BIOLOGY LETTERS

royalsocietypublishing.org/journal/rsbl

Research

Cite this article: Chipman ML, Hu FS. 2019 Resilience of lake biogeochemistry to boreal-forest wildfires during the late Holocene. *Biol. Lett.* **15**: 20190390.
http://dx.doi.org/10.1098/rsbl.2019.0390

Received: 22 May 2019
Accepted: 6 August 2019

Subject Areas:
ecology, environmental science

Keywords:
boreal fires, nitrogen, carbon, $\delta^{15}N$, $\delta^{13}C$, C : N, ecological resilience

Author for correspondence:
Melissa L. Chipman
e-mail: mlchipma@syr.edu

A contribution to the special feature 'Ecological resilience: from theory to empirical observations using long-term datasets' organised by the PAGES EcoRe3 Working Group.

Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4614500.

THE ROYAL SOCIETY PUBLISHING

Global change biology

Resilience of lake biogeochemistry to boreal-forest wildfires during the late Holocene

Melissa L. Chipman[1] and Feng Sheng Hu[2,3,4]

[1]Department of Earth Sciences, Syracuse University, Syracuse, NY, USA
[2]Department of Plant Biology, [3]Department of Geology, and [4]Program in Ecology, Evolution, and Conservation Biology, University of Illinois, Urbana, IL, USA

MLC, 0000-0002-6872-8829; FSH, 0000-0002-7643-1347

Novel fire regimes are expected in many boreal regions, and it is unclear how biogeochemical cycles will respond. We leverage fire and vegetation records from a highly flammable ecoregion in Alaska and present new lake-sediment analyses to examine biogeochemical responses to fire over the past 5300 years. No significant difference exists in $\delta^{13}C$, %C, %N, C : N, or magnetic susceptibility between pre-fire, post-fire, and fire samples. However, $\delta^{15}N$ is related to the timing relative to fire ($\chi^2 = 19.73$, $p < 0.0001$), with higher values for fire-decade samples (3.2 ± 0.3‰) than pre-fire (2.4 ± 0.2‰) and post-fire (2.2 ± 0.1‰) samples. Sediment $\delta^{15}N$ increased gradually from 1.8 ± 0.6 to 3.2 ± 0.2‰ over the late Holocene, probably as a result of terrestrial-ecosystem development. Elevated $\delta^{15}N$ in fire decades likely reflects enhanced terrestrial nitrification and/or deeper permafrost thaw depths immediately following fire. Similar $\delta^{15}N$ values before and after fire decades suggest that N cycling in this lowland-boreal watershed was resilient to fire disturbance. However, this resilience may diminish as boreal ecosystems approach climate-driven thresholds of vegetation structure, permafrost thaw and fire.

1. Introduction

Disturbance plays a key role in mediating the impact of climate change on the structure and function of global ecosystems [1]. Changing disturbance regimes may reduce ecological resilience, which is the capacity for ecosystem structure and function to return to pre-disturbance conditions following perturbation [2]. Wildfires are the major disturbance in boreal forests, impacting plant communities, ecosystem productivity and biogeochemical cycling [3,4]. Boreal forests may experience novel fire regimes in the future, as suggested by strong thresholds in fire–climate relationships [5] and observed increases in the frequency and severity of modern fires [6–9]. Understanding the resilience of boreal forests to fire has implications for assessing ecosystem response to high-latitude warming.

The Yukon Flats ecoregion of Alaska experiences some of the most frequent burning in the North American boreal biome [5,7]. Recent climate-driven burning in this warm and dry region is unprecedented in the context of the past 10 000 years [8]. The region may be an analogue for other flammable boreal areas in the future. Wildfires combust biomass and surface soils, releasing nutrients and other soil-derived materials to nearby waterbodies via erosion and/or leaching [10–12], in addition to losses via combustion [13]. Thus, fires impact biogeochemical pathways linking terrestrial and aquatic systems [14]. Understanding the resilience of boreal watersheds to changing fire regimes is key in lowland-boreal landscapes such as the Yukon Flats, where abundant lakes and

royalsocietypublishing.org/journal/rsbl *Biol. Lett.* **15**: 20190390

Table 1. Mean and standard errors of biogeochemical measurements for all, pre-fire (50 years before fire), fire (within CHAR decade) and post-fire (50 years after fire) samples.

	%C	$\delta^{13}C$ (‰ VPDB)	%N	$\delta^{15}N$ (‰ air N_2)	molar C : N	magnetic susceptibility	age range (years since fire)	no. of samples
pre-fire	26.9 ± 1.5	−32.3 ± 0.2	2.4 ± 0.1	2.4 ± 0.2	13.4 ± 0.2	1.1 ± 0.2	11–54	25
fire	22.1 ± 5.0	−31.3 ± 1.1	1.8 ± 0.4	3.2 ± 0.3	14.2 ± 1.3	2.9 ± 1.9	0	5
post-fire	22.9 ± 2.4	−30.8 ± 0.5	2.0 ± 0.2	2.2 ± 0.1	13.2 ± 0.2	4.2 ± 1.4	11–56	25
all	24.6 ± 1.4	−31.6 ± 0.3	2.2 ± 0.1	2.4 ± 0.1	13.4 ± 0.2	2.7 ± 0.7		55

wetlands provide critical habitat for millions of North American waterfowl [15] and alter regional carbon dynamics [16].

