

REVIEW

The biological controls of soil carbon accumulation following wildfire and harvest in boreal forests: A review

Michael J. Gundale¹  | E. Petter Axelsson²  | Vincent Buness¹  | Timon Callebaut³  |
 Thomas H. DeLuca⁴  | Stefan F. Hupperts¹  | Theresa S. Ibáñez²  |
 Daniel B. Metcalfe³  | Marie-Charlotte Nilsson¹  | Matthias Peichl¹  |
 Clydecia M. Spitzer¹  | Zsofia R. Stangl¹  | Joachim Strengbom⁵  |
 Maja K. Sundqvist¹  | David A. Wardle³  | Björn D. Lindahl⁶ 

¹Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

²Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden

³Department of Environmental Science and Ecology, Umeå University, Umeå, Sweden

⁴College of Forestry, Oregon State University, Corvallis, Oregon, USA

⁵Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

⁶Department of Soil Science, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence

Michael J. Gundale, Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå 90183, Sweden.

Email: michael.gundale@slu.se

Funding information

Svenska Forskningsrådet Formas, Grant/Award Number: 2021-02116 and 2021-02121

Abstract

Boreal forests are frequently subjected to disturbances, including wildfire and clear-cutting. While these disturbances can cause soil carbon (C) losses, the long-term accumulation dynamics of soil C stocks during subsequent stand development is controlled by biological processes related to the balance of net primary production (NPP) and outputs via heterotrophic respiration and leaching, many of which remain poorly understood. We review the biological processes suggested to influence soil C accumulation in boreal forests. Our review indicates that median C accumulation rates following wildfire and clear-cutting are similar (0.15 and 0.20 Mg ha⁻¹ year⁻¹, respectively), however, variation between studies is extremely high. Further, while many individual studies show linear increases in soil C stocks through time after disturbance, there are indications that C stock recovery is fastest early to mid-succession (e.g. 15–80 years) and then slows as forests mature (e.g. >100 years). We indicate that the rapid build-up of soil C in younger stands appears not only driven by higher plant production, but also by a high rate of mycorrhizal hyphal production, and mycorrhizal suppression of saprotrophs. As stands mature, the balance between reductions in plant and mycorrhizal production, increasing plant litter recalcitrance, and ectomycorrhizal decomposers and saprotrophs have been highlighted as key controls on soil C accumulation rates. While some of these controls appear well understood (e.g. temporal patterns in NPP, changes in aboveground litter quality), many others remain research frontiers. Notably, very little data exists describing and comparing successional patterns of root production, mycorrhizal functional traits, mycorrhizal-saprotroph interactions, or C outputs via heterotrophic respiration and dissolved organic C following different disturbances. We argue that these less frequently described controls require attention, as they will be key not only for understanding ecosystem C balances, but also for representing these dynamics more accurately in soil organic C and Earth system models.

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.

© 2024 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd.

KEYWORDS

decomposition, disturbance, forest succession, heterotrophic respiration, humus, mycorrhizae, organic horizon, soil carbon

1 | INTRODUCTION

Boreal forests are expansive carbon (C) rich landscapes that serve as strong net C sinks, and therefore play a pivotal role in the global C cycle (Watts et al., 2023). They cover approximately 17% of the terrestrial land surface area, and account for somewhere between 20% to 40% of terrestrial C stocks (Anderson, 1991; Bradshaw & Warkentin, 2015; Lorenz et al., 2010; Tarnocai et al., 2009), with around 80% of the C in boreal forests found belowground (Pan et al., 2011). Boreal soil C stock sizes vary greatly among sites and regions, with major drivers of stock variation including topography (i.e. affecting hydrology), climate, and parent material (Jandl et al., 2007; Sothe et al., 2022). As such, boreal forests on peat or permafrost soils can contain as much as 1200 and 600 Mg C ha⁻¹, respectively (Bradshaw & Warkentin, 2015; DeLuca & Boisvenue, 2012), whereas those on young and poorly developed boreal Cambisols may contain as little as 130 Mg C ha⁻¹ (DeLuca & Boisvenue, 2012). Indeed, the influence of topography, climate, and parent material, compounded over time, serve as four of the five primary soil development factors (Jenny, 1994).

