

RESEARCH ARTICLE OPEN ACCESS

A Meta-Regression of 18 Wildfire Chronosequences Reveals Key Environmental Drivers and Knowledge Gaps in the Boreal Nitrogen Balance

Stefan F. Hupperts¹  | Frank Berninger²  | Han Y. H. Chen^{3,4}  | Nicole Fenton⁵  | Mélanie Jean⁶  | Kajar Köster²  | Markku Larjavaara⁷  | Michelle C. Mack^{8,9}  | Marie-Charlotte Nilsson¹  | Marjo Palviainen⁷  | Anatoly Prokushkin¹⁰  | Jukka Pumpanen¹¹  | Meelis Seedre^{3,12,13,14}  | Martin Simard¹⁵  | Michael J. Gundale¹ 

¹Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden | ²Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland | ³Faculty of Natural Resources Management, Lakehead University, Thunder Bay, Ontario, Canada | ⁴Institute for Global Change Biology, School for Environment and Sustainability, University of Michigan, Ann Arbor, Michigan, USA | ⁵Institute for Forest Research, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec, Canada | ⁶Département de Biologie, Université de Moncton, Moncton, New Brunswick, Canada | ⁷Department of Forest Sciences, University of Helsinki, Helsinki, Finland | ⁸Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA | ⁹Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA | ¹⁰V.N. Sukachev Institute of Forest SB RAS, Krasnoyarsk, Russia | ¹¹Department of Environmental and Biological Sciences, University of Eastern Finland, Kuopio, Finland | ¹²Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, Alnarp, Sweden | ¹³Forest Department, Ministry of Climate of Estonia, Tallinn, Estonia | ¹⁴KappaZeta Ltd., Kastani, Tartu, Estonia | ¹⁵Department of Geography, Centre for Forest Research, Laval University, Quebec City, Québec, Canada

Correspondence: Stefan F. Hupperts (stefan.hupperts@slu.se)

Received: 13 February 2025 | **Accepted:** 19 July 2025

Funding: S.F.H. and M.J.G. acknowledge funding from the Kempe Foundation (grant no. JCK-1911) and VR (grant no. 2020-03908).

Keywords: biological nitrogen fixation | boreal forest | deciduous | fire regime | nitrogen accumulation | nitrogen stocks

ABSTRACT

Climate change has increased the size and frequency of wildfires across the boreal biome. Severe wildfires in boreal forests have been found to trigger shifts from evergreen to deciduous canopies, which has cascading effects on carbon and nitrogen cycling. Ecosystem productivity and carbon uptake in boreal forests are strongly linked with nitrogen, and Earth system models increasingly depend on our understanding of the nitrogen balance to predict post-fire carbon uptake. To investigate the post-fire boreal nitrogen balance, we combined a mass balance approach and literature synthesis to estimate rates of nitrogen accumulation and nitrogen inputs across a network of 18 boreal wildfire chronosequences that varied in both wildfire regime and post-fire canopy type, comprising 527 forest stands. We found that deciduous- or mixed-dominance boreal forests establishing after severe, stand-replacing fires had the highest nitrogen accumulation rates ($15.7 \pm 3.8 \text{ kg ha}^{-1} \text{ year}^{-1}$), while evergreen-dominated forests establishing after surface- or mixed-severity fires had the lowest nitrogen accumulation rates ($1.4 \pm 1.1 \text{ kg ha}^{-1} \text{ year}^{-1}$). Annual known inputs from nitrogen deposition and biological nitrogen fixation combined, estimated from published data, largely failed to explain the rate of nitrogen accumulation, particularly in deciduous or mixed-dominance forests establishing after stand-replacing fires, suggesting that the origins of most nitrogen in these forest types remain poorly understood. As the frequency of severe wildfires increases across the boreal biome and shifts toward deciduous canopies become more common, our study reveals a large knowledge gap in the resulting nitrogen balance that needs to be resolved in order to improve predictions of forest carbon uptake.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Global Change Biology* published by John Wiley & Sons Ltd.

1 | Introduction

Wildfire is the primary natural disturbance throughout the boreal region (De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013), which can lead to significant carbon (C) and nitrogen (N) losses (Mack et al. 2021). Varying from low-severity surface fires to high-severity stand-replacing fires, historical fire return intervals across the boreal zone have ranged from approximately 43 years in Siberia to more than 500 years in eastern Canada, with most published estimates less than 200 years (Bondarev 1997; Bouchard et al. 2008; De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013; Liski et al. 2001; Maltman et al. 2023). There is increased recognition that both the area and frequency of wildfires are increasing due to climate change (Buma et al. 2022; Natole et al. 2021; Simpson et al. 2011), which was highlighted by the extreme 2023 wildfire season in North American boreal forests. Given that ecosystem C loss is directly related to fire severity, an increase in wildfire severity could also have considerable effects on ecosystem N stocks that are released during fire (Natole et al. 2021; Simpson et al. 2011). Moreover, severe fires may trigger shifts in canopy type from evergreen to deciduous tree species that may result in higher C and N accumulation rates (Mack et al. 2021), but the interactive effect of fire regime and post-fire canopy type on N accumulation remains unknown. Because stand productivity and C uptake are often contingent on N availability (Hungate et al. 2003; Norby et al. 2010), our understanding of the recovery of N inputs throughout post-fire stand succession under various fire regimes and canopy types is crucial for predicting boreal forest productivity and C uptake potential in a changing climate.

Recovery of ecosystem N following disturbance such as wildfire depends partially on new inputs of N from deposition and biological dinitrogen (N_2)-fixation (BNF), as well as inputs from unknown sources (Korhonen et al. 2013; Palviainen et al. 2017). In the circumpolar boreal forest, which comprises approximately 30% of the global forested area and is the largest terrestrial biome on Earth (Brandt 2009; Olson et al. 2001), atmospheric N deposition is generally well quantified and typically very low ($<3 \text{ kg ha}^{-1} \text{ year}^{-1}$), with higher rates concentrated near populated areas in northern Europe and eastern Canada (Dentener et al. 2006; Gundale et al. 2011). Research on BNF in boreal forests has been heavily focused on moss-diazotroph associations (Hupperts et al. 2021). In old-growth (>200 years) evergreen-dominated boreal forests, moss-associated BNF can reach between 2 and $4 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (DeLuca et al. 2002), though some isolated estimates surpass $8 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (Jean et al. 2018). However, the majority of boreal forests experience wildfire or management disturbances at intervals that are shorter than 200 years (Bondarev 1997; Bouchard et al. 2008; De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013; Liski et al. 2001; Maltman et al. 2023), and the proportion of young forest is consistently increasing across the biome (McDowell et al. 2020). The limited number of measured rates from other potential sources (e.g., lichens, deadwood, soils, etc.) of BNF have been low or negligible (Cleveland et al. 2022; Heumann et al. 2025). Alder (*Alnus* spp.) is known to have high rates of BNF in floodplains and riparian areas (Cleve et al. 1971), but the ecosystem-scale contribution of N fixed by alder in upland forests has seldom been quantified, partly because it is often rare or absent in evergreen-dominated stands that comprise much of

the boreal zone (Massey et al. 2023). In comparison to the sparse literature on these other niches, the ecosystem-scale contribution of N fixed by mosses has been quantified in dozens of studies following a study by DeLuca et al. (2002) that first described widespread moss-associated BNF in upland boreal forests. Many studies have also found positive links between precipitation and BNF, including moss-associated BNF (Hupperts et al. 2021), suggesting that wetter climates may support higher rates of N accumulation, but this has not been empirically tested over a broad spatial or temporal scale.

Our study aimed to quantify links between fire regime, canopy type, and the ecosystem N balance (i.e., N accumulation rate compared to N inputs) in boreal forests. We combined a mass balance approach and a literature synthesis to estimate rates of nitrogen accumulation and nitrogen inputs across a network of 18 boreal forest wildfire chronosequences that varied in fire regime and post-fire canopy type. The chronosequences comprised 527 stands in total, spanning the boreal zone in North America, Europe, and Asia (Figure 1 and Table S1). To calculate N accumulation across these chronosequences, we calculated N stocks in living trees, ground vegetation, deadwood, and the soil organic layer up to 200 years since fire. We then compared ecosystem N accumulation rates to published estimates of the two most well-described N inputs, deposition and moss-associated BNF. We focused on mosses for BNF estimates because they are by far the most measured source in boreal forests (Hupperts et al. 2021) and were present in all of the chronosequences we measured, but we also report BNF rates from other sources found in the literature. This approach allowed us to estimate N accumulation rates among different fire regimes and canopy types, and to identify potential knowledge gaps in the N balance of these boreal forests. We asked: (1) How do fire regime and canopy type affect N accumulation rates? (2) How does climate affect N accumulation rates? and (3) How do N accumulation rates compare to N input rates from deposition and moss-associated BNF?

2 | Materials and Methods

2.1 | Chronosequences

Data were compiled from 18 wildfire chronosequences across the boreal region spanning North America, Europe, and Asia ($n = 529$ stands, Figure 1 and Table S1). The commonly used chronosequence approach uses a space-for-time design (Walker et al. 2010), assuming that sites within a chronosequence follow a similar developmental trajectory, which should be considered when making broad inferences. Owing to stand-replacing wildfire regimes in much of the circumpolar boreal forest biome, the age distribution of boreal forests skews relatively young. For example, at least 93.6% of forested areas in boreal Canada (including eastern Canadian boreal forests) are younger than 200 years (Maltman et al. 2023), largely due to wildfire (De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013). Similarly, most boreal forests in Russia are estimated to be less than 200 years old, with an average fire return interval shorter than 100 years (Bondarev 1997; De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013; Glückler et al. 2021). In Fennoscandia, the pre-industrial fire



FIGURE 1 | Ecosystem nitrogen stocks were quantified in 18 boreal wildfire chronosequences, comprising 527 stands. Boreal zone from World Wildlife Fund ecoregions (Olson et al. 2001). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

return interval was approximately 100 years (Zackrisson 1977). Across the biome, the proportion of young forests is increasing (McDowell et al. 2020). Thus, to capture a representative age distribution, we excluded stands that experienced wildfire more than 200 years prior to sampling.

The mean (1901–2020) annual temperature among chronosequences ranges from -9.5° near Tura, Russia, to $+0.9^{\circ}$ in the Clay Belt of Eastern Canada, while the mean summer (June–August) temperature ranges from 7.8° in the Yukon, Canada, to 15.2° in Ontario, Canada. The mean annual precipitation ranges from 248 mm in northern Yukon, Canada, to 824 mm in the Clay Belt of Eastern Canada. Twelve of 18 chronosequences had stand-replacing fire regimes (i.e., all stands in the chronosequence originated from a fire that caused complete overstory mortality). The remaining six chronosequences contained stands with surface fire regimes (i.e., no or incomplete overstory mortality) or were comprised of stands with a mix of surface and stand-replacing fire regimes. Twelve of 18 chronosequences had evergreen-dominated canopies post-fire, while six were dominated by deciduous trees or had

mixed dominance post-fire. Chronosequences were classified as deciduous/mixed if basal area or stem density of deciduous trees was $> 30\%$. Young (< 10 years after fire) sites in the two Alaskan deciduous/mixed chronosequences were classified using a deciduous index, whereby the sum of relative density plus relative biomass of deciduous tree seedlings was divided by two and multiplied by 100, then classified as broadleaf/mix if this index was $> 33.3\%$ (Mack et al. 2021). The Ontario deciduous/mix chronosequence was classified as deciduous/mix because the average deciduous tree stem density in younger stands (9 years after fire) and the average deciduous tree basal area in older stands (27, 92, and 140 years after fire) was $> 30\%$ (Seedre et al. 2014). Four of 18 chronosequences were affected by continuous permafrost. All chronosequences used in this study were located on mineral soils. Soil textures included sand ($n = 4$ chronosequences), loamy sand ($n = 1$ chronosequences), silt loam ($n = 6$ chronosequences), silt clay loam ($n = 4$ chronosequences), clay ($n = 2$ chronosequences), and silty loam sand ($n = 1$ chronosequence). The Global Lithology Map Database suggests varied lithology among our chronosequences (Hartmann and Moosdorf 2012). Sedimentary

lithology, which has been suggested as a potential N source (Houlton et al. 2018), was found to potentially occur (along with non-sedimentary lithologies) among all fire severity and canopy types, but was not overrepresented within any fire severity or canopy type. Additional details of the chronosequences can be found from original publications (Aaltonen et al. 2019; Alexander and Mack 2016; Bond-Lamberty et al. 2006; Köster et al. 2014, 2017, 2018; Larjavaara et al. 2017; Mack et al. 2021; Palviainen et al. 2017; Seedre et al. 2014; Simard et al. 2007; Wirth et al. 2002; Zackrisson et al. 2004).