The capacity for post-disturbance recovery is assumed to be low in retrogressive ecosystems such as mature N-limited boreal forests, where fires can result in nutrient losses that exceed inputs [17]. However, a recent study in the Yukon Flats suggested resilience of lake ecosystems to modern fires on annual timescales [18]. Despite this finding, it remains unclear how resilient boreal watersheds are to fires at longer timescales and under different fire regimes [14]. Palaeoecological archives are valuable for assessing ecosystem resilience to changing disturbance regimes at multiple timescales [12,19]. Lake sediments incorporate watershed materials that enter the lake following disturbance, as well as biogeochemical signals of aquatic nutrient cycling, which may be responsive to changes in the quantity and/or quality of terrestrial inputs. In this study, we use sediment cores from a site in the Yukon Flats with a well-established fire history [8] to examine the impact of fires on ecosystem biogeochemistry and resilience during the past 5300 years.

2. Materials and methods

In 2007, we collected sediment cores from Screaming Lynx Lake (SL07; 66.06815° N, 145.40440° W, 223 m.a.s.l.), Yukon Flats, Alaska (electronic supplementary material, figure S1). The lake has a small surface area (0.03 km^2) within a 0.7-km^2 watershed underlain by discontinuous permafrost [20]. Sediment cores were obtained from the deepest part of the lake (water depth = 7.4 m), and correlated based on visual stratigraphy and magnetic susceptibility (MS), resulting in a continuous 390.5-cm sediment sequence. These sediments were used for a fire-history reconstruction (electronic supplementary material, figure S2a) [8].

In this study, we conducted geochemical analyses on the SL07 sediments spanning the past 5300 years, which capture the regional Holocene establishment of boreal forests (electronic supplementary material, figure S3). We identified sediment samples with significant peaks in charcoal-accumulation rate (CHAR; # charcoal particles $cm^{-2}\,yr^{-1}$), representing fire events within approximately 1 km of the lake [21]. To remove the influence of multiple fires, we identified CHAR peaks in samples with (1) no other significant CHAR peaks within a 50-year interval before the fire decade, and (2) low variability of charcoal concentration in surrounding samples within a 100-year window (electronic supplementary material, figure S2d). We manually chose five CHAR peaks meeting these criteria at 220, 1995, 2630, 3090, and 5190 cal BP to capture a broad temporal range in the record. We subsampled 0.5-cm^3 sediment at contiguous 0.25-cm intervals over a 2.5-cm section centred on each CHAR peak to achieve decadal resolution for sediment deposited ≤50 years before and after fires.

Bulk sediment samples were analysed for weight percentages of C and N, $\delta^{13}C$, $\delta^{15}N$ and MS (electronic supplementary material, table S1). We tested for significant differences in pre-fire, fire, and post-fire values for all measurements using one-way analysis of variance. We examined the effect of time relative to fire on $\delta^{15}N$ with a linear mixed-effects model, accounting for the random effect of long-term variability [model = $\delta^{15}N \sim$ timing + (1 | fire age) + ε]. The model was constructed in the nlme package in R [22], and model significance was assessed using a likelihood-ratio test.

3. Results

Mean C : N and $\delta^{13}C$ of the SL07 sediments are 13.4 ± 0.2‰ and −31.6 ± 0.3‰, respectively (table 1). %C (mean = 24.6 ± 1.4) and %N (mean = 2.2 ± 0.1) are highly correlated (r = 0.97, $p < 0.0001$), with a %N-intercept of 0.0007. No significant difference exists for %N, %C, C : N or $\delta^{13}C$ between pre-fire, fire, and post-fire samples (figure 1). Similarly, MS shows no significant difference between pre-fire, fire, and post-fire samples ($F_{2,52} = 2.48$, $p = 0.094$). MS is overall low (2.7 ± 0.7) in the SL07 sediments. The only exception is high MS following the 1995 cal BP fire (17.6 ± 1.3; electronic supplementary material, figure S4), associated with a 2-cm clay band.

Sediment $\delta^{15}N$ increases through time over the past 5300 years (figure 2*a*). Of all the geochemical measurements, only $\delta^{15}N$ differs significantly ($p < 0.05$) among pre-fire, fire, and post-fire samples ($F_{2,52} = 4.02$, $p = 0.024$), with a mean value of 3.2 ± 0.3‰ for fire decades compared 2.4 ± 0.2‰ and 2.2 ± 0.1‰ for pre- and post-fire, respectively (table 1). Our linear mixed-effects model shows that sediment $\delta^{15}N$ is significantly related to timing relative to fire ($\chi^2_2 = 19.73$, $p < 0.0001$). Specifically, $\delta^{15}N$ in the fire decade (3.2 ± 0.3‰) is significantly higher than pre-fire values (2.4 ± 0.2‰; $t_{48} = 3.76$, $p = 0.0005$). However, post-fire $\delta^{15}N$ (2.2 ± 0.1‰) does not significantly differ from pre-fire values ($t_{48} = -1.80$, $p = 0.0782$).

