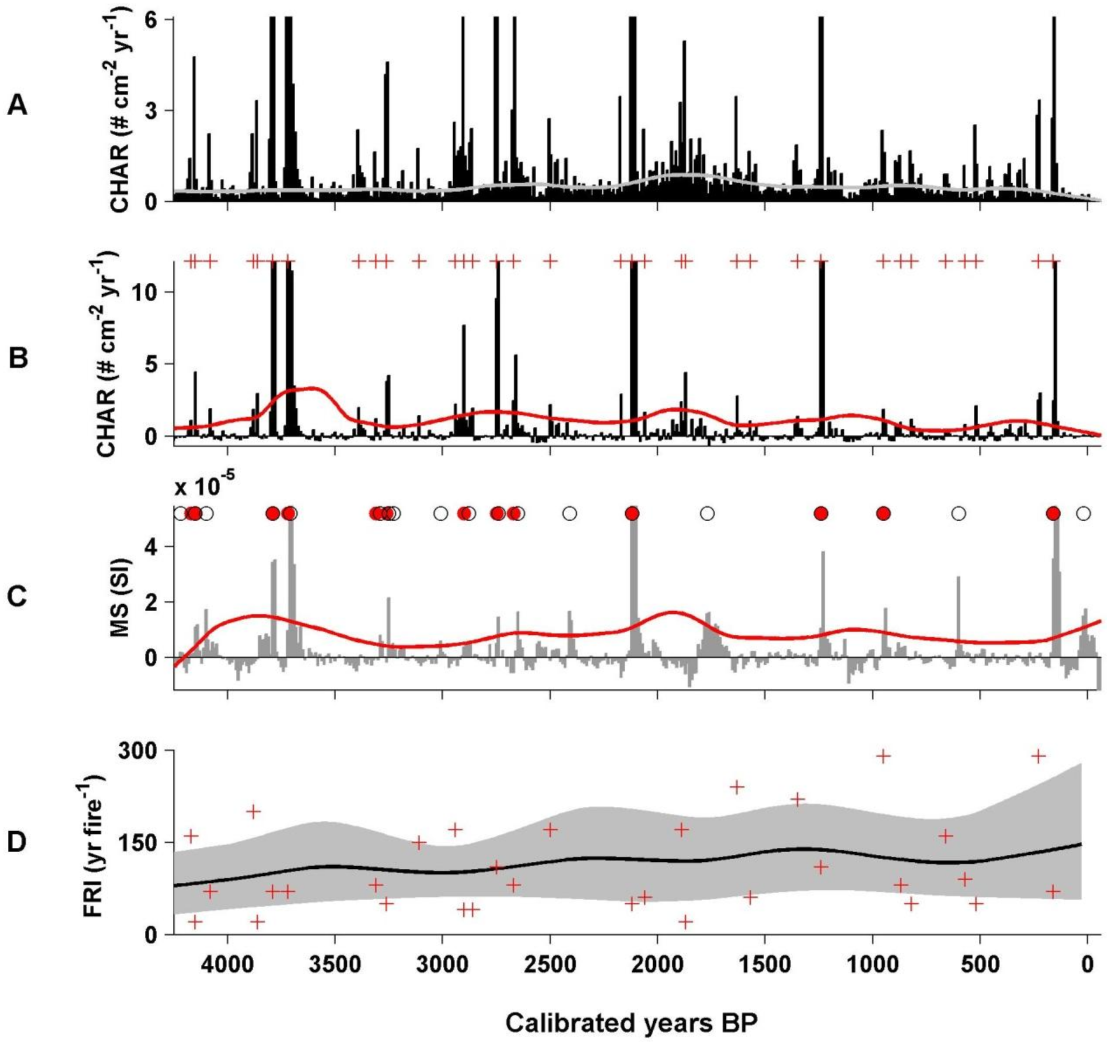

**Figure 3.** Sediment charcoal and magnetic susceptibility (MS) records. (A) Charcoal accumulation rate (CHAR, black line), interpolated to 10 yr intervals, and the 500 yr trend (gray line), representing "background" CHAR. (B) Residual CHAR values (black line), the threshold used to identify potential fire events (red line), and CHAR values exceeding this threshold and thus identified as local fire events (red "+"). (C) Residual MS values (gray line), the threshold used to identify MS peaks (red line), MS values exceeding the threshold and thus identified as MS peaks (open circles), and coincident CHAR and MS peaks identified as high-severity catchment fires (red circles). (D) Individual fire return intervals (FRI; yr/fire, red "+") smoothed over 1000-yr windows (black line), with 95% confidence intervals derived from bootstrap sampling (grey envelope).