In addition to these state factors, boreal forests are also commonly subjected to natural and anthropogenic disturbances, including wildfire and clear-cutting, which determine C dynamics on the scale of decades to centuries. The development and succession of vegetation and its associated soil communities following these disturbances also serve as major controls on soils (i.e. "biota"; Jenny, 1994), through determining soil C stock accumulation between disturbance cycles. Approximately 1% of the boreal biome burns every year (Wooster & Zhang, 2004), often resulting in large releases of soil C (Bill et al., 2023; Granath et al., 2021; Shao et al., 2023); however, burning severity and soil C loss shows substantial spatial variation both among and within fires (Pérez-Izquierdo et al., 2023). In recent decades, boreal fires are becoming more frequent, extensive, and severe because of climate warming and summer drought (Balshi et al., 2009; de Groot et al., 2013; Kasischke & Turetsky, 2006; Turetsky et al., 2011). High severity fires generally release greater quantities of soil C, sometimes also releasing C that accumulated during previous burn intervals, referred to as "legacy C" (Walker et al., 2019). Further intensification of the fire regime could eventually change boreal forests from net C sinks to sources (Walker et al., 2019). However, recovery of vegetation and soil communities, and natural transitions in forest cover types, can counter-balance these losses on the scale of decades to centuries, with rapid accumulation of new organic matter (Mack et al., 2021). In addition to fire, commercial management is now an expansive disturbance in boreal forests, where more than half of the boreal region is subjected to some form of management activity, often even-aged rotational silvicultural systems that are initiated via clear-cutting

(Gauthier et al., 2015; Figure 1). The net impact of rotational forest management on the C sink-source balance is frequently debated, and the magnitude to which short-term soil C losses following clear-cutting are balanced by long-term gains is central to this discussion (Bellassen & Luysaert, 2014; Lindroth, 2023; Peichl et al., 2023).

In this review, we explore the range of biological mechanisms that can impact soil C accumulation patterns following wildfire or clear-cutting, independent of other major state factors (topography, parent material, and climate), which have already been emphasized in previous reviews (Bradshaw & Warkentin, 2015; DeLuca & Boisvenue, 2012). While we focus on post-fire and even-aged stands initiated via clear-cutting, our discussion is relevant to other important disturbance types, such as wind and insect outbreaks, as well as other ecosystems dominated by ectomycorrhizal tree species (e.g. temperate conifer forests). We focus primarily on soil organic horizon C stocks, which are the largest, most vulnerable, and most dynamic soil C pool during intra-disturbance recovery cycles in boreal forests. We discuss plant and microbial properties and processes that influence rates of soil C stock accumulation over decades to century timescales, and compare and contrast how each mechanism may differ between wildfire versus even-aged forest management. In doing so we aim to advance fundamental understanding of soil C dynamics in boreal forests following anthropogenic and natural disturbance, and identify key knowledge gaps to guide future research efforts.

2 | TEMPORAL PATTERNS OF C STOCK RECOVERY AFTER DISTURBANCE

We searched the literature for data on soil organic horizon C accumulation rates from chronosequence studies following wildfire and clear-cutting (see Supporting Information). Estimates of soil C accumulation rates following fire and clear-cutting are highly variable between boreal forest study sites (Table 1). Soil C stock derived from 24 chronosequences over a median duration of 108 years following wildfire ranged between -0.6 and 1.7 Mg ha⁻¹ year⁻¹, with a median accumulation rate of 0.15 Mg C ha⁻¹ year⁻¹ (Table 1). A meta-analysis of post-fire chronosequences by Palviainen et al. (2020), which included a combination of unpublished data and some studies listed in Table 1, indicated that soil C accumulation follows an asymptotic relationship during the first ca. 80 years following wildfire, with a similar average rate of 0.28 Mg C ha⁻¹ year⁻¹. Similarly, a meta-analysis by Pregitzer and Euskirchen (2004) found that organic horizon C accumulation reached an asymptote somewhere between 71 and 120 years after fire. A 5000-year post-fire chronosequence investigated by Wardle et al. (2003) indicated accumulation of ca. 0.05 Mg C ha⁻¹ year⁻¹, that is considerably lower than the majority

FIGURE 1 Photos from Canada and Sweden (left and right column, respectively), depicting recent clear-cuts (a, b), soil scarification (c, d), wildfire (e, f), and mature *Pinus contorta* forest (g), and 375 year old *Pinus sylvestris* & *Picea abies* forest. Photo credits: a, e, f: (Anne McIntosh), b, f, h: (Vincent Bunes), c: (Victor Leifers), and d: (Göran Hallsby).



of shorter chronosequences, further indicating that accumulation rates appear to slow down after ca. 100 years (Table 1). Following logging disturbance, short-term C losses on the scale of decades are sometimes observed, as indicated by parabolic accumulation curves (Table 1). However, over longer time scales ranging from decades to a full stand rotation age (often around one century), average C accumulation rates are positive and show a similar magnitude to those of post-fire chronosequences (median rate of $0.20 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ over a median chronosequence duration of 74 years, derived from 15 chronosequences; Table 1).