4. Discussion

(a) Millennial-scale trends reflect long-term terrestrial processes

Bulk $\delta^{15}N$ of lake sediments integrates signals from aquatic and terrestrial sources and from processes over multiple timescales [23,24]. We use other geochemical data to constrain our interpretation of $\delta^{15}N$ from SL07. Overall low MS and lack of significant differences in MS among pre-fire, post-fire, and fire samples suggest limited erosion of lithic material into the lake following fire, with the exception of a clay layer with high MS and $\delta^{13}C$ immediately following the 1995 cal BP CHAR peak (electronic supplementary material, figure S4). CHAR peaks

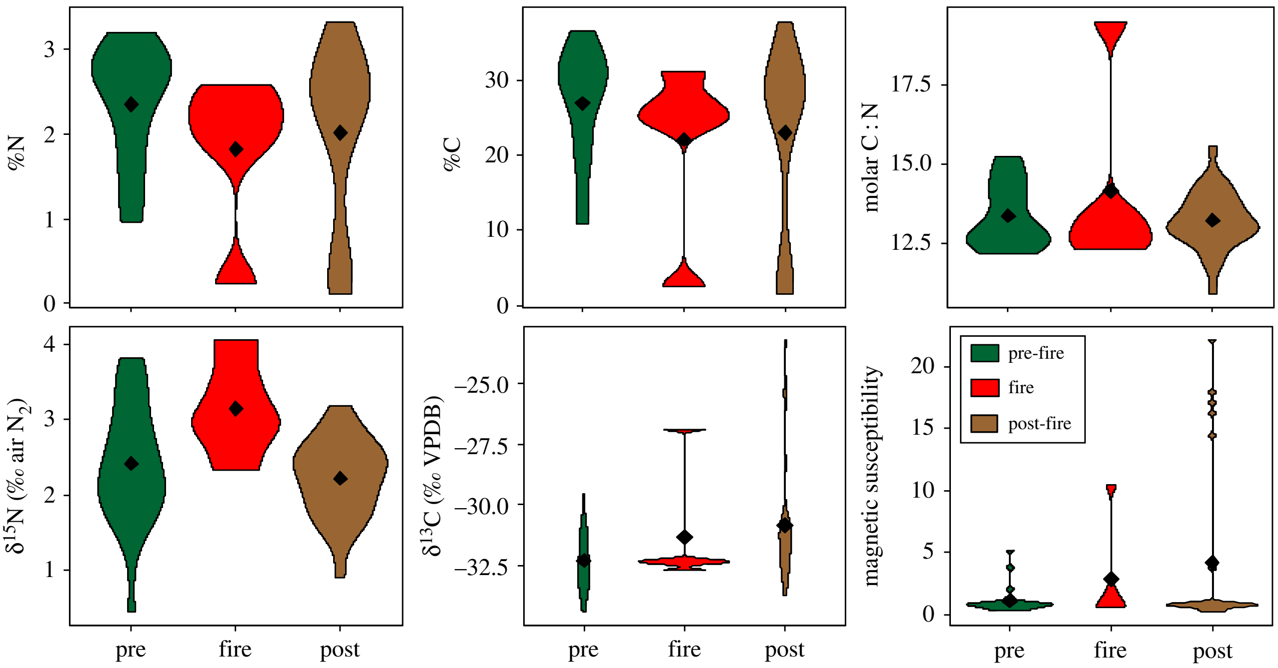

Figure 1. Boxplots (diamond = mean, circle = outlier) of SL07 biogeochemical proxies for pre-fire, fire and post-fire samples. (Online version in colour.)