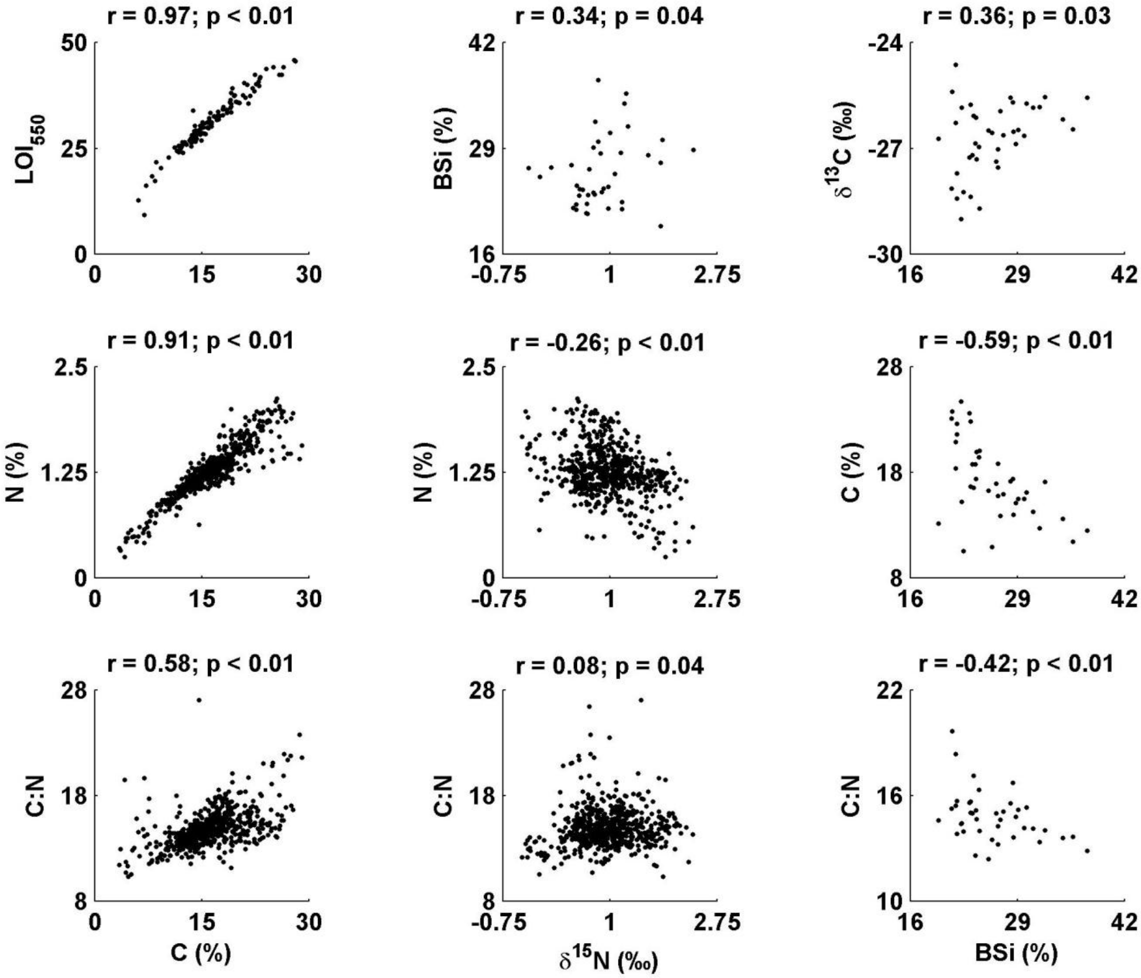

**Figure 4.** Spearman correlation coefficients (r) characterizing key relationships between bulk sediment biogeochemical proxies. Reported p-values account for reduced sample sizes due to temporal autocorrelation (see Methods).