2.2 | Climate

Average summer (June–August) climate data were retrieved from the Climate Research Unit (0.5° spatial resolution for 1901–2020) and included precipitation, precipitation frequency (i.e., number of days with precipitation ≥ 0.1 mm) temperature, potential evapotranspiration (PET), and the Palmer Drought Severity Index (PDSI) (Harris et al. 2020). Because many widely used Earth system models link BNF with actual evapotranspiration (AET) (Hupperts et al. 2021), we also retrieved average summer AET data from the TerraClimate (Abatzoglou et al. 2017) database (0.042° spatial resolution for 1981–2010).

2.3 | Nitrogen Stocks

We calculated total ecosystem N stocks using the sum of four main pools: living trees, deadwood (standing and lying), ground layer vegetation, and the soil organic layer. Ten chronosequences reported mineral soil layer N stocks data up to a depth of 30 cm (total $n=80$), depending on the chronosequence. However, because this represents only 15% of all stands in our chronosequence network (i.e., 80/527), we excluded mineral soil N from our calculation of total ecosystem N and analyzed mineral soil N stocks separately. Living tree and deadwood N pools were estimated from plots that ranged from 50 to 5000 m² among the chronosequences and were calculated by multiplying estimated biomass with tissue-specific N concentrations. Detailed descriptions of which pools were estimated with primary measurements, allometric equations, or sourced from the literature are available in the Data S1 (https://figshare.com/projects/Boreal_nitrogen_stocks/178236). Aboveground biomass of living trees was estimated using allometric equations derived from the study or from the literature (Marklund 1988; Paré et al. 2013). Coarse root biomass was either measured from soil cores or estimated using allometric equations. However, five of 16 chronosequences did not measure or estimate coarse root biomass. Fine root biomass was measured from soil cores or included in the soil organic layer N pool, but three chronosequences did not measure or estimate fine root N pools. The biomass of standing and lying deadwood was estimated using allometric equations or direct biomass measurements. The N concentrations of different living and deadwood tree tissue types were obtained from the literature or field measurements. Ground layer vegetation N pools were measured from 2 to 10 plots per stand and ranged in size from 0.005 to 1.0 m² (Table S1). Aboveground vegetation was clipped at the base and oven dried before weighing to obtain biomass. Species- or functional group-specific N concentrations were obtained from the literature or direct measurements

(See Data S1). Six chronosequences did not measure or estimate ground layer vegetation N pools. Soil organic layer N pools were quantified from 1 to 22 soil measurements per stand. All measured N concentrations were obtained using elemental analyzers (varioMAX CN elemental analyzer, Elementar Analysensysteme GmbH, Germany; LECO CNS 2000 analyzer, LECO Corporation, St. Joseph, MI, USA; or Costech ECS4010, Valencia, CA, USA).

2.4 | Nitrogen Inputs

To estimate BNF, we first conducted a literature search of studies that measured BNF in boreal forests. In April 2024, we searched the Web of Science database using search terms “(biological nitrogen fixation OR nitrogen fixation OR BNF OR dinitrogen fixation OR N₂-fixation) AND boreal forest”. This initial search yielded 294 publications. We then filtered the studies using additional criteria: (1) the study involved primary measurements of BNF; (2) the study took place in a boreal forest; and (3) the study was field-based (not greenhouse, lab, or climate chamber). Applying these criteria yielded 57 unique publications (see Data S1). We then recorded which sources of BNF were measured (e.g., moss, alder, lichen, etc.). Some studies measured multiple sources, and some studies measured one BNF rate from samples that included both mosses and the organic layer; all sources were then recorded as having been measured.

From the list of 57 studies that measured BNF, we again applied filters with the following criteria: (1) the reported BNF rate could be up-scaled to the stand level (kg ha⁻¹ year⁻¹); (2) the study reports that the stand was less than or equal to 200 years old (i.e., to match the age range of stands in our chronosequence network), and when a range was given for site age, we used the average value; (3) a relevant control could be used if treatments were applied; and (4) if *Sphagnum* was investigated, the authors used ¹⁵N incorporation rather than acetylene reduction (due to known methodological drawbacks; Saiz et al. 2019). This final filtering criteria yielded 20 studies (see Data S1). The average stand age among the studies was 95 years since disturbance, indicating that the stand age distribution among moss BNF studies was not skewed toward either young or old sites within our 200 year timeframe. If studies used acetylene reduction, BNF was calculated using a conversion factor of 3:1 (3 moles of acetylene reduced to 1 mole of N₂ reduced) (DeLuca et al. 2002). Upscaling to annual rates was done using the number of growing season days reported in the respective study (see Data S1). From these 20 studies we calculated the median annual BNF rate, as commonly done in similar studies to retain all data (e.g., potential outliers) but avoid false inflation of the central tendency when data are skewed (Figure S1). We also calculated the average rate, in which case one outlier was removed from the moss BNF data because it was more than eight standard deviations from the average moss-associated BNF rate. Ninety-five per cent confidence intervals were calculated for all sources with bootstrapping of 10,000 iterations.

To directly compare moss-associated BNF and ecosystem N accumulation within the same stand types, we further grouped moss-associated BNF rates by fire regime (stand-replacing or surface/mixed) and canopy type (evergreen or deciduous/mixed)

if these parameters were reported in the respective studies. We found the following number of moss-associated BNF rates for each stand type: 17 observations in evergreen-dominated stands of stand-replacing fire regimes; 3 observations in deciduous/mixed stands of stand-replacing fire regimes; 12 observations in evergreen stands of surface/mixed fire regimes; and 0 observations in deciduous/mixed stands of surface/mixed fire regimes. The remaining 39 observations of moss-associated BNF were from stands of harvest or unspecified origin. Median input rates for each stand type were calculated with bootstrapping of 10,000 iterations.

Some evidence suggests that mosses use vanadium-based nitrogenase, rather than molybdenum-based nitrogenase, under certain conditions (Darnajoux et al. 2019). For acetylene reduction assays, the conversion factor of vanadium-based nitrogenase is 1:1, rather than 3:1 that is used for molybdenum-based nitrogenase. We have no way of knowing whether mosses in compiled studies were using vanadium-based nitrogenase. However, to account for potential use of vanadium-based nitrogenase, we also calculated BNF rates of all studies that used acetylene reduction assays using a liberal assumption of vanadium-based nitrogenase. We did this by multiplying upscaled BNF rates by 3 (essentially back-transforming the rates), therefore using a 1:1 conversion factor rather than 3:1.

To ensure that compiled moss BNF rates were from similar climatic niches as the chronosequences used in the present study, we extracted climate data for the BNF studies using the same climate variables described above. We then performed a principal components analysis (PCA) of the climate data with the BNF studies and nitrogen stocks studies pooled. Data were transformed by centering (i.e., given a mean of 0) and scaling (i.e., given a standard deviation of 1) in a z-score type matrix using the scale function in R version 4.2 (R core Development Team 2022) prior to PCA analysis (Oksanen et al. 2018). The resulting PCA indicates that the BNF studies and N stocks studies occupy similar climates (Figure S2). A permutational analysis of variance (PERMANOVA) with Euclidean dissimilarity measure (using the adonis function in the vegan package of R; Oksanen et al. 2018) on the centered and scaled data confirms that there is no significant difference in climate between BNF studies and N stocks studies ($F = 0.3$, $p = 0.8$, Figure S2).

Inorganic N deposition (NO_y and NH_x) data was retrieved from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP), which models spatially explicit N deposition annually from 1861 to 2005 (Lamarque et al. 2013; Warszawski et al. 2014). Specifically, we used publicly available datasets “ndep_noy_histsoc_annual_1861_2005.nc4” and “ndep_nhx_histsoc_annual_1861_2005.nc4” from the ISIMIP2b simulation round. The ISIMIP model accounts for dry and wet deposition, including N inputs from wildfire emissions and lightning. Stands originating earlier than the data range were given the same value as 1861, and stands that were surveyed later than the data range were given the same value as 2005. Organic N deposition is not well studied, but was assumed to account for 30% of total N deposition (Neff et al. 2002). Palviainen et al. (2017) reported N deposition for the Finland chronosequence, and ISIMIP data was therefore not used for this chronosequence. We then calculated the average N deposition rate in the oldest stand

within each chronosequence, followed by calculating the average and median N deposition rate among all chronosequences to obtain a boreal-wide long-term estimate of N deposition.

2.5 | Data Analysis

To investigate our first question, asking how fire regime and canopy type affect N accumulation rates, we fit a mixed effects model using the lme function in the nlme package (Pinheiro et al. 2018) of R version 4.2. Time since fire (years), fire regime, canopy type, and their interactions served as fixed effects. We tested linear and logarithmic functions and selected the model with the lowest AIC score. Total ecosystem N (i.e., sum of living tree N, ground-layer N, deadwood N, and soil organic soil layer N [kg ha^{-1}]) was the response variable, and the raw (non-transformed) data were used. Chronosequence was included as a random effect (intercept) to account for differences in sampling depth among chronosequences and spatial autocorrelation among stands nested within respective chronosequences. Residuals were visually inspected to assess normal distribution and homogeneity of variance among fixed effects. Residuals indicated that the levels within fire regime and canopy type had different variance (i.e., heteroscedasticity); we therefore included the constant variance function “varIdent” within the mixed effects model to account for the distinct variance structure among levels of both fire regime and canopy type. The varIdent function estimates a different variance for each level of a given categorical variable and scales the variance relative to the first level within the respective categorical variable. We also included the exponential variance function “varExp” to account for time-dependent variance. The varExp function allows exponential change in residual variance along a continuous variable (e.g., time). Two outliers were removed (final $n = 527$ stands) because they disproportionately skewed the residuals; their inclusion would actually increase the overall N accumulation rate, meaning that our analysis is conservative. The marginal R^2 (fixed effects only) and conditional R^2 (fixed and random effects) were calculated using the MuMIn (Barton 2023) package in R. Six chronosequences did not quantify ground-layer N; we therefore repeated these analyses but excluded ground-layer N from total ecosystem N stocks. Results are shown in Table S2. Estimates of N stocks, N accumulation rates, and 95% confidence intervals were performed by calculating estimated means (N stocks) and estimated slopes (N accumulation rates) using the emmeans and emtrends functions of the emmeans package (Lenth 2018) in R, which controls for all fixed and random effects. Post hoc comparisons of N stocks and accumulation rates among levels of fire regime and canopy type were performed with Tukey corrections using the emmeans function (N stocks) and emtrends function (N accumulation rates). To evaluate mineral soil N accumulation, we again used a linear mixed effects model with time since fire as a fixed effect and chronosequence as a random effect.