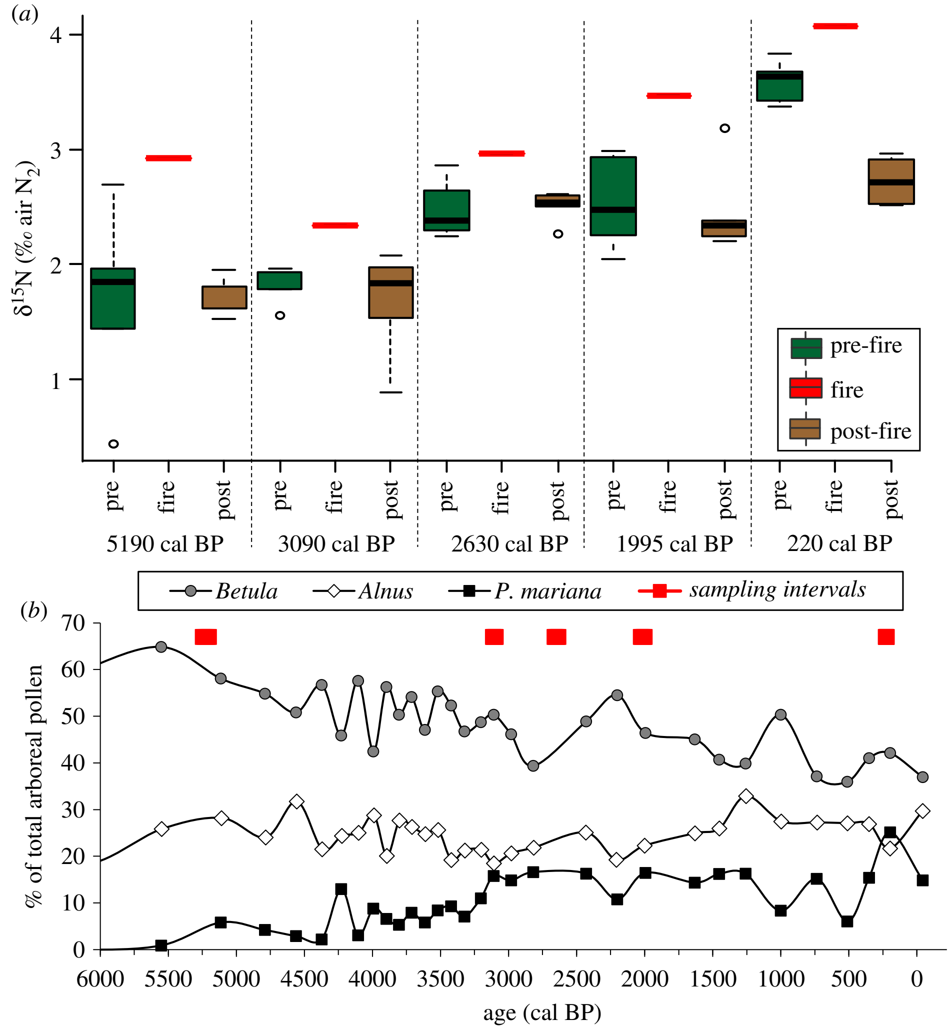

Figure 2. (*a*) Boxplots of $\delta^{15}N$ for pre-fire, fire and post-fire samples for each fire event, showing a temporal trend. (*b*) *Betula*, *Alnus* and *P. mariana* relative pollen abundance, with sampling intervals for fires in this study. (Online version in colour.)

represent atmospheric deposition of particles from fires within approximately 1 km of the lake [21], and thus the lack of eroded material for most peaks could either reflect that fires did not burn on the lake margin and/or that fires did not burn deeply into the soils. The strong relationship between %C and %N, and the low *y*-intercept value, indicates little to no influence of inorganically bound nitrogen on sediment $\delta^{15}N$ [23]. Furthermore, relatively low C : N (13.4 ± 0.2)

and $\delta^{13}C$ (−31.6 ± 0.3‰) suggest limited contribution of terrestrial (C : N > 20) compared to aquatic (C : N < 10) organic material [25]. Thus, we interpret $\delta^{15}N$ as predominately reflecting changes in the isotopic composition of aquatic material incorporated into the sediment.

The gradual $\delta^{15}N$ increase over the past 5300 years (figure 2*a*) is probably related to terrestrial processes in the watershed. Positive relationships between soil, foliar and lake-sediment $\delta^{15}N$ have been identified in non-boreal settings where $\delta^{15}N$ may be an indicator of ecosystem-scale N availability [26–28]. However, increasing N availability is not a plausible explanation for the late-Holocene $\delta^{15}N$ increase at our site. In boreal ecosystems, declining N availability typically characterizes retrogressive stages of ecosystem development [29,30]. In Alaska, such retrogressive development occurred with the late-Holocene establishment of *Picea mariana*-dominated forests [31,32]. At SL07, *P. mariana* increased from 1 to 14% of the pollen sum over the past 5300 years (figure 2*b*). Foliar and soil $\delta^{15}N$ values can be decoupled in boreal forests because *P. mariana* (black spruce) uses organic N via ectomycorrhizae, which strongly fractionates against ^{15}N [33], compared to ecosystems that primarily rely on inorganic ammonium and nitrate [27]. *Picea mariana* foliage and litter are thus extremely depleted in ^{15}N, while soils become progressively enriched [33,34] as this species increased in abundance over the late Holocene. Thus, we interpret the late-Holocene increase in $\delta^{15}N$ as a signal of soil development associated with the expansion of *P. mariana* and the delivery of isotopically heavier soil-derived N to the lake.