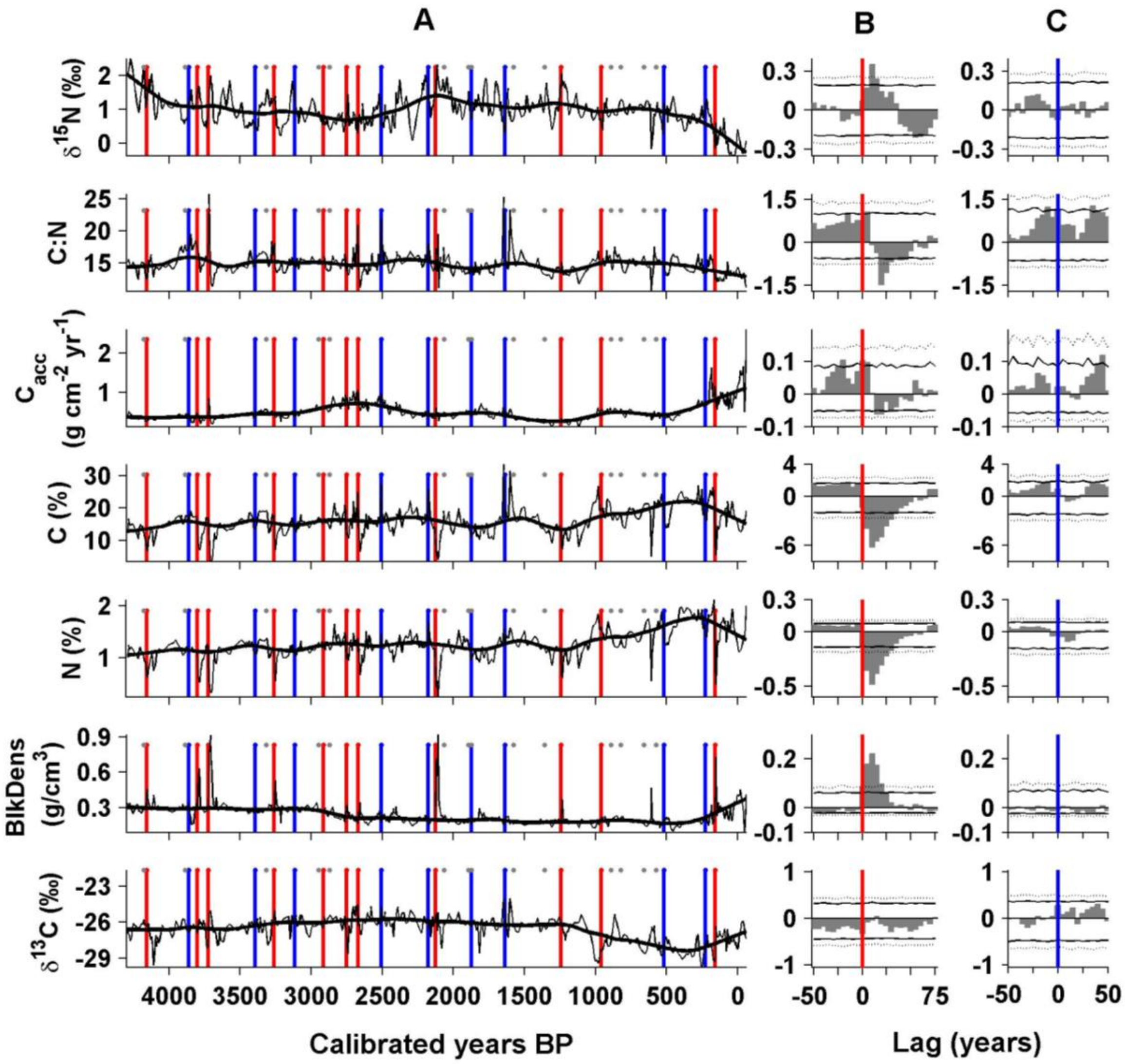

**Figure 5.** Results of Superposed Epoch Analysis. (A) Raw and smoothed (500 yr trend; bold line) time series, with vertical solid lines denoting high-severity catchment fires (n = 11) and vertical blue dotted lines denoting lower-severity/extra local fires (n = 9). Grey dots represent lower-severity/extra local fires not included in the analysis (see Methods). (B) Composite residual response values (y axis) before and after high-severity catchment fires (solid red lines) and (C) lower-severity/extra local fires (dotted blue lines). The horizontal dotted and solid lines in B and C represent Monte Carlo-derived 99% and 95% confidence intervals, respectively.