To investigate the potential contribution of N from alder-diazotroph symbioses, we also modeled N stocks as a function of alder presence using the same mixed effects model structure described above. Owing to multi-collinearity, we could not include fire regime and alder presence in the same model, and therefore tested the effect of fire regime and alder presence in separate models and compared F values.

To investigate our second question, asking how climate affects N accumulation rates, we investigated the relationship between average summer (June–August) climate and total ecosystem N accumulation. First, we tested for multi-collinearity among summer climate variables by conducting a PCA using the “pr-comp” function in R on centered and scaled data, as described above. Variables included mean temperature, mean precipitation, mean precipitation frequency, mean PET, mean AET, and mean PDSI. The first axis of the PCA explained 55.4% of variation and the second axis explained an additional 25.0% of variation (Table S3 and Figure S3). There was clear multi-collinearity among variables; we therefore used first and second axis scores as composite explanatory variables, thus integrating multiple aspects of climate. We then applied the same linear mixed model structure described above and included scores from the first and second PCA axes. The first axis, PCA1, had neither a significant main effect nor interactive effect (with time) on N stocks and was therefore removed from the model (Table S4).

We then investigated our third question, asking how N accumulation rates compared to N input rates from deposition and moss-associated BNF. Estimated N accumulation rates were compared to the median and average input rates of N deposition and moss-associated BNF (individually and combined), estimated from the literature review described above, with bootstrapped 95% confidence intervals of 10,000 iterations. Bootstrapping employs a resampling with replacement technique and does not rely on assumptions of normal distribution. Comparing estimated N accumulation rates with estimated N input rates enabled us to calculate the proportion of N that is explained by N deposition and moss-associated BNF. We also estimated the median N deposition rate and moss-associated BNF rate within each fire regime \times canopy type, with bootstrapped 95% confidence intervals, and compared them to the estimated N accumulation rate of each fire regime \times canopy type. All figures were made with the ggplot2 (Wickham 2016) and cowplot (Wilke 2020) packages in R.

3 | Results

3.1 | Nitrogen Accumulation

Across the chronosequence network, our model estimated that ecosystem N stocks increased at an annual rate of 6.9 kg ha^{-1} (95% confidence interval (CI) = $5.7\text{--}8.0 \text{ kg ha}^{-1}$, Figure 2a and Table 1). The fixed effects in our model (fire severity, canopy type, and time since fire) explained over half of the variation in ecosystem N stocks (Figure 2a and Table S5). The highest N accumulation rate was found in deciduous- and mixed-dominance forests (i.e., $> 30\%$ average proportion of *Betula*, *Populus*, or *Larix*) following stand-replacing fires ($15.7 \pm 3.8 \text{ kg N ha}^{-1} \text{ year}^{-1}$), while the lowest was found in evergreen-dominated forests following surface- or mixed-severity fires ($1.4 \pm 1.1 \text{ kg N ha}^{-1} \text{ year}^{-1}$, Figure 2b–e and Figure S4). In separate models (due to collinearity), fire regime explained more than twice the variation in N accumulation rates than was explained by *Alnus* presence (Table S6a,b). Among the chronosequences that measured mineral soil N, the overall mineral soil N accumulation rate was $5.3 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $2.3\text{--}8.3 \text{ kg ha}^{-1} \text{ year}^{-1}$, Figure S5 and Table S7). Across all stands regardless of age, most ecosystem N was found in the soil organic layer ($74.7\% \pm 0.02\%$, Figures S6 and S7).

When controlling for fire regime and canopy type, the N accumulation rate was related to the second axis of the principal components analysis (PCA) that primarily represented summer precipitation frequency (i.e., the average number of days with at least 0.1 mm precipitation), summer actual evapotranspiration, and the Palmer Drought Severity Index (PDSI, Figure S8 and Table S4).

3.2 | Nitrogen Inputs

Our literature synthesis identified 57 original field-based studies that measured BNF in boreal forests, and 40 of these studies (70%) focused on moss-associated BNF (Figure 3a). Other measured sources of BNF included *Alnus* (9 studies), deadwood (5 studies), organic soil layer (4 studies), lichen (3 studies), foliar endophytes (2 studies), roots (2 studies), mineral soil layer (1 study), litter (1 study), bark (1 study), and biocrust (1 study). Up-scaled rates of BNF that met our additional filtering criteria (e.g., conducted in forests younger than 200 years to match the age range of our chronosequence network; see 2. Methods) were reported in only 20 of the 57 studies (Figure 3b). Of these 20 studies, moss-associated BNF was measured in 15 studies from at least 42 different stand ages. Other up-scaled rates of BNF that met our filtering criteria included *Alnus* (4 studies from 6 stand ages), organic soil layer (2 studies from 6 stand ages), foliar endophytes (2 studies from 3 stand ages), roots (2 studies from 6 stand ages), deadwood (1 study from 3 stand ages), mineral soil layer (1 study from 3 stand ages), litter (1 study from 3 stand ages), bark (1 study from 3 stand ages), and biocrust (1 study from 1 stand).

Among the 15 studies quantifying moss-associated BNF that met our filtering criteria, the median moss-associated BNF rate was $0.19 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $0.09\text{--}0.25 \text{ kg ha}^{-1} \text{ year}^{-1}$, Table 2 and Figure 3c), and the average rate was $0.44 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $0.29\text{--}0.61 \text{ kg ha}^{-1} \text{ year}^{-1}$). Across our chronosequence network, the median long-term N deposition rate was $1.55 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $1.18\text{--}2.35 \text{ kg ha}^{-1} \text{ year}^{-1}$, Table 2) and the average rate was $1.88 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $1.50\text{--}2.29 \text{ kg ha}^{-1} \text{ year}^{-1}$). The combined N input from moss-associated BNF and N deposition (median rates with bootstrapped 95% confidence intervals) was $1.74 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $1.35\text{--}2.51 \text{ kg ha}^{-1} \text{ year}^{-1}$, Figure 4a and Table 1). The combined input using average rates was $2.32 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $1.91\text{--}2.76 \text{ kg ha}^{-1} \text{ year}^{-1}$).

3.3 | Comparing Nitrogen Accumulation Rates With Inputs

By comparing the overall N accumulation rate ($6.9 \pm 1.1 \text{ kg ha}^{-1} \text{ year}^{-1}$) with median N inputs from deposition and moss-associated BNF ($1.7 \text{ kg ha}^{-1} \text{ year}^{-1}$ [bootstrapped 95% CI = $1.3\text{--}2.5 \text{ kg ha}^{-1} \text{ year}^{-1}$]), we found that 25% (95% CI = $16.9\text{--}43.8\%$) of accumulated N was explained by moss BNF and N deposition combined (Figure 4a). Thus, approximately 75% (95% CI = $56.2\text{--}83.1\%$) of annual N inputs were unexplained. In deciduous and mixed-dominance forests following stand-replacing fires, approximately 90% (95% CI = $65\text{--}94\%$) of annual inputs were unexplained, while approximately 0% (95% CI = $0\text{--}28\%$) of annual N inputs were unexplained in evergreen-dominated

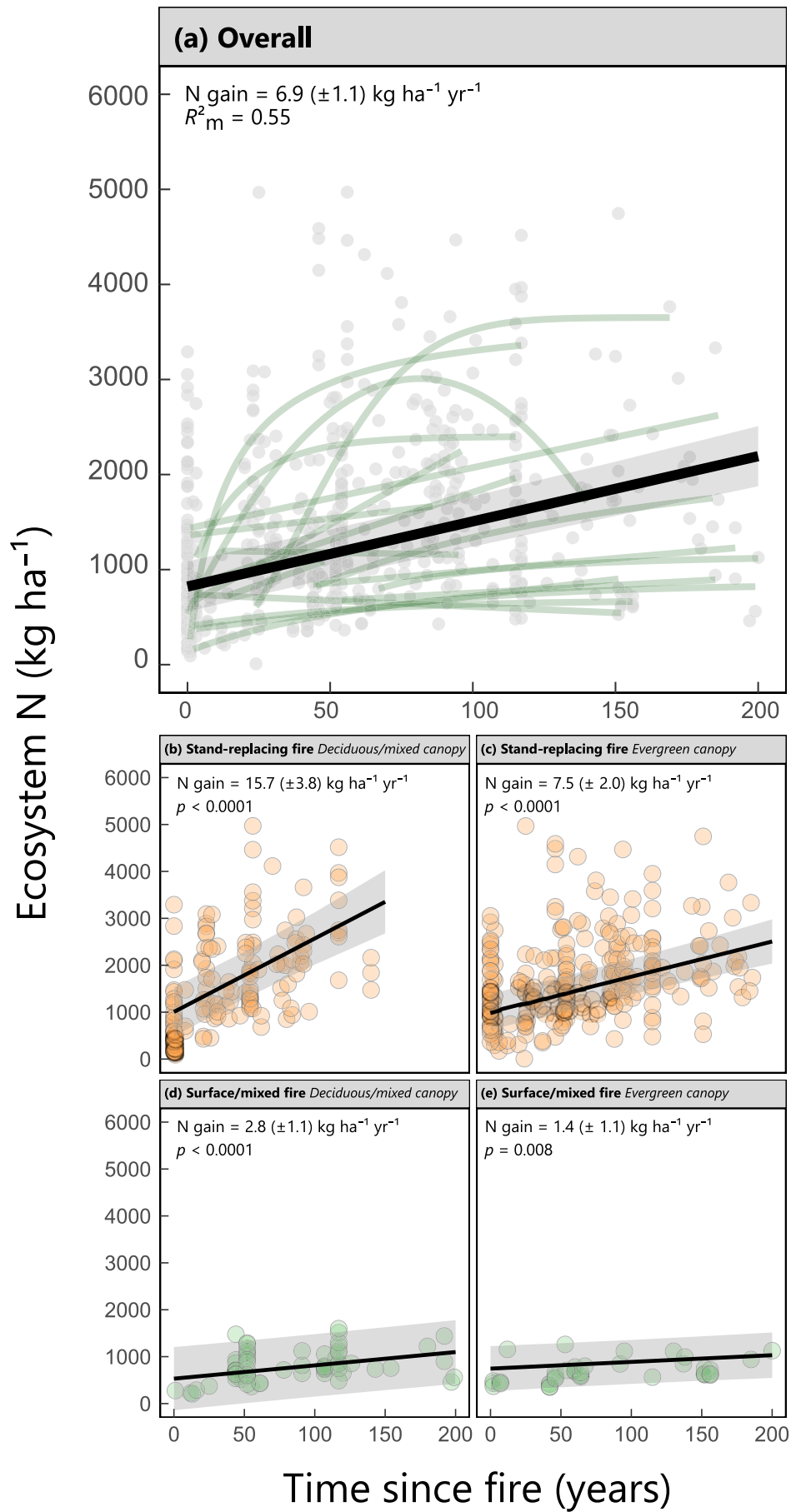


FIGURE 2 | Legend on next page.

FIGURE 2 | (a) Overall ecosystem nitrogen (N) stocks following wildfire. The thick black line depicts the modeled N stocks of 18 pooled chronosequences ($n = 527$ forest stands), accounting for all fixed and random effects. The marginal R -squared (R^2_m) accounts for fixed effects only. The green lines represent modeled N stocks of each chronosequence from individual models. (b–e) Ecosystem nitrogen N stocks depending on fire regime and canopy type. Regression lines represent modeled N stocks from full mixed effects model, controlling for all fixed and random effects in the model. Shading around regression lines denote 95% confidence intervals.

forests following surface- and mixed-severity fires (Table 1 and Figure 4b,e). When using average N input rates, we found that 66% (95% CI = 51.9%–76.1%) of the overall N accumulation rate was unexplained by known N inputs.