Other interpretations may explain the late-Holocene increasing trend in sediment $\delta^{15}N$. For example, the mid-Holocene expansion of N-fixing *Alnus* increased lake productivity and lake-sediment $\delta^{15}N$ in southwestern Alaska [35,36]. However, *Alnus* pollen percentages were relatively stable over the past 5300 years at SL07 (electronic supplementary material, figure S3). *Picea mariana* grows in cool/wet soils that are more acidic, poorly drained and recalcitrant than soils beneath deciduous vegetation [37]. These conditions can enhance denitrification, which discriminates strongly against ^{15}N [23]. However, *P. mariana* forests have lower mineralization and nitrification rates than deciduous stands [37,38], and low available nitrate limits denitrification [39]. Fire-regime changes may have also played a role in driving the late-Holocene $\delta^{15}N$ increase, given that charcoal records suggest increased burning over the past 5300 years in the Yukon Flats (electronic supplementary material, figure S2c). However, this interpretation is inconsistent with the return of post-fire $\delta^{15}N$ to pre-fire values after each fire at SL07 (discussed below). Yet, another explanation is progressive deepening of the lake, resulting in stratification and anoxic bottom waters, and thus increasing within-lake denitrification. This interpretation is not supported by palaeorecords from this region indicating variable moisture conditions and lake levels over the late Holocene [40,41]. Furthermore, it is unlikely that this shallow lake remained stratified during spring and autumn overturns.

(b) Decadal-scale patterns suggest ecological resilience to fire

Our results suggest ecosystem resilience to fire on decadal timescales over the late Holocene. Specifically, we find no change in all of the sediment indicators following fires at SL07, with the exception of $\delta^{15}N$, which quickly recovered. These results contrast with recent work on fire-induced nutrient dynamics in a subalpine watershed during the late Holocene, which showed marked multidecadal changes in lake-sediment %C, %N, C : N and $\delta^{15}N$ following high-severity fires [12]. Differences in topography and hydrology may explain these contrasting results. Terrestrial and aquatic systems in steep subalpine watersheds are tightly coupled, promoting rapid fluxes of terrestrial debris to lakes following fires. Similarly, upland boreal watersheds also experienced elevated nutrients over several decades in response to fires [11]. By contrast, the SL07 watershed is characterized by low surface relief, which may have inhibited post-fire erosion of terrestrial debris to the lake despite the relatively large drainage basin (watershed : lake area = 23.3; electronic supplementary material, figure S1), highlighting the role of landforms in modulating aquatic linkages to terrestrial disturbance.

Low-relief boreal and wetland environments such as the Yukon Flats have poorly developed fluvial networks, which can minimize the impact of fires on adjacent lakes [18]. However, elevated $\delta^{15}N$ during fire decades at SL07 indicates increased nutrient influx to the lake. One mechanism that may enhance nutrient leaching from terrestrial to aquatic pools is an increase in soil infiltration depths and subsurface drainage associated with increased permafrost thaw depths [42,43]. Removal of organic matter during fire increases soil thermal conductivity, which can result in deepening of the permafrost active layer [44]. In addition to enhancing subsurface flow, lowering of the permafrost table from fire-driven soil warming could increase the availability of deeper N pools, which are ^{15}N-enriched relative to surface organic soils removed during fire [42,45]. Our record suggests that increased thaw depths following fire can be an important indirect hydrologic pathway connecting lakes to terrestrial disturbance in low-lying boreal areas.

In addition to enhancing subsurface hydrological connectivity, fires can increase short-term N availability in the soil by converting organic N to ammonium and nitrate [46]. Although soil ammonium increases are short-lived (less than 2 years), nitrification of ammonium can elevate soil nitrate pools for several years after fire [46,47], which can be rapidly leached into nearby lakes and streams in boreal settings [10,11]. Nitrification strongly discriminates against ^{15}N, and thus leached nitrate could increase the $\delta^{15}N$ of aquatic material [23]. In addition, terrestrial N losses from biomass volatilization may be offset by N fixation via *Alnus*, which is a major early post-fire colonizer. Enhanced early successional N availability from *Alnus* N-fixation could accelerate N cycling and $\delta^{15}N$ fractionation in soils and/or in the aquatic environment [35,36]. Enhanced nitrogen export and nitrate leaching from boreal soils in interior Alaska have also been linked to increased permafrost thaw depths [42,43,48], which could be further exacerbated by fire activity.

The rapid return of sediment $\delta^{15}N$ to pre-fire values within 50 years following fire suggests that N cycling in lowland-boreal watersheds is resilient to fire. This finding is not surprising, given that post-fire successional plants have a high capacity for N uptake [49] and that soils can rapidly return to N-limited conditions. The rapid recovery of $\delta^{15}N$ following fire is consistent with recent findings regarding post-fire vegetation succession in boreal forests, which suggest a substantial seed bank following fire, rapid stand self-replacement (3–10 years), and stabilizing fire–soil–vegetation feedbacks that promote resilience [50,51].

Recent studies in other forested ecosystems revealed evidence of decreasing resilience to recent burning. For example, temperate forests near the edge of their climatic tolerances have shown diminished seedling densities and high regeneration failures following fire [52]. Despite evidence for resilience as demonstrated in this study, boreal forests in Alaska may already be approaching thresholds of vegetation structure, carbon cycling and fire regimes in response to climate change and climate–fire feedbacks [53,54]. For example, enhanced fire regimes may promote deciduous vegetation and/or alter soil carbon storage, representing a fundamental shift in ecosystem state that can alter nutrient cycling [53,55]. Furthermore, ongoing increases in summer temperatures and fire may increase permafrost active-layer depths in lowland areas and alter subsurface hydrological networks, which could enhance the connectivity and nutrient fluxes. Future studies should assess the vulnerability and resilience of boreal landscapes in the context of altered vegetation, permafrost and hydrology in response to novel climate conditions and fire regimes.