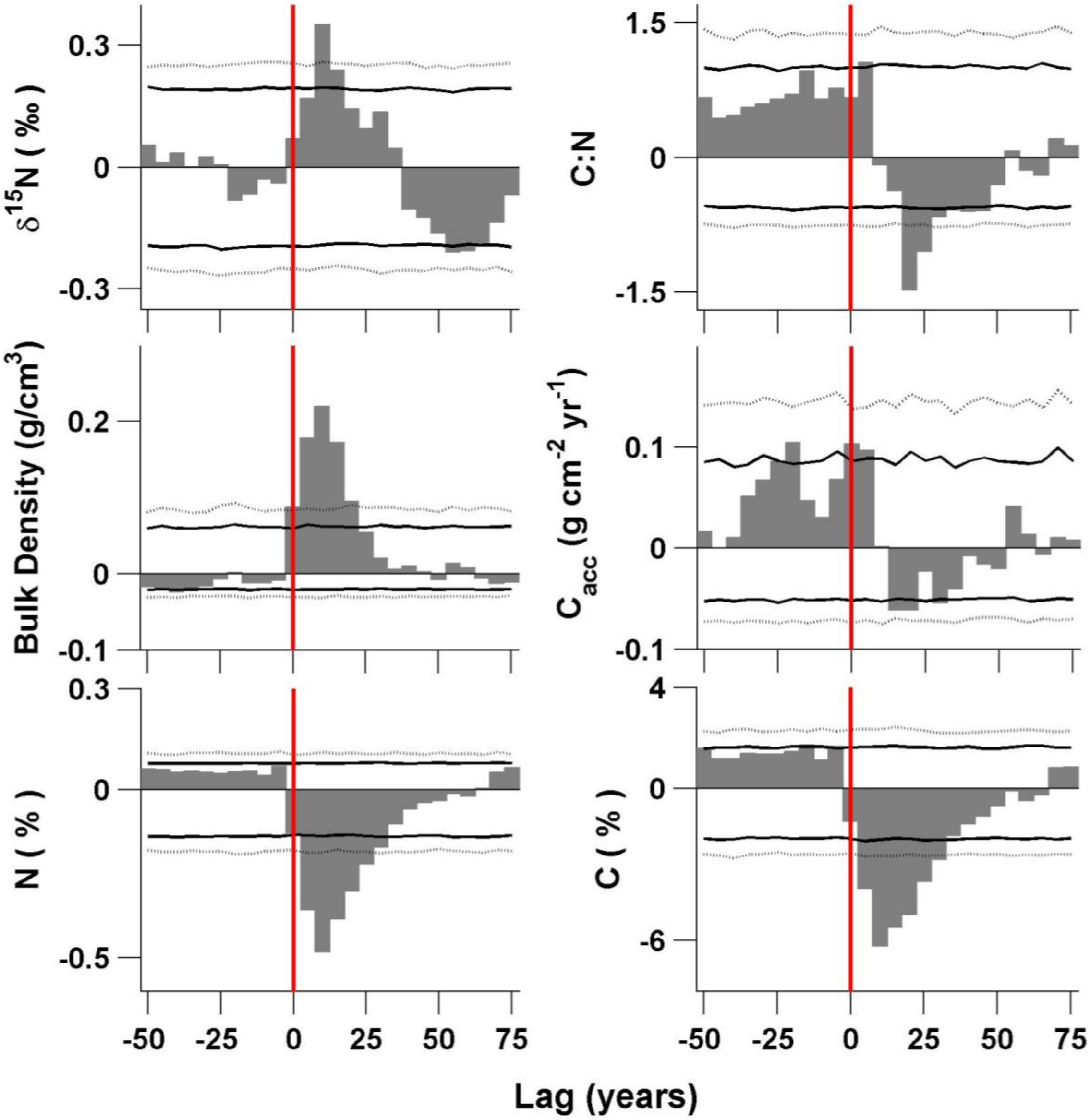

**Figure 6.** Results of Superposed Epoch Analysis. Residual response values (y axis) before and after high-severity catchment fires (solid red lines). The horizontal dotted and solid lines represent Monte Carlo-derived 99% and 95% confidence intervals, respectively (see Methods).

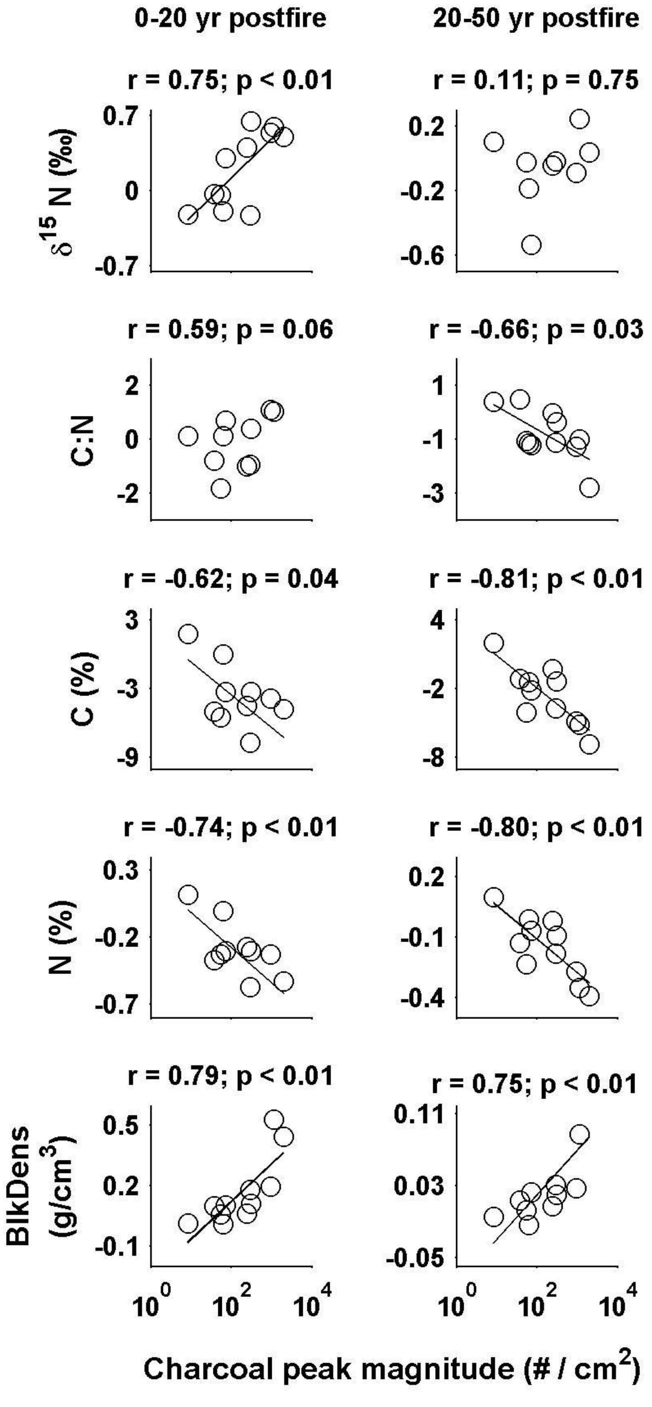

**Figure 7.** Relationships between high-severity catchment fire charcoal peak magnitude and the magnitude of proxy responses over two post-fire time intervals. Pearson correlation coefficients (r) were calculated using the log-transformed peak magnitude of each fire event and mean residual response variable values between 0 and 20 yr (left column) and 20 and 50 yr (right column) after each event.