4 | Discussion

Post-fire N accumulation rate was related to both fire regime and post-fire canopy type, but was largely unexplained by known N inputs. To our knowledge, this is the first post-fire N balance estimate from replicated chronosequences spanning many sites across multiple continents. Previous studies that focused on individual chronosequences (not necessarily related to fire) have reported highly variable rates of N accumulation, with variation seemingly caused by factors such as ecosystem type, disturbance history, and pools measured. An earlier review (Binkley et al. 2000) encompassing a variety of biomes revealed that the majority of studies with robust experimental designs found N accumulation rates under $6 \text{ kg ha}^{-1} \text{ year}^{-1}$, but some individual chronosequences reported rates as high as $80 \text{ kg ha}^{-1} \text{ year}^{-1}$. Our overall estimate of N accumulation ($6.9 \text{ kg ha}^{-1} \text{ year}^{-1}$) falls within this range, and is further strengthened by the wide geographical, climatic, and temporal scope of our data.

4.1 | Fire Regime and Canopy Type Control N Accumulation Rates

Our first question asked how fire regime and canopy type affect N accumulation rates. We found that the N accumulation rate depended on both fire regime and canopy type, and their interaction. Nitrogen accumulated faster in forests developing after stand-replacing fires compared to those with surface/mixed fire regimes, suggesting that environmental and biogeochemical conditions after stand-replacing fires may favor free-living asymbiotic BNF. There may be several reasons why stand-replacing fires favor BNF. First, though residual ash is rich in ammonium and nitrate, this effect is very transient as N becomes immobilized in microbial biomass within only a few years (Ibáñez et al. 2022). Residual ash has also been found to increase phosphorus, molybdenum, and iron availability (Certini 2005; Harden et al. 2004; Wong et al. 2021), which may subsequently promote BNF (Dynarski and Houlton 2018; Holloway et al. 2020; Houlton et al. 2008). Further, high severity fires have been shown to transform soil organic N into highly stable polyaromatic N compounds that are less available to plants (Roth et al. 2023), therefore potentially promoting N limitation that favors diazotroph activity. Consistent with this hypothesis, previous work found higher diazotroph abundance in recently burnt boreal soils compared to unburnt boreal soils (Su et al. 2022). Higher surface soil temperature, light availability, and abundant deadwood in recently burned sites have also

been associated with diazotroph activity (Benoist et al. 2022; Holloway et al. 2020; Kalamees et al. 2005; Rinne et al. 2017). These findings have important implications for forest growth under climate change; with already increasing wildfire severity across the boreal zone (Buma et al. 2022; De Groot, Cantin, et al. 2013; De Groot, Flannigan, and Cantin 2013; Natole et al. 2021), our data suggest that higher post-fire BNF appears to compensate for N loss from more severe fires, leading to recovery of N stocks.

We also found that stands with deciduous/mixed canopies had considerably higher N accumulation rates compared to evergreen-dominated stands, which could be a result of higher asymbiotic BNF rates, but direct measurements are still needed. The higher N tissue concentrations, N turnover, and N mineralization rates found in deciduous trees and forests reflect different N redistribution patterns within the ecosystem, but do not explain the origin of N. Mosses are an unlikely source of BNF in these forests, as they are considerably less abundant in deciduous-dominated stands compared to evergreen-dominated stands (Jean, Melvin, et al. 2020), and deciduous leaf litter has been shown to suppress moss-associated BNF in boreal forests (Gundale et al. 2009; Jean, Holland-Moritz, et al. 2020). Other sources of BNF associated with deciduous trees may be an overlooked N source that can explain high rates of N accumulation. For example, previous work in Finland has found N_2 -fixing bacteria associated with soil under *Betula* trees (Rönkko et al. 1993; Smolander 1990). *Betula* is a ubiquitous deciduous genus in boreal forests and is phylogenetically closely related to *Alnus*, and both are members of the Betulaceae family in the order Fagales. Over evolutionary time, Fagales has experienced numerous losses in the genetic capacity to form symbioses via nodules (Griesmann et al. 2018). We therefore speculate that the ancestral capacity to form nodulating symbioses with diazotrophs, coupled with our study results, suggests that this evolutionary branch may also support non-nodulating asymbiotic diazotrophs in the rhizosphere. Alternatively, some of the N budget discrepancy might be explained by the presence of *Alnus* in these stands or from deep mineral soil (discussed in greater detail below). Regardless of the origin of N, severe wildfires are already shifting some boreal forests towards deciduous canopies (Mack et al. 2021), and our findings, using data from across the boreal region, indicate that such shifts promote ecosystem N accumulation.

4.2 | Links Between Climate and N Accumulation

Our second question asked how climate affects N accumulation rates. The wide geographical spread of our chronosequence network enabled us to evaluate key bioclimatic controls on N accumulation, several of which are increasingly incorporated into coupled C-N Earth system models to control N inputs and

TABLE 1 | Modeled ecosystem nitrogen (N) stocks, recovery rates, and inputs in boreal forests. The N gap indicates the amount of N that remains unexplained by the known N input rate. Numbers in parentheses indicate 95% confidence interval. Letters denote significant differences among fire regime and canopy type within each column, based on post hoc tests with Tukey's adjustment ($\alpha=0.05$). Estimates are from the full model, controlling for all fixed and random effects. Sample size (n) indicates the number of stands.

	Nitrogen stocks (kg ha ⁻¹)		Nitrogen accumulation (kg ha ⁻¹ year ⁻¹)	Nitrogen inputs (kg ha ⁻¹ year ⁻¹)		Nitrogen gap (kg ha ⁻¹ year ⁻¹)	
	Year 0	Year 200		BNF	Deposition		
Overall (<i>n</i> = 527)	822 (±265)	2193 (±317)	6.9 (±1.1)	0.2 (0.1–0.3)	1.6 (1.2–2.4)	5.1 (3.2–6.6)	
Stand-replacing fire regime	Evergreen canopy (<i>n</i> = 260)	1017 (±347) a	2521 (±436) b	7.5 (±2.0) b	<0.01 (0.0–0.9)	1.6 (1.1–3.3)	5.9 (2.3–8.4)
	Deciduous/Mixed canopy (<i>n</i> = 159)	1004 (±461) a	4138 (±789) a	15.7 (±3.8) a	0.2 (0.01–0.50)	1.3 (1.2–3.6)	14.2 (7.3–18.3)
Surface/Mixed fire regime	Evergreen canopy (<i>n</i> = 66)	744 (±413) a	1030 (±417) c	1.4 (±1.1) c	0.2 (0.1–0.5)	2.2 (1.6–2.5)	0 (0–0.7)
	Deciduous/Mixed canopy (<i>n</i> = 42)	531 (±573) a	1099 (±582) c	2.8 (±1.1) c	No data	1.1 (1.0–1.2)	1.7 (0.5–2.9)

limitations and are subsequently used to make climate change predictions (Meyerholt and Zaehle 2018). Our PCA analysis indicated that N accumulation rates were positively related to summer precipitation frequency (i.e., the average number of days with at least 0.1 mm precipitation), summer evapotranspiration, and the Palmer Drought Severity Index. In contrast to potential evapotranspiration, which quantifies evaporation and transpiration if water is continuously supplied, actual evapotranspiration quantifies the amount of water that is lost given existing water limitations. Most coupled C–N Earth system models control BNF using direct positive linkages to actual evapotranspiration or net primary productivity, which are primarily based on global-scale patterns (Cleveland et al. 1999). In agreement with Earth system models, our study provides robust empirical evidence to suggest that N accumulation rate, serving as a coarse indicator of whole ecosystem BNF in boreal forests, may be similarly predicted by integrated climate variables such as actual evapotranspiration. Another variable integrated in the PCA axis, precipitation frequency, has often been found by field and greenhouse studies to have positive effects on moss-associated BNF (Hupperts et al. 2021), and our data suggest this may serve as a general control on total BNF (beyond just mosses) likely because hydration is essential for moss and diazotroph activity (Turetsky 2003). The Palmer Drought Severity Index, in which higher values correspond to less severe drought conditions, was also a significant component of the second PCA axis, reflecting greater precipitation frequency and consequently greater rates of N accumulation. Earth system model predictions of BNF have been identified as most uncertain in high-latitude ecosystems, including boreal forests, owing to a lack of data (Meyerholt et al. 2016). By revealing an empirical link between climate and N accumulation, our results may help strengthen these predictions.

4.3 | Nitrogen Inputs

Our third question asked how N accumulation rates compared to N input rates from deposition and moss-associated BNF. We found that known N inputs largely failed to explain N accumulation rates, particularly in deciduous/mixed forests establishing after stand-replacing fires, where 65%–94% of accumulating N was unexplained. This finding indicates a large knowledge gap regarding where the remaining N originates. Our literature synthesis demonstrated that moss-associated BNF is clearly the most widely studied and measured source of BNF in boreal forests, particularly following the study by DeLuca et al. (2002). However, our mass balance analysis suggests that moss-associated BNF explains very little N accumulation (only 3%) across our chronosequence network, and even less in deciduous/mixed stands from stand-replacing fire regimes, where N accumulation rates were much higher. Other BNF niches may help explain this other “missing” fraction of inputs; however, the few published rates from other potential sources fall short of explaining the large discrepancy that we discovered. Our literature synthesis found that diazotroph communities associated with live foliage, dead wood, litter, bark, crusts, roots, organic soil, and mineral soil may collectively fix approximately $0.37 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (sum of median values in Table 2), but this estimate is based on very few published data points and still fails to explain

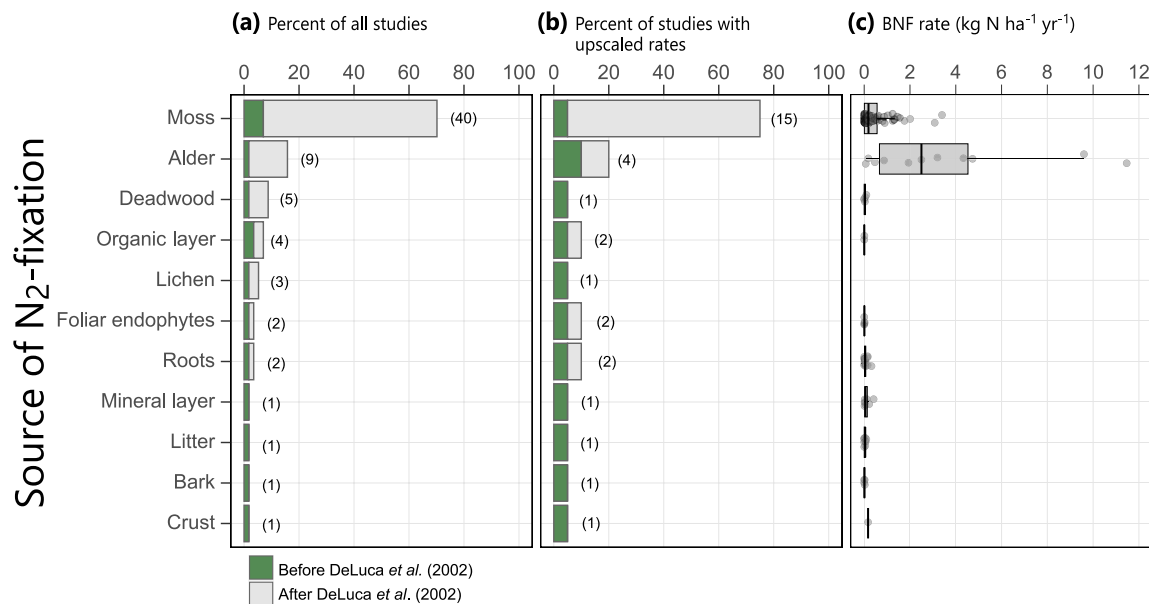


FIGURE 3 | (a) Published studies that measured biological BNF (BNF) in boreal forests. Studies are further identified by whether they were published before or after DeLuca et al. (22), which prompted a strong focus on moss BNF research. Numbers in parentheses denote the number of studies. (b) Studies that measured BNF in boreal forests younger than 200 years (i.e., to match the age range of stands in our chronosequence network), and also reported upscaled rates of BNF. Published studies were compiled from a Web of Science literature search (see Methods). (c) Measured rates of BNF from studies in panel (b). The middle vertical line indicates the median value, the maximum and minimum lines indicate the first and third quartiles, respectively, and the whiskers extend to the largest value that is not further than 1.5 times the interquartile range. One outlier under the “Moss” category is not shown (rate = 30.1 kg N ha⁻¹ year⁻¹), but was included in the analysis. Lichen was measured alongside mosses; we therefore report the rate under the “Moss” category.