A few research priorities emerge from these data compilation. First, similar chronosequence studies are needed from other disturbance types, such as following insect outbreaks, which our literature review identified were nearly completely absent for the boreal forest zone. Further, a clear research priority is to understand the mechanisms underlying the large variation that exists among

chronosequences. While some of this variation could be due to site selection error in individual chronosequences (i.e. chronosequences constructed from stands with inherently different site properties), the initial soil C stock size and the effect of stand removal on soil moisture, among other factors, may also influence whether soil C stocks increase or decrease through time. We now discuss the key controls on these accumulation patterns.

3 | CARBON INPUTS

While plants serve as the origin of soil C, different aspects of plant production have been emphasized as dominant controls on soil C accumulation. First, net primary productivity (NPP) has long been considered the ultimate driver of soil C stock accumulation in ecosystem ecology, whereby biomass production and soil C accumulation are

TABLE 1 Reported organic horizon C accumulation rates from chronosequence studies initiated via wildfire or clear-cutting in boreal forests. Studies for each disturbance type (fire vs. even-aged management) are ordered in rank from lowest to highest C accumulation rate. The column “relationship” refers to the shape of the response curve, linear, hump shaped, parabolic, or asymptotic. Asymptotic refers to C accumulation patterns that decelerate through time, whereas parabolic relationship initially decrease and then increase. When an asymptotic relationship was found, the approximate inflection point is reported in parentheses, when possible to distinguish. Reported accumulation rates are estimated averages covering the whole time-series, except for relationships that reached an asymptote, in which case the time to the asymptote was instead used to estimate the average rate. When relationships were asymptotic, but the asymptote was not reached within the time series, then the entire time series was used to estimate an average. Data used for the two meta-analysis include a combination of studies listed in the table, non-chronosequence references, and unpublished data. Search methods and references are reported in the [Supporting Information](#).

Reference	Mg C ha ⁻¹ year ⁻¹	Relationship (inflection)	Species	Time series	Location
Fire					
Bill et al. (2023)	-0.56	Linear	Mixed (hydric shield)	100	Northwest Territories, CA
Moroni et al. (2010)	-0.07	Hump	<i>P. mariana</i>	74	Newfoundland, CA
Trumbore and Harden (1997)	-0.05	Asymptotic (-)	<i>P. banksiana</i>	100	Manitoba, CA
Wardle et al. (2003)	0.05	Linear	Mixed forest	5000	Sweden
Trumbore and Harden (1997)	0.03	Asymptotic (-)	<i>P. mariana poorly drained</i>	117	Manitoba, CA
Wirth et al. (2002)	0.02	Asymptotic (ca. 70)	<i>Pinus sylvestris</i>	95	Siberia, RU
Goulden et al. (2011)	0.07	Asymptotic	<i>Picea mariana</i>	154	Manitoba, CA
Larjavaara et al. (2017)	0.10	Linear	Larix mixed	218	Siberia, RU
Trumbore and Harden (1997)	0.12	Asymptotic (-)	<i>P. mariana well drained</i>	117	Manitoba, CA
Andrieux et al. (2018)	0.13	Linear	<i>Picea mariana</i>	300	Quebec, CA
Mack et al. (2021)	0.13	Linear	Mixed	100	Alaska, USA
Mack et al. (2021)	0.14	Linear	Deciduous	100	Alaska, USA
Mack et al. (2021)	0.15	Linear	<i>P. mariana</i>	100	Alaska, USA
Harden et al. (2012)	0.20	Linear	<i>Picea mariana</i>	116	Alaska, USA
Harden et al. (2012)	0.20	Linear	<i>Picea mariana</i>	116	Alaska, USA
Rapalee et al. (1998)	0.28	Asymptotic (-)	<i>P. mariana</i> & <i>P. banksiana</i>	100	Manitoba, CA
Harden et al. (2012)	0.29	Linear	<i>Picea mariana</i>	198	Alaska, USA
Harden et al. (2012)	0.30	Linear	<i>Picea mariana</i>	132	Manitoba, CA
Bill et al. (2023)	0.31	Linear	Mixed (xeric shield)	100	Northwest Territories, CA
Bill et al. (2023)	0.38	Linear	Mixed (mesic shield)	100	Northwest Territories, CA
Bill et al. (2023)	0.44	Linear	Mixed (plains)	100	Northwest Territories, CA
O'Neill et al. (2003)	0.50	Linear	<i>P. mariana</i>	140	Alaska, USA
Lecomte et al. (2006)	0.58	Linear	<i>P. mariana</i>	750	Quebec, CA
Seedre et al. (2014)	1.73	Linear	Mixed	27	Ontario, CA
Median value	0.15			108	
Even-aged management					
Martin et al. (2005)	-0.58	Linear	Mixed	30	Manitoba, CA
Howard et al. (2004)	-0.23	Negative exponential	<i>Pinus banksiana</i>	79	Saskatchewan, CA
Krause (1998)	-0.16	Parabolic	<i>Pinus banksiana</i>	18	New Brunswick, CA
Senez-Gagnon et al. (2018)	-0.02	Linear	<i>Abies balsamea</i>	80	Quebec, CA
Moroni et al. (2010)	0.00	Parabolic	<i>P. mariana</i>	74	Newfoundland, CA
Peltoniemi et al. (2004)	0.05	Linear	<i>Pinus sylvestris</i>	124	Finland
Taylor et al. (2007)	0.05	Hump	<i>Picea rubens</i>	140	Nova Scotia, CA