# APPENDIX A. SUPPLEMENTARY METHODS

## Precision and Accuracy of Isotopic Measurements

Analytical precision of isotopic measurements was evaluated using within-run and between-run standard deviations from repeat analysis of a lake sediment standard and laboratory standards at the Idaho Stable Isotopes Laboratory, University of Idaho (UI), and the Stable Isotope Core Laboratory, Washington State University (WSU). Accuracy was assessed by calculating the mean difference between observed and known values for standards calibrated with internationally distributed reference materials. Error associated with sediment subsampling was evaluated by analyzing replicates taken from the same samples.

The mean within-run standard deviation for the sediment standard was +/- 0.07‰ for $\delta^{13}C$ and +/- 0.14 ‰ for $\delta^{15}N$ at UI (n = 12 runs) and +/- 0.04‰ for $\delta^{13}C$ and +/- 0.17‰ for $\delta^{15}N$ at WSU (n = 4 runs). The between-run standard deviation for mean lake sediment standard values was +/- 0.09‰ for $\delta^{13}C$ and +/- 0.22‰ for $\delta^{15}N$ at UI (n = 12) and +/- 0.02 ‰ for $\delta^{13}C$ and +/- 0.12‰ for $\delta^{15}N$ at WSU (n = 4). The mean within-run standard deviation for acetanilide lab standards was +/- 0.08‰ for $\delta^{15}N$ and +/- 0.07‰ $\delta^{13}C$ at UI and +/- 0.21‰ for $\delta^{15}N$ and +/- 0.08‰ $\delta^{13}C$ at WSU. Accuracy was 0.05‰ for $\delta^{13}C$ and 0.19‰ for $\delta^{15}N$ at UI and 0.09‰ for both $\delta^{13}C$ and $\delta^{15}N$ at WSU. Sediment subsampling error was +/- 0.11‰ for $\delta^{13}C$ and +/- 0.12‰ for $\delta^{15}N$ (five sets of n = 4 replicates; run at UI).

## Peak Analysis of Charcoal and Magnetic Susceptibility Records

Fires and erosion events were inferred from statistically significant peaks in charcoal accumulation rate (CHAR) and magnetic susceptibility (MS), respectively, using CharAnalysis version 1.1 (Higuera et al. 2009), which decomposes a time series into a low frequency background component and a high-frequency peak component. Prior to statistical analysis, CHAR and MS values were re-sampled to continuous 10-yr resolution. MS data were also transformed to positive values by adding the minimum observed value (SI units) to all measurements. Background CHAR and MS were estimated within 500-yr windows using a locally weighted regression robust to outliers (Cleveland 1979). Residual CHAR and MS were calculated by subtracting background values from the interpolated values to create a peak series composed of two populations: distinct peaks caused by local fires or erosion events (with a mean significantly higher than zero), and variability (i.e., “noise”) associated with other factors (with a mean near zero). Within overlapping 500-yr sections, peak CHAR and MS samples exceeding the 99.9th percentile of the local noise distribution estimated using a Gaussian mixture model were identified as potential fires or erosion events (Higuera et al. 2010). A charcoal peak exceeding this threshold was interpreted as a fire only if its maximum value 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).