TABLE 2 | Annual nitrogen (N) inputs from published literature. Biological nitrogen fixation (BNF) rates were calculated using published data from forests younger than 200 years (i.e., to match the age range of our chronosequence network), retrieved from a Web of Science literature search (see Methods). Long-term inorganic N deposition was estimated using the Inter-Sectoral Model Intercomparison Project (ISIMIP) database, and organic N deposition was assumed to account for 30% of total N deposition. Confidence intervals (CIs) were estimated with bootstrapping of 10,000 iterations. Sample size (n) indicates the number of data points for each source.

Annual nitrogen inputs (kg ha ⁻¹ year ⁻¹)						
Input	Source	Median	95% CI	Average	95% CI	n
Biological nitrogen fixation (BNF)	Moss	0.19	0.09–0.25	0.44	0.29–0.61	70/71*
	Alder	2.50	0.47–4.73	3.58	1.63–5.91	11
	Bark	0.01	0–0.02	0.01	0–0.02	4
	Crust	0.17	—	0.17	—	1
	Deadwood	0.03	0–0.10	0.04	0.01–0.07	5
	Foliar endophytes	0.01	0–0.02	0.01	0–0.01	5
	Litter	0.05	0–0.06	0.03	0.01–0.05	9
	Mineral layer	0.05	0.02–0.22	0.11	0.04–0.21	8
	Organic layer	0.005	0–0.01	0.005	0–0.01	2
	Roots	0.04	0.01–0.06	0.07	0.03–0.11	17
N deposition	Inorganic + organic	1.55*	1.18–2.35	1.88	1.50–2.29	18

*One outlier under the “Moss” category was removed from the calculation of the average (rate = 30.1 kg N ha⁻¹ year⁻¹), but retained for calculation of the median.

N accumulation rates in most scenarios, even when pooled with mosses. Foliar endophytic N₂-fixing diazotrophs have been suggested as an important source of BNF, but we found only two studies that quantified stand-scale BNF

rates from foliar endophytes in boreal forests, averaging approximately only 0.01 kg N ha⁻¹ year⁻¹ (Bizjak et al. 2023; Granhall and Lindberg 1978). Another potential source may lie belowground; some research has suggested associations

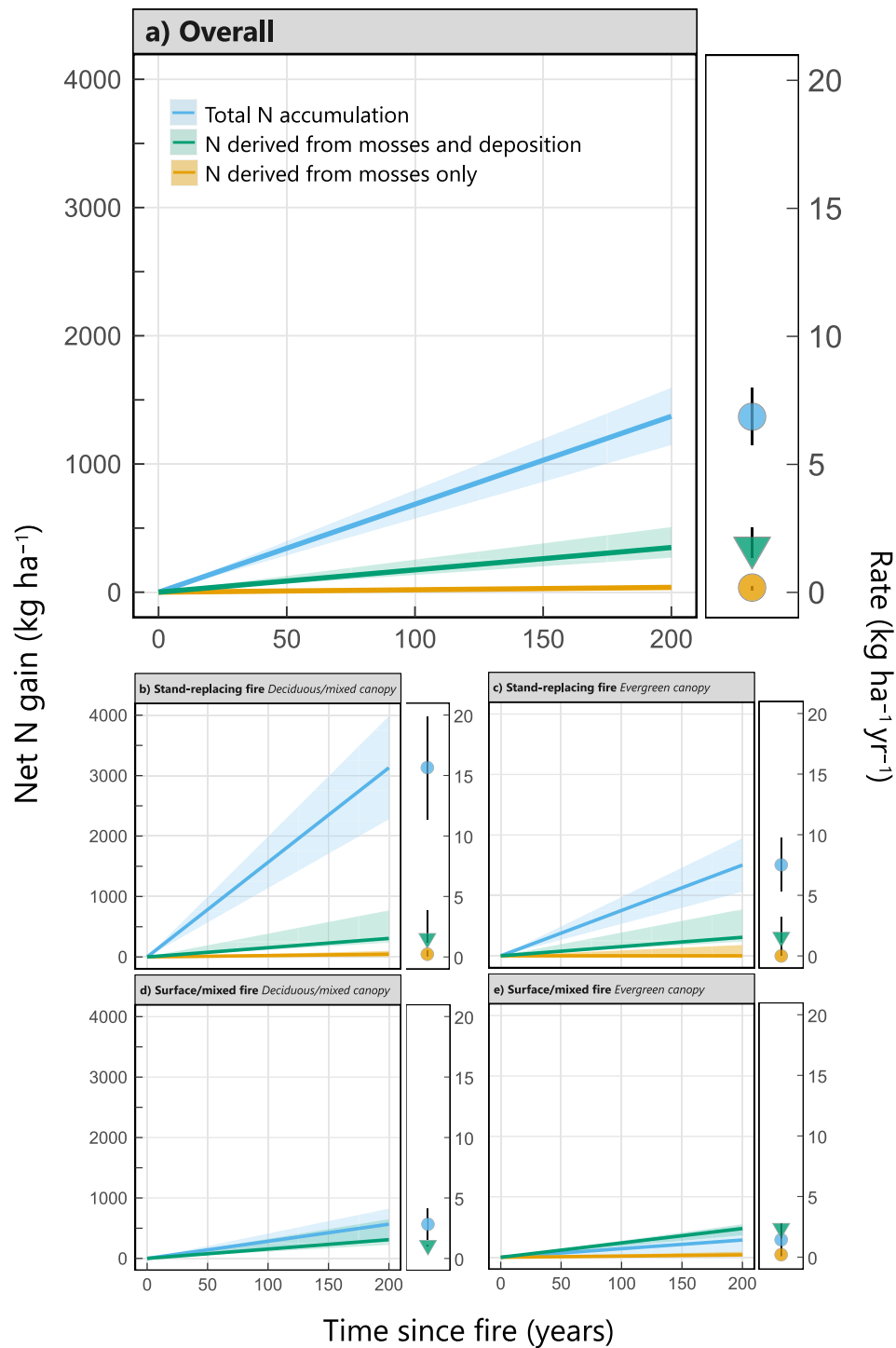


FIGURE 4 | The net N accumulation rates across our chronosequence network ($\pm 95\%$ confidence intervals, $n = 18$ chronosequences comprising 527 stands), compared with the rate of known N inputs estimated from published data (\pm bootstrapped 95% confidence intervals) in (a) all stands pooled; (b) deciduous/mixed canopy stands after stand-replacing fire; (c) evergreen canopy stands after stand-replacing fire; (d) deciduous/mixed canopy stands after surface/mixed severity fire; and (e) evergreen canopy stands after surface/mixed severity fire. Nitrogen inputs in panel (d) only include deposition because we found no published moss-associated BNF rates from this specific stand type.

between diazotrophs and ectomycorrhizal fungi (Frey-Klett et al. 2007), but the stand-scale ecological relevance remains unclear. A recent study in Yellowstone National Park similarly found that pooled BNF rates from lichen, litter, moss, surface mineral soil, and wood explained less than 10% of the N accumulation rate following wildfire (Heumann et al. 2025).

Moss-associated BNF is clearly an important N source in old evergreen boreal forests (DeLuca et al. 2002), but our present study has revealed a marked paucity of research on other sources of BNF in boreal forests younger than 200 years, particularly those with deciduous-dominated canopies establishing after stand-replacing fires.

The discrepancy between N accumulation rates and known N input rates persisted even under more conservative assumptions, such as assuming the presence of alternative nitrogenase co-factors with moss BNF (Darnajoux et al. 2019). Another conservative aspect of our calculations derives from the fact that modest N losses from boreal forests also occur, including leaching (usually $<1 \text{ kg ha}^{-1} \text{ year}^{-1}$, but pulses up to $6 \text{ kg ha}^{-1} \text{ year}^{-1}$ immediately after fire; Kortelainen et al. 2006; Sponseller et al. 2016) and N_2O emissions (up to $0.5 \text{ kg ha}^{-1} \text{ year}^{-1}$; Köster et al. 2017; Mason et al. 2019). Within the mass balance framework that we used to estimate N accumulation and BNF, any such losses would equate to an additional equivalent fraction of input by BNF, meaning that the actual amount of unexplained N inputs may be higher than our estimate.

4.4 | *Alnus*

Alnus spp. is often considered to be an important source of fixed N in high-latitude forests. Indeed, high rates of BNF by *Alnus* have been found in the Tanana River floodplain of interior Alaska (Cleve et al. 1971), but few studies have quantified stand-scale BNF rates by *Alnus* in upland boreal forests. Our literature search found only four such studies: two in interior Alaska (average BNF rate = $3.8 \text{ kg ha}^{-1} \text{ year}^{-1}$; Houseman et al. 2020; Mitchell and Ruess 2009), one in interior British Columbia (average BNF rate = $9.6 \text{ kg ha}^{-1} \text{ year}^{-1}$; Sanborn et al. 2002), and one in Sweden (average BNF rate = $0.2 \text{ kg ha}^{-1} \text{ year}^{-1}$; Granhall and Lindberg 1978).

In contrast to mosses, which were present in all chronosequences, *Alnus* was present in 10 of 18 chronosequences. We found that chronosequences with *Alnus* accumulated N faster than chronosequences without *Alnus*, but this effect was confounded with fire regime. In separate models, fire regime explained more than twice the variation in N accumulation rates than was explained by *Alnus* presence, demonstrating that *Alnus* was a less important factor explaining N stock recovery. Rather than contributing toward biomass and organic soil layer N stock accumulation (the pools that we measured), *Alnus* might exhibit lower BNF rates than described for floodplains and temperate forest ecosystems (Binkley et al. 1994; Silvester 1983), or the N_2 it fixes may be more readily lost from the ecosystem. One study in Alaska found that *Alnus* usually exhibited BNF rates less than $1.0 \text{ kg ha}^{-1} \text{ year}^{-1}$, except when it occurred in self-replacing deciduous-dominated stands (i.e., deciduous-dominated stands that were already deciduous-dominated prior to wildfire; Houseman et al. 2020). In these specific stand types, the study found that N inputs from *Alnus* ranged between 4.7 and $11.5 \text{ kg ha}^{-1} \text{ year}^{-1}$, indicating that *Alnus* can be a very important source of N in specific contexts, but there is very little research to demonstrate this outside of Alaska. Ultimately, our data provide insufficient evidence to conclude that *Alnus* is a major contributor to N inputs in the majority of chronosequences that we studied. High-severity wildfires are already triggering shifts toward deciduous dominance in boreal regions (Mekonnen et al. 2019; Tautenhahn et al. 2016), and our data suggest that largely overlooked sources of N associated with deciduous trees (including deep mineral soil accessed by deeper rooting patterns, described further below) are compensating for N that is lost during combustion.