Data accessibility. Raw data and a copy of the electronic supplementary file can be accessed from the Dryad Digital Repository: https://doi.org/10.5061/dryad.440rk01 [56].

Authors' contributions. F.S.H. conceived of the study, M.L.C. carried out laboratory work and statistical analyses, and both authors drafted the manuscript. Both authors give final approval for publication and agree to be held accountable for work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by NSF grant no. 1636476 (F.S.H.).

Acknowledgements. We thank Michael Masters, University of Illinois, for EA-IRMS analyses.

References

1. Turner MG. 2010 Disturbance and landscape dynamics in a changing world. *Ecology* **91**, 2833–2849. (doi:10.1890/10-0097.1)
2. Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA. 2016 Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* **53**, 120–129. (doi:10.1111/1365-2664.12511)
3. Mcguire AD *et al.* 2009 Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol. Monogr.* **79**, 523–555.
4. Mann DH, Scott Rupp T, Olson MA, Duffy PA. 2012 Is Alaska's boreal forest now crossing a major ecological threshold? *Arct Antarct. Alp. Res.* **44**, 319–331. (doi:10.1657/1938-4246-44.3.319)
5. Young AM, Higuera PE, Duffy PA, Hu FS. 2017 Climatic thresholds shape northern high-latitude fire regimes and imply vulnerability to future climate change. *Ecography* (*Cop.*). 40, 606–617. (doi:10.1111/ecog.02205)
6. Kasischke ES, Turetsky MR. 2006 Recent changes in the fire regime across the North American boreal region—spatial and temporal patterns of burning across Canada and Alaska. *Geophys. Res. Lett.* **33**, L09703. (doi:10.1029/2006GL025677)
7. Kasischke ES *et al.* 2010 Alaska's changing fire regime—implications for the vulnerability of its boreal forests. *Can. J. For. Res.* **40**, 1313–1324. (doi:10.1139/X10-098)
8. Kelly R, Chipman ML, Higuera PE, Stefanova I, Brubaker LB, Hu FS. 2013 Recent burning of boreal forests exceeds fire regime limits of the past 10,000 years. *Proc. Natl Acad. Sci. USA* **110**, 13 055–13 060. (doi:10.1073/pnas.1305069110)
9. Veraverbeke S, Rogers BM, Goulden ML, Jandt RR, Miller CE, Wiggins EB, Randerson JT. 2017 Lightning as a major driver of recent large fire years in North American boreal forests. *Nat. Clim. Chang.* **7**, 529–534. (doi:10.1038/nclimate3329)
10. Betts EF, Jones JB. 2009 Impact of wildfire on stream nutrient chemistry and ecosystem metabolism in boreal forest catchments of interior Alaska. *Arct. Antarct. Alp. Res.* **41**, 407–417. (doi:10.1657/1938-4246-41.4.407)
11. McEachern P, Prepas EE, Gibson JJ, Dinsmore WP. 2000 Forest fire induced impacts on phosphorus, nitrogen, and chlorophyll concentrations in boreal subarctic lakes of northern Alberta. *Can. J. Fish. Aquat. Sci.* **57**, 73–81. (doi:10.1139/cjfas-57-S2-73)
12. Dunnette PV, Higuera PE, Mclauchlan KK, Derr KM, Briles CE, Keefe MH. 2014 Biogeochemical impacts of wildfires over four millennia in a Rocky Mountain subalpine watershed. *New Phytol.* **203**, 900–912. (doi:10.1111/nph.12828)
13. Harden JW, Mack M, Veldhuis H, Gower ST. 2003 Fire dynamics and implications for nitrogen cycling in boreal forests. *J. Geophys. Res.* **107**, 8223. (doi:10.1029/2001JD000494)
14. Bixby RJ, Cooper SD, Gresswell RE, Brown LE, Dahm CN, Dwire KA. 2015 Fire effects on aquatic ecosystems: an assessment of the current state of the science. *Freshw. Sci.* **34**, 1340–1350. (doi:10.1086/684073)
15. Lewis TL, Schmutz JA, Amundson CL, Lindberg MS. 2016 Waterfowl populations are resilient to immediate and lagged impacts of wildfires in the boreal forest, *J. Appl. Ecol.* **53**, 1746–1754. (doi:10.1111/1365-2664.12705)
16. Douglas TA, Jones MC, Hiemstra CA, Arnold JR. 2014 Sources and sinks of carbon in boreal ecosystems of interior Alaska: a review. *Elem. Sci. Anthr.* **2**, 000032. (doi:10.12952/journal.elementa.000032)
17. Peltzer DA *et al.* 2010 Understanding ecosystem retrogression. *Ecol. Monogr.* **80**, 509–529. (doi:10.1890/09-1552.1)
18. Lewis TL, Lindberg MS, Schmutz JA, Bertram MR. 2014 Multi-trophic resilience of boreal lake ecosystems to forest fires. *Ecology* **95**, 1253–1263. (doi:10.1890/13-1170.1)
19. McLauchlan KK *et al.* 2014 Reconstructing disturbances and their biogeochemical consequences over multiple timescales. *Bioscience* **64**, 105–116. (doi:10.1093/biosci/bit017)
20. Olefeldt D *et al.* 2016 Circumpolar distribution and carbon storage of thermokarst landscapes. *Nat. Commun.* **7**, 1–11. (doi:10.1038/ncomms13043)
21. Higuera PE, Peters ME, Brubaker LB, Gavin DG. 2007 Understanding the origin and analysis of sediment-charcoal records with a simulation model. *Quat. Sci. Rev.* **26**, 1790–1809. (doi:10.1016/j.quascirev.2007.03.010)
22. Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team. 2018 nlme: Linear and nonlinear mixed effects models. R package version 3.1–137. See https://CRAN.R-project.org/package=nlme.
23. Talbot MR. 2001 Nitrogen isotopes in palaeolimnology. *Tracking Environmental Change Using Lake Sediments* **2**, 401–439. (doi:10.1007/0-306-47670-3_15)
24. McLauchlan KK, Williams JJ, Engstrom DR. 2013 Nutrient cycling in the paleorecord: fluxes from terrestrial to aquatic ecosystems. *Holocene* **23**, 1635–1643. (doi:10.1177/0953613496289)
25. Meyers PA, Lallier-Vergès E. 1999 Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. *J. Paleolimnol.* **21**, 345–372. (doi:10.1023/A:1008073732192)
26. McLauchlan KK, Craine JM, Oswald WW, Leavitt PR, Likens GE. 2007 Changes in nitrogen cycling during the past century in a northern hardwood forest. *Proc. Natl Acad. Sci. USA* **104**, 7466–7470. (doi:10.1073/pnas.0701779104)
27. Craine JM, Brookshire ENJ, Cramer MD, Hasselquist NJ, Koba K, Marin-Spiotta E, Wang L. 2015 Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils. *Plant Soil* **396**, 1–26. (doi:10.1007/s11104-015-2542-1)
28. Kim SL, Shuman BN, Minckley TA, Marsicek JP. 2016 Biogeochemical change during climate-driven afforestation: a paleoecological perspective from the