## APPENDIX B. SUPPLEMENTARY RESULTS

**Table B1.** Radiometric dates for Chickaree Lake, CO.

| Sample Depth (cm) | Material | Laboratory ID[a] | $^{210}$Pb Activity (dpm g$^{-1}$) or $^{14}$C date (yr BP)[b] | | | Modeled or Calibrated date (cal. yr BP) 95% CI[c] | | |
|---|---|---|---|---|---|---|---|---|
| 0.8-2.4 | Bulk sediment | Flett Research | 77.33 | ± | 1.31 | -57 | (-58 | -56) |
| 2.4-3.5 | Bulk sediment | Flett Research | 77.85 | ± | 1.18 | -53 | (-53 | -52) |
| 3.5-4.6 | Bulk sediment | Flett Research | 66.27 | ± | 0.82 | -48 | (-49 | -48) |
| 4.6-6.7 | Bulk sediment | Flett Research | 57.99 | ± | 0.86 | -43 | (-44 | -42) |
| 6.7-8.9 | Bulk sediment | Flett Research | 45.53 | ± | 0.71 | -37 | (-38 | -36) |
| 8.9-11.0 | Bulk sediment | Flett Research | 45.88 | ± | 1.09 | -31 | (-32 | -30) |
| 11.0-13.2 | Bulk sediment | Flett Research | 30.27 | ± | 0.63 | -23 | (-25 | -22) |
| 13.2-15.4 | Bulk sediment | Flett Research | 25.48 | ± | 0.55 | -16 | (-17 | -15) |
| 15.4-18.6 | Bulk sediment | Flett Research | 19.88 | ± | 0.50 | -7 | (-9 | -6) |
| 18.6-20.8 | Bulk sediment | Flett Research | 23.28 | ± | 0.47 | 8 | (6 | 10) |
| 20.8-21.9 | Bulk sediment | Flett Research | 19.57 | ± | 0.45 | 23 | (20 | 25) |
| 21.9-25.1 | Bulk sediment | Flett Research | 15.90 | ± | 0.44 | 30 | (27 | 33) |
| 25.1-26.2 | Bulk sediment | Flett Research | 12.35 | ± | 0.37 | 58 | (52 | 63) |
| 58.0-59.5 | Charcoal | CAMS 139054 | 120 | ± | 100 | 150 | (3 | 406) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 61.6-62.1 | Plant remains | CAMS 155252 | 165 | ± | 35 | 173 | (3 | 283) |
| 81.5-83.5 | Charcoal | CAMS 139055 | 230 | ± | 70 | 233 | (3 | 456) |
| 83.0-83.5 | Bulk sediment | CAMS 139056 | 395 | ± | 30 | 466 | (330 | 505) |
| 116.0-117.5 | Charcoal | CAMS 139057 | 620 | ± | 70 | 601 | (525 | 679) |
| 116.5-117.0 | Bulk sediment | CAMS 139058 | 750 | ± | 35 | 686 | (659 | 731) |
| 124.5-125.0 | Bulk sediment | CAMS 155253 | 840 | ± | 30 | 746 | (693 | 879) |
| 155.0-156.5 | Charcoal | CAMS 139059 | 1010 | ± | 50 | 924 | (798 | 1043) |
| 191.0-191.5 | Bulk sediment | CAMS 155254 | 1310 | ± | 30 | 1251 | (1181 | 1291) |
| 191.5-192.0 | Charcoal | CAMS 155255 | 1245 | ± | 45 | 1183 | (1066 | 1274) |
| 240.0-240.5 | Bulk sediment | CAMS 159645 | 1810 | ± | 30 | 1752 | (1637 | 1821) |
| 290.0-290.5 | Bulk sediment | CAMS 159646 | 1975 | ± | 30 | 1924 | (1863 | 1989) |
| 340.0-340.5 | Bulk sediment | CAMS 159647 | 2375 | ± | 35 | 2410 | (2344 | 2665) |
| 380.0-380.5 | Wood | CAMS 155256 | 2495 | ± | 35 | 2580 | (2392 | 2719) |
| 423.5-424.0 | Bulk sediment | CAMS 155257 | 2685 | ± | 35 | 2788 | (2752 | 2855) |
| 424.0-424.5 | Charcoal | CAMS 155258 | 2555 | ± | 35 | 2661 | (2503 | 2747) |
| 452.0-453.0 | Charcoal | CAMS 155259 | 2740 | ± | 70 | 2847 | (2754 | 3032) |
| 488.5-489.0 | Bulk sediment | CAMS 155260 | 3045 | ± | 35 | 3269 | (3147 | 3351) |
| 530.0-530.5 | Bulk sediment | CAMS 159648 | 3390 | ± | 30 | 3636 | (3565 | 3704) |
| 570.5-571.0 | Bulk sediment | CAMS 159649 | 3805 | ± | 35 | 4194 | (4092 | 4359) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 605.5-606.0 | Bulk sediment | CAMS 159650 | 4050 | ± | 30 | 4522 | (4439 | 4777) |
| 639.5-640.0 | Bulk sediment | CAMS 155261 | 4245 | ± | 40 | 4825 | (4647 | 4865) |
| 680.5-681.0 | Bulk sediment | CAMS 159651 | 4675 | ± | 35 | 5399 | (5322 | 5567) |
| 720.5-721.0 | Bulk sediment | CAMS 159652 | 5175 | ± | 35 | 5933 | (5794 | 5992) |
| 763.5-764.0 | Bulk sediment | CAMS 159653 | 5610 | ± | 40 | 6379 | (6310 | 6476) |

---

[a] CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA.

[b] Lead-210 activity, with standard deviation, or conventional radiocarbon years before present (CE 1950), with standard deviation.

[c] See Methods for details on $^{210}$Pb modeling and calibration of $^{14}$C dates.

**Table B2.** Mean (standard deviation) biogeochemical composition of forest organic matter

| | Organic soil (n = 4) | Litter/conifer needles (n = 4) | Tree cores (n = 338) |
|---|---|---|---|
| $\delta^{15}N$ (‰) | 0.74 (1.07) | -3.62 (0.64) | -1.80 (0.40) |
| $\delta^{13}C$ (‰) | -26.19 (0.36) | -28.05 (1.35) | N/A |
| C:N | 40.97 (15.86) | 50.60 (9.42) | N/A |

**Table B3.** Spearman correlation coefficients [a,b] among $\delta^{13}$C, %C, C:N, and BSi over time.

1300 cal yr BP-Present

| | %BSi | $\delta^{13}$C | C:N |
|---|---|---|---|
| %C | **-0.82** | **-0.68** | **0.67** |
| C:N | -0.38 | **-0.32** | |
| $\delta^{13}$C | **0.69** | | |

2800-1300 cal yr BP

| | %BSi | $\delta^{13}$C | C:N |
|---|---|---|---|
| %C | **-0.57** | **0.42** | **0.79** |
| C:N | **-0.70** | **0.49** | |
| $\delta^{13}$C | -0.07 | | |

4250-2800 cal yr BP

| | %BSi | $\delta^{13}$C | C:N |
|---|---|---|---|
| %C | 0.03 | 0.05 | **0.69** |
| C:N | 0.02 | 0.12 | |
| $\delta^{13}$C | -0.03 | | |

[a] Correlations reflect reduced sample sizes to account for autocorrelation (see Methods).