4.5 | Mineral Soil

Redistribution of N from the mineral soil is another potential source of N that might explain the N budget discrepancy we report (Heumann et al. 2025), but direct evidence to support this hypothesis is lacking. Among the 10 chronosequences in which mineral soil N was measured (up to 30 cm depth), we found that it increased by approximately $5.3 \text{ kg ha}^{-1} \text{ year}^{-1}$ (95% CI = $2.3\text{--}8.3 \text{ kg ha}^{-1} \text{ year}^{-1}$), rather than decreased, indicating that net redistribution from mineral soil does not explain the “missing” N input. However, there was high variation in the mineral soil N accumulation rate despite a statistically significant increase. Nitrogen redistributed from deeper soil may contribute toward ecosystem N accumulation, but would need to be relatively large to sustain the increases of N that we found in the upper mineral layer, the organic layer, and aboveground biomass that was not already accounted for by N deposition and moss BNF. Specifically, the accumulation of N that we found in upper mineral soil ($5.3 \text{ kg ha}^{-1} \text{ year}^{-1}$) pooled with the organic layer and aboveground biomass ($6.9 \text{ kg ha}^{-1} \text{ year}^{-1}$) collectively equals approximately $12.2 \text{ kg ha}^{-1} \text{ year}^{-1}$. Accounting for N inputs from deposition and moss BNF (together approximately $1.7 \text{ kg ha}^{-1} \text{ year}^{-1}$) leaves approximately $10.5 \text{ kg ha}^{-1} \text{ year}^{-1}$ that would potentially come from deeper mineral soil. A redistribution of this magnitude would require over 2 Mg N ha^{-1} over a 200-year timespan (i.e., $10.5 \text{ kg ha}^{-1} \text{ year}^{-1}$ multiplied by 200 years), or approximately the entire mineral soil N stock found in this and other studies. There is currently no evidence from boreal chronosequences younger than 200 years that such redistribution is occurring. Nevertheless, estimating N stock changes over time in deep ($>50 \text{ cm}$) mineral soil represents a clear research frontier, but there is little agreement about the depth at which conclusions can be drawn.

Rock weathering may also be a source of N in boreal forests. Across the entire boreal forest, rock weathering may provide an average of approximately $0.8\text{--}1.1 \text{ kg N ha}^{-1} \text{ year}^{-1}$ (i.e., dividing the value reported for boreal forest in Table 2 of (Houlton et al. 2018) by the areal extent of the boreal zone (excluding water bodies) from the World Wildlife Fund ecoregions; Olson et al. 2001). However, it is very spatially heterogeneous, with higher rates of N from rock weathering found in areas with marine sedimentary lithology (Houlton et al. 2018). According to the Global Lithology Map Database (Hartmann and Moosdorf 2012), pockets of sedimentary lithology (along with several other non-sedimentary lithologies) potentially occur among all stand types, but were not overrepresented within any fire severity or canopy type.

4.6 | Future Directions

Our data revealed that deciduous-dominated forests establishing after stand-replacing fires had significantly higher N accumulation rates than other forest types, but 65%–94% of the accumulating N remained unexplained by the known inputs. This finding highlights a clear need to quantify N inputs from other sources besides mosses and N deposition in forests developing after stand-replacing fires. We speculate that deciduous trees such as *Betula*, which rapidly colonize recently disturbed sites, may support non-nodulating symbiotic diazotrophs in the

rhizosphere and thus represent a key source of N in young boreal forests following wildfire. *Betula* does not form nodulating symbioses, but is within the same taxonomic family (Betulaceae) as a known nodulating N₂-fixing genus (*Alnus*), and within a taxonomic order (Fagales) that has experienced numerous losses of the nodulating symbiosis over evolutionary time (Griesmann et al. 2018). Our study also revealed a paucity of research that quantifies stand-scale BNF in other niches that may prove to be important contributors to the N budget of wildfire-affected forests. Stand-scale BNF associated with deadwood, the organic layer, lichen, foliar endophytes, roots, the mineral soil layer, litter, bark, and biocrusts has only been quantified in boreal forests in one or two studies each. Consequently, there remains a considerable opportunity to quantify the contribution of these niches to the boreal forest N budget following wildfire. The role of deep mineral soil and rock weathering as N sources should also be investigated further.

5 | Conclusions

The productivity and CO₂ uptake of terrestrial ecosystems, including boreal forests, are contingent on the availability of N (Norby et al. 2010; Wang and Houlton 2009), which originates from N deposition and BNF. Given the increasing extent and severity of wildfires that are occurring in boreal forests, identifying and quantifying the sources of N stock recovery among different wildfire regimes and canopy types is important for modeling and predicting boreal forest C uptake, storage, and productivity in a changing climate. By combining a mass balance approach with a literature synthesis, this study revealed that the most widely measured source of boreal BNF, mosses, explained only 1%–6% of accumulating N in forests <200 years old, highlighting the importance of other N sources in young boreal forests, particularly deciduous/mixed dominance forests establishing after stand-replacing fires. Higher tissue N concentrations, N turnover, and N mineralization rates in deciduous trees and forests reflect different N redistribution patterns within the ecosystem, but do not explain where the N originates. Our analysis therefore points to other sources of N such as deep mineral soil, rock weathering, and non-nodulating free-living diazotrophs that are associated with severe post-fire environments and deciduous trees (e.g., *Betula* or *Larix*), thus opening a new research frontier. Identifying these sources of N, and understanding how they respond to climate change factors (e.g., elevated CO₂ and temperature, altered precipitation, etc.) is needed for refinement of coupled C-N Earth system models, and will help improve predictions of C and N cycle interactions in boreal forests under changing climate and intensifying disturbance regimes.

Author Contributions

Stefan F. Hupperts: conceptualization, formal analysis, writing – original draft, writing – review and editing. **Frank Berninger:** data curation, writing – review and editing. **Han Y. H. Chen:** data curation, writing – review and editing. **Nicole Fenton:** data curation, writing – review and editing. **Mélanie Jean:** data curation, writing – review and editing. **Kajar Köster:** data curation, writing – review and editing. **Markku Larjavaara:** data curation, writing – review and editing. **Michelle C. Mack:** data curation, writing – review and editing.

Marie-Charlotte Nilsson: data curation, writing – review and editing. **Marjo Palviainen:** data curation, writing – review and editing. **Anatoly Prokushkin:** data curation, writing – review and editing. **Jukka Pumpanen:** data curation, writing – review and editing. **Meelis Seedre:** data curation, writing – review and editing. **Martin Simard:** data curation, writing – review and editing. **Michael J. Gundale:** conceptualization, data curation, funding acquisition, writing – original draft, writing – review and editing.

Acknowledgments

S.F.H. and M.J.G. acknowledge funding from the Kempe Foundation (grant no. JCK-1911) and VR (grant no. 2020-03908). We thank the ISIMIP team for producing and publishing the nitrogen deposition data. We also acknowledge Lindo et al. (2013), the USGS Powell Center Nitrogen Fixation Working Group, and Hupperts et al. (2021) for bibliographic lists of biological nitrogen fixation publications in boreal forests up to 2012, 2020, and 2021, respectively. Data extraction and upscaling were done independently of these previous literature reviews.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and R code that support the findings of this study are openly available in the Figshare repository at <https://doi.org/10.6084/m9.figshare.24126546.v6> and <https://doi.org/10.6084/m9.figshare.24131379.v5>, respectively.

References

- Aaltonen, H., K. Köster, E. Köster, et al. 2019. “Forest Fires in Canadian Permafrost Region: The Combined Effects of Fire and Permafrost Dynamics on Soil Organic Matter Quality.” *Biogeochemistry* 143, no. 2: 257–274. <https://doi.org/10.1007/s10533-019-00560-x>.
- Abatzoglou, J. T., S. Z. Dobrowski, S. A. Parks, and K. C. Hegewisch. 2017. “Data Descriptor: TerraClimate, a High-Resolution Global Dataset of Monthly Climate and Climatic Water Balance From 1958–2015.”
- Alexander, H. D., and M. C. Mack. 2016. “A Canopy Shift in Interior Alaskan Boreal Forests: Consequences for Above- and Belowground Carbon and Nitrogen Pools During Post-Fire Succession.” *Ecosystems* 19, no. 1: 98–114. <https://doi.org/10.1007/s10021-015-9920-7>.
- Bartoń, K. 2023. “_MuMIn: Multi-Model Inference_.” R Package Version 1.47.5. <https://cran.r-project.org/package=MuMIn>.
- Benoist, A., D. Houle, R. L. Bradley, and J. P. Bellenger. 2022. “Evaluation of Biological Nitrogen Fixation in Coarse Woody Debris From Eastern Canadian Boreal Forests.” *Soil Biology and Biochemistry* 165: 108531. <https://doi.org/10.1016/j.soilbio.2021.108531>.
- Binkley, D., K. Cromack, and D. D. Baker. 1994. “Nitrogen Fixation by Red Alder: Biology, Rates, and Controls.” In *The Biology and Management of Red Alder*, edited by D. E. Hibbs, 57–72. Oregon State University Press.
- Binkley, D., Y. Son, and D. W. Valentine. 2000. “Do Forests Receive Occult Inputs of Nitrogen?” *Ecosystems* 3, no. 4: 321–331. <https://doi.org/10.1007/s100210000029>.
- Bizjak, T., A. Sellstedt, R. Gratz, and A. Nordin. 2023. “Presence and Activity of Nitrogen-Fixing Bacteria in Scots Pine Needles in a Boreal Forest: A Nitrogen-Addition Experiment.” *Tree Physiology* 43, no. 8: 1354–1364. <https://doi.org/10.1093/treephys/tpad048>.
- Bondarev, A. 1997. “Age Distribution Patterns in Open Boreal Dahurican Larch Forests of Central Siberia.” *Forest Ecology and Management* 93, no. 3: 205–214. [https://doi.org/10.1016/S0378-1127\(96\)03952-7](https://doi.org/10.1016/S0378-1127(96)03952-7).