TABLE 1 (Continued)

Reference	Mg C ha ⁻¹ year ⁻¹	Relationship (inflection)	Species	Time series	Location
Grunzweig et al. (2014)	0.20	Linear	<i>Picea glauca</i>	110	Alaska, US
Lindroos et al. (2022)	0.33	Asymptotic (-)	<i>Picea abies</i>	21	Finland
Lindroos et al. (2022)	0.40	Asymptotic (-)	<i>Pinus sylvestris</i>	21	Finland
Seedre et al. (2014)	0.48	Parabolic	Mixed	27	Ontario, CA
Hagemann et al. (2010)	0.50	Asymptotic (ca. 17)	<i>Picea mariana</i>	ca. 140	Labrador, CA
Strukelj et al. (2015)	0.66	Unknown	<i>Populus tremuloides</i>	9	Quebec, CA
Krause (1998)	0.78	Parabolic	<i>Picea mariana</i>	18	New Brunswick, CA
Martinez-Garcia et al. (2022)	0.80	Asymptotic (ca. 100)	<i>P. abies</i> & <i>P. sylvestris</i>	200	Sweden
Median value	0.20			74	
Meta-analyses					
Palviainen et al. (2020)	0.28	Asymptotic (ca. 80)	Multiple species—Fire	150	Boreal-wide (16)
Pregitzer and Euskirchen (2004)	~0.29	Asymptotic (ca. 71–120)	Multiple species & disturbance types	>200	Boreal-wide (7)

predicted to positively co-vary (Pregitzer & Euskirchen, 2004). This perspective, originating from Odum's theory of ecosystem succession (Odum, 1969), predicts that NPP follows a hump-shaped relationship, whereas heterotrophic respiration is less variable and gradually increases through time as organic matter accumulates. Second, in contrast to this production-focused perspective, emphasis has more recently been placed on the quality of litter inputs. Here, a negative trade-off between plant growth and defense is emphasized, whereby species with highly defended biomass have inherently lower production rates and produce litter inputs that are more recalcitrant (e.g. higher lignin content, C:N ratios and lignin:N ratios; Cornwell et al., 2008; Jonsson & Wardle, 2010). Here, variation in heterotrophic respiration (i.e. decomposition) due to litter quality is emphasized as a strong control on the C accumulation rate. Third, increasing emphasis has been placed on the key role of belowground C inputs (e.g. root turnover and exudation) relative to aboveground inputs in controlling soil C accumulation, as well as on mycelial production and necromass traits of mycorrhizal fungi (Clemmensen et al., 2013; Fernandez & Kennedy, 2015). Each of these aspects of C inputs may influence the trajectory of soil C accumulation following disturbance, as discussed in further detail below.