[b] Correlations significant at the $p \leq 0.05$ level are bold.

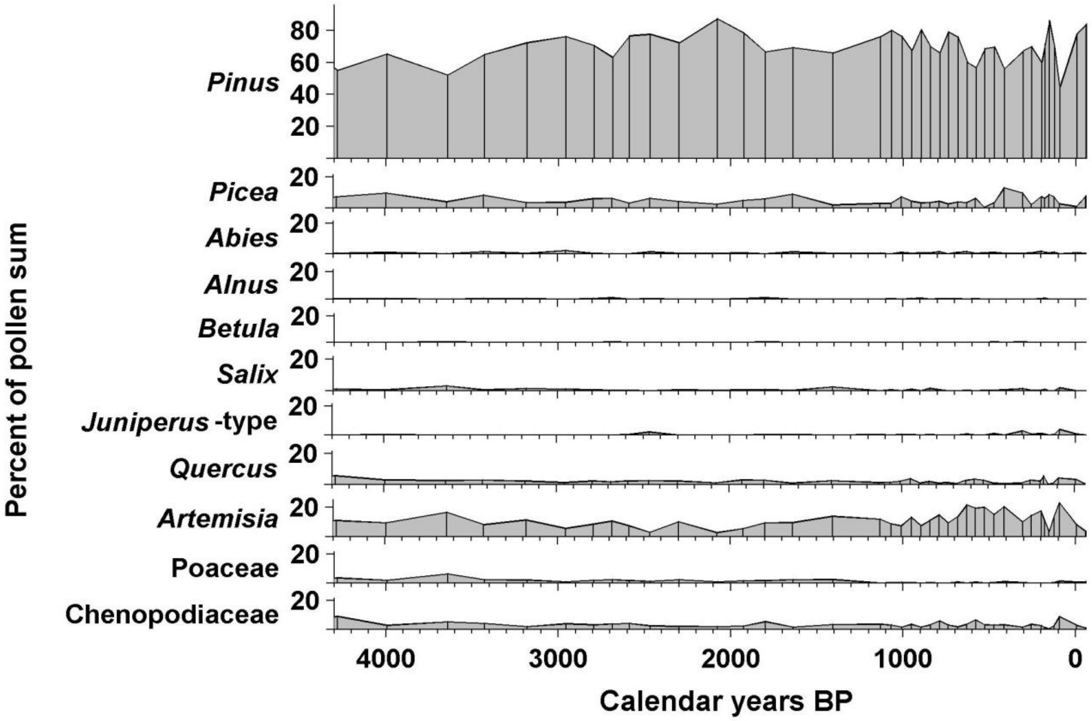

**Figure B1**. Pollen percentage diagram for Chickaree Lake, CO, showing major pollen taxa identified. Percentage abundance (y axis) is shown by time (x axis). Percent abundance was calculated relative to total terrestrial pollen.