Rocky Mountains. *Ecosystems* **19**, 615–624. (doi:10.1007/s10021-015-9955-9)

29. Chapin FS, Walker LR, Fastie CL, Sharman LC. 1994 Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* **64**, 149–175. (doi:10.2307/2937039)
30. Wardle DA, Zackrisson O, Hornberg G, Gallett C. 1997 The influence of island size on ecosystem properties. *Science* **277**, 1296–1299. (doi:10.1126/science.277.5330.1296)
31. Anderson PM, Brubaker LB. 1994 Vegetation history of northcentral Alaska: a mapped summary of Late-Quaternary pollen data. *Quat. Sci. Rev.* **13**, 71–92. (doi:10.1016/0277-3791(94)90125-2)
32. Hu FS, Brubaker LB. 1996 Boreal ecosystem development in northwestern Alaska Range since 11,000 yr B.P. *Quat. Res.* **45**, 188–201. (doi:10.1006/qres.1996.0019)
33. Hobbie JE, Hobbie EA, Drossman H, Conte M, Weber JC, Shamhart J, Weinrobe M. 2009 Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and boreal forests: ^{15}N is the key signal. *Can. J. Microbiol.* **55**, 84–94. (doi:10.1139/W08-127)
34. Mayor JR *et al.* 2012 Nitrogen isotope patterns in Alaskan black spruce reflect organic nitrogen sources and the activity of ectomycorrhizal fungi. *Ecosystems* **15**, 819–831. (doi:10.1007/sl0021-012-9548-9)
35. Hu FS, Finney BP, Brubaker LB. 2001 Effects of Holocene *Alnus* expansion on aquatic productivity, nitrogen cycling, and soil development in southwestern Alaska. *Ecosystems* **4**, 358–368. (doi:10.1007/s10021-001-0017-0)
36. Perren BB, Axford Y, Kaufman DS. 2017 Alder, nitrogen, and lake ecology: terrestrial–aquatic linkages in the postglacial history of Lone Spruce Pond, Southwestern Alaska. *PLoS ONE* **12**, e0169106. (doi:10.1371/journal.pone.0169106)
37. Van Cleve K, Yarie J. 1986 Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. In *Forest ecosystems in the Alaskan taiga: a synthesis of structure and function* (eds K Van Cleave, FS Chapin III, PW Flanagan, LA Viereck, CT Dyrness), pp. 160–189. New York, NY: Springer-Verlag, Inc.
38. Bonan G. 1990 Carbon and nitrogen cycling in North American boreal forests. I. Litter quality and soil thermal effects in Interior Alaska. *Biogeochemistry* **3**, 1–28. (doi:10.1007/bf00000889)
39. Del Grosso SJ, Parton WJ, Moiser AR, Oijima DS, Kulmala AE, Phongpan S. 2000 General model for N_2O and N_2 gas emissions from soils due to denitrification. *Global Biogeochem. Cy.* **14**, 1045–1060. (doi:10.1029/1999gb001225)
40. Chipman ML, Clegg BF, Hu FS. 2012 Variation in the moisture regime of northeastern interior Alaska and possible linkages to the Aleutian Low: inferences from a late-Holocene $\delta^{18}O$ record. *J. Paleolimnol.* **48**, 69–81. (doi:10.1007/s10933-012-9599-0)
41. Anderson L, Finney BP, Shapley MD. 2018 Lake levels in a discontinuous permafrost landscape: late Holocene variations inferred from sediment oxygen isotopes, Yukon Flats, Alaska. *Arct. Antarct. Alp. Res.* **50**, e1496565. (doi:10.1080/15230430.2018.1496565)