- Bond-Lamberty, B., S. T. Gower, C. Wang, P. Cyr, and H. Veldhuis. 2006. "Nitrogen Dynamics of a Boreal Black Spruce Wildfire Chronosequence." *Biogeochemistry* 81, no. 1: 1–16. <https://doi.org/10.1007/s10533-006-9025-7>.
- Bouchard, M., D. Pothier, and S. Gauthier. 2008. "Fire Return Intervals and Tree Species Succession in the North Shore Region of Eastern Quebec." *Canadian Journal of Forest Research* 38, no. 6: 1621–1633. <https://doi.org/10.1139/X07-201>.
- Brandt, J. P. 2009. "The Extent of the North American Boreal Zone." *Environmental Reviews* 17: 101–161. <https://doi.org/10.1139/A09-004>.
- Buma, B., K. Hayes, and M. Lucash. 2022. "Short-Interval Fires Increasing in the Alaskan Boreal Forest as Fire Self-Regulation Decays Across Forest Types." *Scientific Reports* 12: 56789. <https://doi.org/10.1038/s41598-022-08912-8>.
- Certini, G. 2005. "Effects of Fire on Properties of Forest Soils: A Review." *Oecologia* 143, no. 1: 1–10. <https://doi.org/10.1007/s00442-004-1788-8>.
- Cleveland, C. C., C. R. G. Reis, S. S. Perakis, et al. 2022. "Exploring the Role of Cryptic Nitrogen Fixers in Terrestrial Ecosystems: A Frontier in Nitrogen Cycling Research." *Ecosystems* 25: 1653–1669. <https://doi.org/10.1007/s10021-022-00804-2>.
- Cleveland, C. C., A. R. Townsend, D. S. Schimel, et al. 1999. "Global Patterns of Terrestrial Biological Nitrogen (N₂) Fixation in Natural Ecosystems." *Global Biogeochemical Cycles* 13, no. 2: 623–645. [https://doi.org/10.1002/\(ISSN\)1944-9224](https://doi.org/10.1002/(ISSN)1944-9224).
- Darnajoux, R., N. Magain, M. Renaudin, F. Lutzoni, J. P. Bellenger, and X. Zhang. 2019. "Molybdenum Threshold for Ecosystem Scale Alternative Vanadium Nitrogenase Activity in Boreal Forests." *Proceedings of the National Academy of Sciences of the United States of America* 116, no. 49: 24682–24688. <https://doi.org/10.1073/pnas.1913314116>.
- De Groot, W. J., A. S. Cantin, M. D. Flannigan, A. J. Soja, L. M. Gowman, and A. Newbery. 2013. "A Comparison of Canadian and Russian Boreal Forest Fire Regimes." *Forest Ecology and Management* 294: 23–34. <https://doi.org/10.1016/j.foreco.2012.07.033>.
- De Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. "Climate Change Impacts on Future Boreal Fire Regimes." *Forest Ecology and Management* 294: 35–44. <https://doi.org/10.1016/j.foreco.2012.09.027>.
- DeLuca, T. H., O. Zackrisson, M. C. Nilsson, and A. Sellstedt. 2002. "Quantifying Nitrogen-Fixation in Feather Moss Carpets of Boreal Forests." *Nature* 419, no. 6910: 917–920. <https://doi.org/10.1038/nature01051>.
- Dentener, F., J. Drevet, J. F. Lamarque, et al. 2006. "Nitrogen and Sulfur Deposition on Regional and Global Scales: A Multimodel Evaluation." *Global Biogeochemical Cycles* 20, no. 4: 2005GB002672. <https://doi.org/10.1029/2005GB002672>.
- Dynarski, K. A., and B. Z. Houlton. 2018. "Nutrient Limitation of Terrestrial Free-Living Nitrogen Fixation." *New Phytologist* 217: 1050–1061. <https://doi.org/10.1111/nph.14905>.
- Frey-Klett, P., J. Garbaye, and M. Tarkka. 2007. "The Mycorrhiza Helper Bacteria Revisited." *New Phytologist* 176: 22–36.
- Glückler, R., U. Herzschuh, S. Kruse, et al. 2021. "Wildfire History of the Boreal Forest of South-Western Yakutia (Siberia) Over the Last Two Millennia Documented by a Lake-Sediment Charcoal Record." *Biogeosciences* 18, no. 13: 4185–4209. <https://doi.org/10.5194/bg-18-4185-2021>.
- Granhall, U., and T. Lindberg. 1978. "Nitrogen Fixation in Some Coniferous Forest Ecosystems." *Ecological Bulletins* 26: 178–192.
- Griesmann, M., Y. Chang, X. Liu, et al. 2018. "Phylogenomics Reveals Multiple Losses of Nitrogen-Fixing Root Nodule Symbiosis." *Science* 361, no. 6398: eaat1743. <https://doi.org/10.1126/science.aat1743>.
- Gundale, M. J., T. H. Deluca, and A. Nordin. 2011. "Bryophytes Attenuate Anthropogenic Nitrogen Inputs in Boreal Forests." *Global Change Biology* 17, no. 8: 2743–2753. <https://doi.org/10.1111/j.1365-2486.2011.02407.x>.
- Gundale, M. J., H. Gustafsson, and M. C. Nilsson. 2009. "The Sensitivity of Nitrogen Fixation by a Feathermoss-Cyanobacteria Association to Litter and Moisture Variability in Young and Old Boreal Forests." *Canadian Journal of Forest Research* 39, no. 12: 2542–2549. <https://doi.org/10.1139/X09-160>.
- Harden, J. W., J. C. Neff, D. V. Sandberg, et al. 2004. "Chemistry of Burning the Forest Floor During the FROSTFIRE Experimental Burn, Interior Alaska, 1999." *Global Biogeochemical Cycles* 18: 2003GB002194. <https://doi.org/10.1029/2003GB002194>.
- Harris, I., T. J. Osborn, P. Jones, and D. Lister. 2020. "Version 4 of the CRU TS Monthly High-Resolution Gridded Multivariate Climate Dataset." *Scientific Data* 7, no. 1: 1–18. <https://doi.org/10.1038/s41597-020-0453-3>.
- Hartmann, J., and N. Moosdorf. 2012. "The New Global Lithological Map Database GLiM: A Representation of Rock Properties at the Earth Surface." *Geochemistry, Geophysics, Geosystems* 13, no. 12: 1–37. <https://doi.org/10.1029/2012GC004370>.
- Heumann, R. E., M. G. Turner, and C. C. Cleveland. 2025. "Rates and Controls of Nitrogen Fixation in Postfire Lodgepole Pine Forests." *Ecology* 106, no. 2: e70016. <https://doi.org/10.1002/ecy.70016>.
- Holloway, J. E., A. G. Lewkowicz, T. A. Douglas, et al. 2020. "Impact of Wildfire on Permafrost Landscapes: A Review of Recent Advances and Future Prospects." *Permafrost and Periglacial Processes* 31, no. 3: 371–382. <https://doi.org/10.1002/ppp.2048>.
- Houlton, B. Z., S. L. Morford, and R. A. Dahlgren. 2018. "Convergent Evidence for Widespread Rock Nitrogen Sources in Earth's Surface Environment." *Science* 62, no. April: 58–62. <https://doi.org/10.1126/science.aan4399>.
- Houlton, B. Z., Y. P. Wang, P. M. Vitousek, and C. B. Field. 2008. "A Unifying Framework for Dinitrogen Fixation in the Terrestrial Biosphere." *Nature* 454: 327–330. <https://doi.org/10.1038/nature07028>.
- Houseman, B., R. Ruess, T. Hollingsworth, and D. Verbyla. 2020. "Can Siberian Alder N-Fixation Offset N-Loss After Severe Fire? Quantifying Post-Fire Siberian Alder Distribution, Growth, and N-Fixation in Boreal Alaska." *PLoS One* 15, no. 9: 1–22. <https://doi.org/10.1371/journal.pone.0238004>.
- Hungate, B. a., J. S. Dukes, M. R. Shaw, Y. Luo, and C. B. Field. 2003. "Nitrogen and Climate Change." *Science* 302: 1512–1513. <https://doi.org/10.1016/j.buildenv.2005.09.015>.
- Hupperts, S. F., S. Gerber, M.-C. Nilsson, and M. J. Gundale. 2021. "Empirical and Earth System Model Estimates of Boreal Nitrogen Fixation Often Differ: A Pathway Toward Reconciliation." *Global Change Biology* 27: 5711–5725. <https://doi.org/10.1111/gcb.15836>.
- Ibáñez, T. S., T. Rütting, M. C. Nilsson, D. A. Wardle, and M. J. Gundale. 2022. "Mid-Term Effects of Wildfire and Salvage Logging on Gross and Net Soil Nitrogen Transformation Rates in a Swedish Boreal Forest." *Forest Ecology and Management* 517: 120240. <https://doi.org/10.1016/j.foreco.2022.120240>.
- Jean, M., H. Holland-Moritz, A. M. Melvin, J. F. Johnstone, and M. C. Mack. 2020. "Experimental Assessment of Tree Canopy and Leaf Litter Controls on the Microbiome and Nitrogen Fixation Rates of Two Boreal Mosses." *New Phytologist* 227, no. 5: 1335–1349. <https://doi.org/10.1111/nph.16611>.
- Jean, M., M. C. Mack, and J. F. Johnstone. 2018. "Spatial and Temporal Variation in Moss-Associated Dinitrogen Fixation in Coniferous- and Deciduous-Dominated Alaskan Boreal Forests." *Plant Ecology* 219, no. 7: 837–851. <https://doi.org/10.1007/s11258-018-0838-y>.
- Jean, M., A. M. Melvin, M. C. Mack, and J. F. Johnstone. 2020. "Broadleaf Litter Controls Feather Moss Growth in Black Spruce and Birch Forests