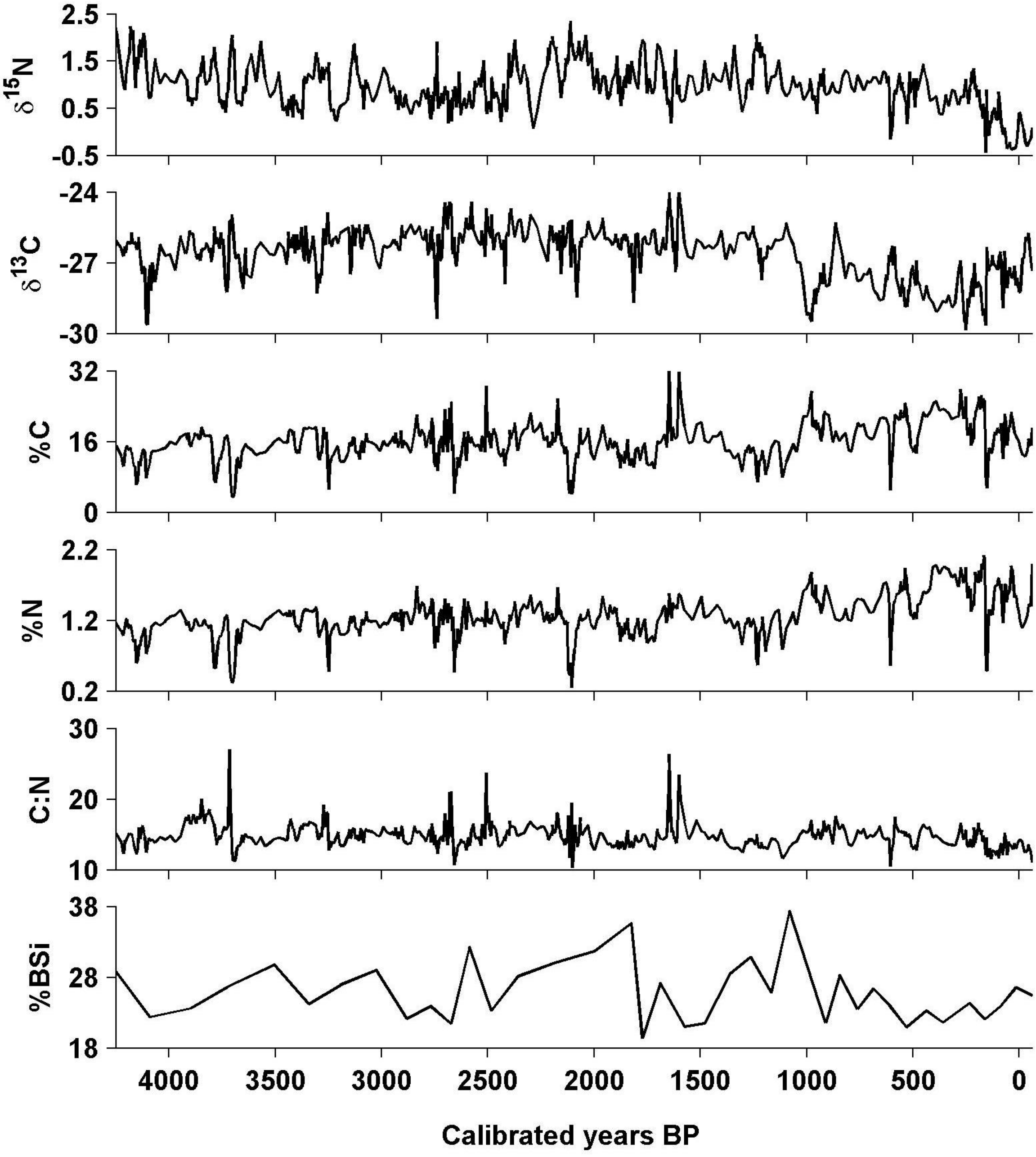

**Figure B2.** Biogeochemical time series for Chickaree Lake, CO, 4250 cal yr BP to present. See Methods for proxy descriptions.

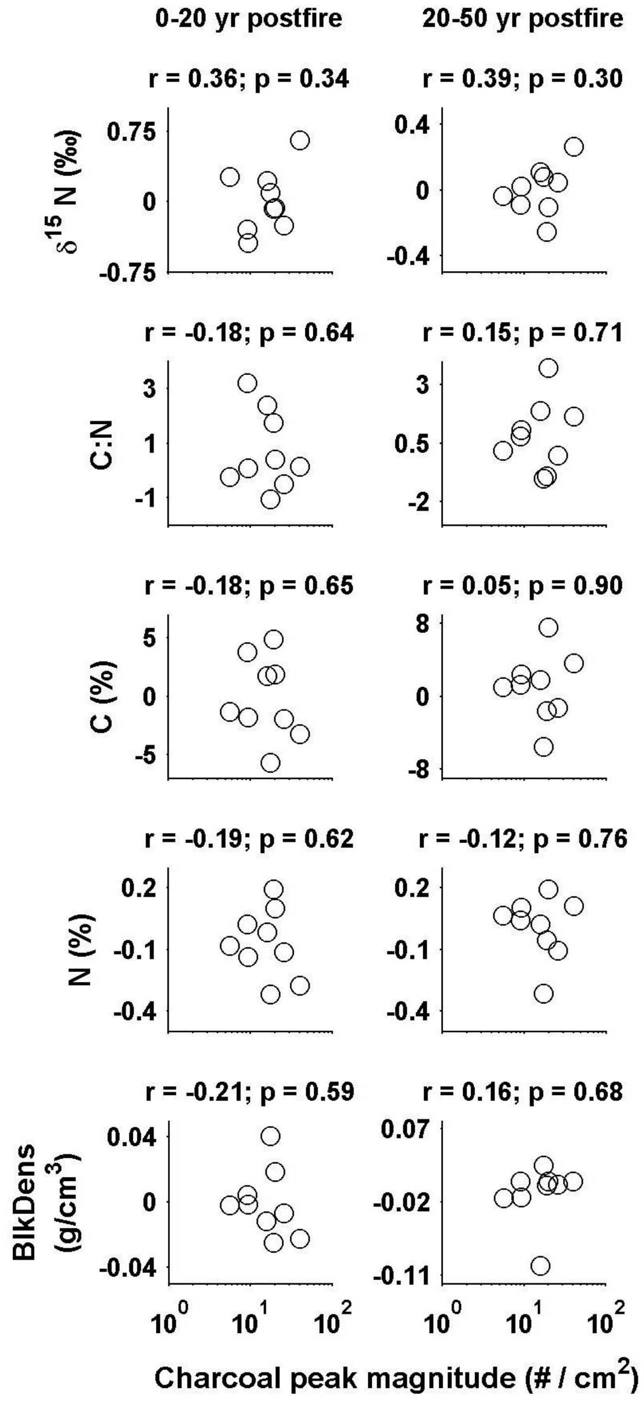

**Figure B3.** Relationships between lower-severity/extra local fire charcoal peak magnitude and the magnitude of proxy responses during two post-fire periods. Pearson correlation coefficients (r) were calculated using the log-transformed peak magnitude of each fire and mean residual response variable values between 0 and 20 yr (left column) and 20 and 50 yr (right column) after each event.