42. Harms TK, Edmonds JW, Genet H, Creed IF, Aldred D, Balser A, Jones JB. 2016 Catchment influence on nitrate and dissolved organic matter in Alaskan streams across and altitudinal gradient. *J. Geophys. Res. Biogeosci.* **121**, 350–369 (doi:10.1002/2015JG003201)
43. Petrone KC, Jones JB, Hinzman LD, Boone RD. 2006 Seasonal export of carbon, nitrogen, and major solutes from Alaskan catchments with discontinuous permafrost. *J. Geophys. Res. Biogeosci.* **111**, 1–13. (doi:10.1029/2005JG000055)
44. Yoshikawa K, Bolton WR, Romanovsky VE, Fukuda M, Hinzman LD. 2002 Impacts of wildfire on the permafrost in the boreal forests of Interior Alaska. *J. Geophys. Res.* **108**, 8148. (doi:10.1029/2001JD000438)
45. Finger RA, Turetsky MR, Kielland K, Ruess RW, Mack MC, Euskirchen ES. 2016 Effects of permafrost thaw on nitrogen availability and plant–soil interactions in a boreal Alaskan lowland, *J. Ecol.* **104**, 1542–1554. (doi:10.1111/1365-2475.12639)
46. Wan S, Hui D, Luo Y. 2001 Fire effect on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol. Appl.* **11**,1349–1365. (doi:10.1890/1051-0761(2001)011[1349:FEONPA]2.0.CO;2)
47. Turner MG, Smithwick EAH, Metzger KL, Tinker DB, Romme WH. 2007 Inorganic nitrogen availability after severe stand-replacing fire in the Greater Yellowstone ecosystem. *Proc. Natl Acad. Sci. USA* **104**, 4782–4789. (doi:10.1073/pnas.0700180104)
48. Jones JB, Petrone KC, Finlay JC, Hinzman LD, Bolton WR. 2005 Nitrogen loss from watersheds of interior Alaska underlain with discontinuous permafrost. *Geophys. Res. Lett.* **32**, L02401. (doi:10.1029/2004GL021734)
49. Chapin III FS, Matson PA, Mooney HA. 2002 *Principles of terrestrial ecosystem ecology*. New York, NY: Springer.
50. Johnstone JF, Chapin III FS, Foote J, Kemmett S, Price K, Viereck L. 2004 Decadal observations of tree regeneration following fire in boreal forests. *Can. J. For. Res.* **34**, 267–273. (doi:10.1139/x03-183)
51. Johnstone JF, Chapin FS, Hollingsworth TN, Mack MC, Romanovsky V, Turetsky M. 2010 Fire, climate change, and forest resilience in interior Alaska. *Can. J. For. Res.* **40**, 1302–1312. (doi:10.1139/X10-061)
52. Stevens-Rumann CS, Kemp KB, Higuera PE, Harvey BJ, Rother MT, Donato DC, Morgan P, Veblen TT. 2018 Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.* **21**, 243–252. (doi:10.1111/ele.12889)
53. Johnstone JF, Hollingsworth TN, Chapin III FS, Mack MC. 2010 Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. *Glob. Chang. Biol.* **16**, 1281–1295. (doi:10.1111/j.1365-2486.2009.02051.x)
54. Turetsky MR, Kane ES, Harden JW, Ottmar RD, Manies KL, Hoy E, Kasischke ES. 2011 Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nat. Geosci.* **4**, 27–31. (doi:10.1038/ngeo1027)
55. Hoy EE, Turetsky MR, Kasischke ES. 2016. More frequent burning increases the vulnerability of Alaskan boreal black spruce forests. *Environ. Res. Lett.* **11**, 095001. (doi:10.1088/1748-9326/9/095001)
56. Chipman JG, Hu FS. 2019 Data from: Resilience of lake biogeochemistry to boreal-forest wildfires during the late Holocene. Dryad Digital Repository. (doi:10.5061/dryad.440rk01)