- of Interior Alaska." *Ecosystems* 23, no. 1: 18–33. <https://doi.org/10.1007/s10021-019-00384-8>.
- Kalamees, R., K. Piissa, I. Vanha-majamaa, and K. Zobel. 2005. "The Effects of Fire and Stand Age on Seedling Establishment of *Pulsatilla patens* in a Pine-Dominated Boreal Forest." *Canadian Journal of Botany* 83, no. 6: 688–693. <https://doi.org/10.1139/B05-038>.
- Korhonen, J. F. J., M. Pihlatie, J. Pumpanen, et al. 2013. "Nitrogen Balance of a Boreal Scots Pine Forest." *Biogeosciences* 10, no. 2: 1083–1095. <https://doi.org/10.5194/bg-10-1083-2013>.
- Kortelainen, P., T. Mattsson, L. Finér, M. Ahtiainen, S. Saukkonen, and T. Sallantausta. 2006. "Controls on the Export of C, N, P and Fe From Undisturbed Boreal Catchments, Finland." *Aquatic Sciences* 68, no. 4: 453–468. <https://doi.org/10.1007/s00027-006-0833-6>.
- Köster, E., K. Köster, F. Berninger, H. Aaltonen, X. Zhou, and J. Pumpanen. 2017. "Carbon Dioxide, Methane and Nitrous Oxide Fluxes From a Fire Chronosequence in Subarctic Boreal Forests of Canada." *Science of the Total Environment* 601: 895–905. <https://doi.org/10.1016/j.scitotenv.2017.05.246>.
- Köster, E., K. Köster, F. Berninger, et al. 2018. "Changes in Fluxes of Carbon Dioxide and Methane Caused by Fire in Siberian Boreal Forest With Continuous Permafrost." *Journal of Environmental Management* 228: 405–415. <https://doi.org/10.1016/j.jenvman.2018.09.051>.
- Köster, K., F. Berninger, A. Lindén, E. Köster, and J. Pumpanen. 2014. "Recovery in Fungal Biomass Is Related to Decrease in Soil Organic Matter Turnover Time in a Boreal Fire Chronosequence." *Geoderma* 235: 74–82. <https://doi.org/10.1016/j.geoderma.2014.07.001>.
- Lamarque, J. F., D. T. Shindell, B. Josse, et al. 2013. "The Atmospheric Chemistry and Climate Model Intercomparison Project (ACCMIP): Overview and Description of Models, Simulations and Climate Diagnostics." *Geoscientific Model Development* 6, no. 1: 179–206. <https://doi.org/10.5194/gmd-6-179-2013>.
- Larjavaara, M., F. Berninger, M. Palviainen, A. Prokushkin, and T. Wallenius. 2017. "Post-Fire Carbon and Nitrogen Accumulation and Succession in Central Siberia." *Scientific Reports* 7, no. 1: 1–11. <https://doi.org/10.1038/s41598-017-13039-2>.
- Lenth, R. 2018. "emmeans: Estimated Marginal Means, Aka Least-Squares Means." R Package Version 1.3.1.
- Lindo, Z., M.-C. Nilsson, and M. J. Gundale. 2013. "Bryophyte-Cyanobacteria Associations as Regulators of the Northern Latitude Carbon Balance in Response to Global Change." *Global Change Biology* 19: 2022–2035. <https://doi.org/10.1111/gcb.12175>.
- Liski, J., A. Pussinen, K. Pingoud, R. Mäkipää, and T. Karjalainen. 2001. "Which Rotation Length Is Favourable to Carbon Sequestration?" *Canadian Journal of Forest Research* 31, no. 11: 2004–2013. <https://doi.org/10.1139/cjfr-31-11-2004>.
- Mack, M. C., X. J. Walker, J. F. Johnstone, et al. 2021. "Carbon Loss From Boreal Forest Wildfires Offset by Increased Dominance of Deciduous Trees." *Science* 372: 280–283.
- Maltman, J. C., T. Hermosilla, M. A. Wulder, N. C. Coops, and J. C. White. 2023. "Estimating and Mapping Forest Age Across Canada's Forested Ecosystems." *Remote Sensing of Environment* 290: 113529. <https://doi.org/10.1016/j.rse.2023.113529>.
- Marklund, L. 1988. *Biomassfunktioner för Tall, Gran Och björk i Sverige (Biomass Functions for Pine, Spruce and Birch in Sweden)*, Vol. 73, Department of Forest Survey, Report 45. Swedish University of Agricultural Sciences.
- Mason, K. E., S. Oakley, L. E. Street, et al. 2019. "Boreal Forest Floor Greenhouse Gas Emissions Across a *Pleurozium schreberi*-Dominated, Wildfire-Disturbed Chronosequence." *Ecosystems* 22, no. 6: 1381–1392. <https://doi.org/10.1007/s10021-019-00344-2>.
- Massey, R., B. M. Rogers, L. T. Berner, et al. 2023. "Deciduous Fractional Cover and Tree Canopy Cover for Boreal North America, 1992–2015." ORNL DAAC. <https://doi.org/10.3334/ORNLDAAAC/2296>.
- McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science* 368: eaaz9463. <https://doi.org/10.1126/science.aaz9463>.
- Mekonnen, Z. A., W. J. Riley, J. T. Randerson, R. F. Grant, and B. M. Rogers. 2019. "Expansion of High-Latitude Deciduous Forests Driven by Interactions Between Climate Warming and Fire." *Nature Plants* 5: 952–958. <https://doi.org/10.1038/s41477-019-0495-8>.
- Meyerholt, J., and S. Zaehle. 2018. "Controls of Terrestrial Ecosystem Nitrogen Loss on Simulated Productivity Responses to Elevated CO₂." *Biogeosciences* 15: 5677–5698.
- Meyerholt, J., S. Zaehle, and M. J. Smith. 2016. "Variability of Projected Terrestrial Biosphere Responses to Elevated Levels of Atmospheric CO₂ due to Uncertainty in Biological Nitrogen Fixation." *Biogeosciences* 13, no. 5: 1491–1518. <https://doi.org/10.5194/bg-13-1491-2016>.
- Mitchell, J. S., and R. W. Ruess. 2009. "N₂ Fixing Alder (*Alnus viridis* spp. Fruticosa) Effects on Soil Properties Across a Secondary Successional Chronosequence in Interior Alaska." *Biogeochemistry* 95, no. 2: 215–229. <https://doi.org/10.1007/s10533-009-9332-x>.
- Natole, M., Y. Ying, A. Buyantuev, M. Stessin, V. Buyantuev, and A. Lapenis. 2021. "Patterns of Mega-Forest Fires in East Siberia Will Become Less Predictable With Climate Warming." *Environmental Advances* 4: 100041. <https://doi.org/10.1016/j.envadv.2021.100041>.
- Neff, J. C., E. A. Holland, F. J. Dentener, W. H. McDowell, and K. M. Russell. 2002. "The Origin, Composition and Rates of Organic Nitrogen Deposition: A Missing Piece of the Nitrogen Cycle?" *Biogeochemistry* 5: 99–136. <https://doi.org/10.1023/A:1015791622742>.
- Norby, R. J., J. M. Warren, C. M. Iversen, B. E. Medlyn, and R. E. McMurtrie. 2010. "CO₂ Enhancement of Forest Productivity Constrained by Limited Nitrogen Availability." *Proceedings of the National Academy of Sciences of the United States of America* 107, no. 45: 19368–19373. <https://doi.org/10.1073/pnas.1006463107>.
- Oksanen, J., F. G. Blanchet, M. Friendly, et al. 2018. "vegan: Community Ecology Package." R Package Version 2.5-1.
- Olson, D. M., E. Dinerstein, E. D. Wikramanayake, et al. 2001. "Terrestrial Ecoregions of the World: A New Map of Life on Earth." *BioScience* 51, no. 11: 933–938.
- Palviainen, M., J. Pumpanen, F. Berninger, et al. 2017. "Nitrogen Balance Along a Northern Boreal Forest Fire Chronosequence." *PLoS One* 12, no. 3: 1–21. <https://doi.org/10.1371/journal.pone.0174720>.
- Paré, D., P. Bernier, B. Lafleur, et al. 2013. "Estimating Stand-Scale Biomass, Nutrient Contents, and Associated Uncertainties for Tree Species of Canadian Forests." *Canadian Journal of Forest Research* 43: 599–608.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2018. "_nlme: Linear and Nonlinear Mixed Effects Models_." R Package Version 3: 1–137.
- R Core Development Team. 2022. "R: A Language and Environment for Statistical Computing." *R Foundation for Statistical Computing* 1: 409. <https://doi.org/10.1007/978-3-540-74686-7>.
- Rinne, K. T., T. Rajala, K. Peltoniemi, J. Chen, A. Smolander, and R. Mäkipää. 2017. "Accumulation Rates and Sources of External Nitrogen in Decaying Wood in a Norway Spruce Dominated Forest." *Functional Ecology* 31, no. 2: 530–541. <https://doi.org/10.1111/1365-2435.12734>.
- Rönkkö, R., A. Smolander, E. L. Nurmiäho-Lassila, and K. Haahtela. 1993. "Frankia in the Rhizosphere of Nonhost Plants: A Comparison with Root-Associated N₂-Fixing Enterobacter." *Klebsiella and Pseudomonas. Plant and Soil* 153, no. 1: 85–95. <https://doi.org/10.1007/BF00010547>.

- Roth, H. K., A. M. McKenna, M. J. Simpson, et al. 2023. "Effects of Burn Severity on Organic Nitrogen and Carbon Chemistry in High-Elevation Forest Soils." *Soil & Environmental Health* 1, no. 3: 100023. <https://doi.org/10.1016/j.seh.2023.100023>.
- Saiz, E., F. Sgouridis, F. P. Drijfhout, and S. Ullah. 2019. "Biological Nitrogen Fixation in Peatlands: Comparison Between Acetylene Reduction Assay and $^{15}\text{N}_2$ Assimilation Methods." *Soil Biology and Biochemistry* 131: 157–165. <https://doi.org/10.1016/j.soilbio.2019.01.011>.
- Sanborn, P., C. Preston, and R. Brockley. 2002. " N_2 -Fixation by Sitka Alder in a Young Lodgepole Pine Stand in Central Interior British Columbia, Canada." *Forest Ecology and Management* 167: 223–231. [https://doi.org/10.1016/S0378-1127\(01\)00695-8](https://doi.org/10.1016/S0378-1127(01)00695-8).
- Seedre, M., A. R. Taylor, B. W. Brassard, H. Y. H. Chen, and K. Jögiste. 2014. "Recovery of Ecosystem Carbon Stocks in Young Boreal Forests: A Comparison of Harvesting and Wildfire Disturbance." *Ecosystems* 17, no. 5: 851–863. <https://doi.org/10.1007/s10021-014-9763-7>.
- Silvester, W. B. 1983. "Analysis of Nitrogen Fixation." In *Biological Nitrogen Fixation in Forest Ecosystems: Foundations and Applications*, edited by J. C. Gordon and C. T. Wheeler, 173–212. Springer. https://doi.org/10.1007/978-94-009-6878-3_6.
- Simard, M., N. Lecomte, Y. Bergeron, P. Y. Bernier, and D. Paré. 2007. "Forest Productivity Decline Caused by Successional Paludification of Boreal Soils." *Ecological Applications* 17, no. 6: 1619–1637. <https://doi.org/10.1890/06-1795.1>.
- Simpson, I. J., S. K. Akagi, B. Barletta, et al. 2011. "Boreal Forest Fire Emissions in Fresh Canadian Smoke Plumes: C_1 – C_{10} Volatile Organic Compounds (VOCs), CO_2 , CO , NO_2 , NO , HCN and CH_3CN ." *Atmospheric Chemistry and Physics* 11, no. 13: 6445–6463. <https://doi.org/10.5194/acp-11-6445-2011>.
- Smolander, A. 1990. "Frankia Populations in Soils Under Different Tree Species-with Special Emphasis on Soils Under *Betula pendula*." *Plant and Soil* 121, no. 1: 1–10. <https://doi.org/10.1007/BF00013091>.
- Sponseller, R. A., M. J. Gundale, M. Futter, et al. 2016. "Nitrogen Dynamics in Managed Boreal Forests: Recent Advances and Future Research Directions." *Ambio* 45: 175–187. <https://doi.org/10.1007/s13280-015-0755-4>.
- Su, W. Q., M. Yu, J. Lin, C. Tang, and J. Xu. 2022. "Fire Decreases Gross Mineralization Rate but Does Not Alter Gross Nitrification Rate in Boreal Forest Soils." *Soil Biology and Biochemistry* 175: 108838. <https://doi.org/10.1016/j.soilbio.2022.108838>.
- Tautenhahn, S., J. W. Lichstein, M. Jung, et al. 2016. "Dispersal Limitation Drives Successional Pathways in Central Siberian Forests Under Current and Intensified Fire Regimes." *Global Change Biology* 22: 2178. <https://doi.org/10.1111/gcb.13181>.
- Turetsky, M. R. 2003. "The Role of Bryophytes in Carbon and Nitrogen Cycling." *Bryologist* 106, no. 3: 395–409.
- Van Cleve, K., L. A. Viereck, and R. L. Schlentner. 1971. "Accumulation of Nitrogen in Alder (*Alnus*) Ecosystems Near Fairbanks, Alaska." *Arctic and Alpine Research* 3, no. 2: 101. <https://doi.org/10.2307/1549980>.
- Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. "The Use of Chronosequences in Studies of Ecological Succession and Soil Development." *Journal of Ecology* 98: 725–736. <https://doi.org/10.1111/j.1365-2745.2010.01664.x>.
- Wang, Y. P., and B. Z. Houlton. 2009. "Nitrogen Constraints on Terrestrial Carbon Uptake: Implications for the Global Carbon-Climate Feedback." *Geophysical Research Letters* 36, no. 24: 1009. <https://doi.org/10.1029/2009GL041009>.
- Warszawski, L., K. Frieler, V. Huber, F. Piontek, O. Serdeczny, and J. Schewe. 2014. "The Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP): Project Framework." *Proceedings of the National Academy of Sciences of the United States of America* 111, no. 9: 3228–3232. <https://doi.org/10.1073/pnas.1312330110>.
- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.
- Wilke, C. 2020. "_cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'." R Package Version 1.1.1. <https://cran.r-project.org/package=cowplot>.
- Wirth, C., E. D. Schulze, B. Lühker, et al. 2002. "Fire and Site Type Effects on the Long-Term Carbon and Nitrogen Balance in Pristine Siberian Scots Pine Forests." *Plant and Soil* 242, no. 1: 41–63. <https://doi.org/10.1023/A:1020813505203>.
- Wong, M. Y., S. D. Rathod, R. Marino, and L. Li. 2021. "Anthropogenic Perturbations to the Atmospheric Molybdenum Cycle Global Biogeochemical Cycles." *Global Biogeochemical Cycles* 2: 1–25. <https://doi.org/10.1029/2020GB006787>.
- Zackrisson, O. 1977. "Influence of Forest Fires on the North Swedish Boreal Forest." *Oikos* 29, no. 1: 22–32.
- 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, no. 12: 3327–3334. <https://doi.org/10.1890/04-0461>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** gcb70398-sup-0001-supinfo.pdf.