3.1 | Quantity of carbon input (net primary productivity)

The various components contributing to total forest NPP include the above- and belowground biomass production of trees and understory vegetation, C transferred through herbivory, litter, emission of volatile organic compounds and methane, and exudation from roots allocated to mycorrhizal fungi (Clark et al., 2001; Luysaert et al., 2007). Most commonly, empirical estimates of NPP are limited to the components of above- and belowground tree biomass production (Anderson-Teixeira et al., 2021; Luysaert et al., 2007). In

the currently most comprehensive Global Forest Carbon Database (ForC), mean NPP of mature (i.e. >100 years) boreal forests is 2.7 ± 0.9 Mg C ha⁻¹year⁻¹ ($n=23$; Anderson-Teixeira et al., 2021). Across boreal forests, NPP has been estimated to average (\pm SD) at 2.8 ± 1.6 Mg C ha⁻¹year⁻¹ ($n=7$; Pregitzer & Euskirchen, 2004), 4.2 ± 2.2 Mg C ha⁻¹year⁻¹ ($n=24$; Gower et al., 2001) and 3.7 ± 1.5 Mg C ha⁻¹year⁻¹ ($n=21$; Pappas et al., 2020), with considerable variation between boreal humid evergreen (2.7 Mg C ha⁻¹year⁻¹; $n=38$), semi-arid evergreen (3.3 Mg C ha⁻¹year⁻¹; $n=14$) and semiarid deciduous (5.4 Mg C ha⁻¹year⁻¹; $n=6$) forests (Luysaert et al., 2007). Mean NPP for boreal forests in Siberia is at the lower end with 1.2 Mg C ha⁻¹year⁻¹ ($n=4$; Schulze et al., 1999) compared to 3.6 ± 1.1 Mg C ha⁻¹year⁻¹ ($n=50$; Pechl et al., 2023) and 5.6 ± 1.8 Mg C ha⁻¹year⁻¹ (Zheng et al., 2004) estimated for managed boreal forests in Scandinavia. The largest uncertainty in empirical NPP estimates lie in the challenge of quantifying fine root production (representing about 30%–70% of NPP; Kalyn & Van Rees, 2006; Yuan & Chen, 2010), various other plant C loss components (Clark et al., 2001; Luysaert et al., 2007), and contributions from ground vegetation, which sometimes accounts for over 50% of NPP (Bond-Lamberty et al., 2004b; Gower et al., 2001; Nilsson & Wardle, 2005; Pechl et al., 2022).

Regarding disturbance, estimates of boreal forest NPP ranges from <1.0 Mg C ha⁻¹year⁻¹ soon after stand-replacing disturbance (i.e., via harvest, fire, or wind throw) to peak rates of 6.0 to 9.0 Mg C ha⁻¹year⁻¹ after initial stand development (Anderson-Teixeira et al., 2021; Gower et al., 2001; Luysaert et al., 2007; Pechl et al., 2022; Zheng et al., 2004). While differences in stand development stage (i.e., stand age) is clearly a major driver for the observed range (Anderson-Teixeira et al., 2021; Chen et al., 2002; Goulden et al., 2011; Pechl et al., 2022), climate (Luysaert et al., 2007; Schulze et al., 1999), site fertility (Chen et al., 2002; Schulze et al., 1999; Wirth et al., 2002), and types of tree species (e.g. deciduous vs. coniferous; Gower et al., 2001; Mack et al., 2021) are also important. After a sharp reduction in NPP following stand-replacing

disturbance, a rapid increase in ground vegetation production occurs (Amiro et al., 2003; Peichl et al., 2022), followed by the recovery of tree NPP (Bond-Lamberty et al., 2004b; Goulden et al., 2011; Hicke et al., 2003; Peichl et al., 2022; Wirth et al., 2002). During stand development, NPP has been reported to peak at approximately 50–100 years across different studies (Chen et al., 2002; Goulden et al., 2011; Peichl et al., 2022; Pregitzer & Euskirchen, 2004; Wirth et al., 2002). In older stands (i.e. 150–200 years-old), NPP decreases (Chen et al., 2002; Wirth et al., 2002) but may remain as high as 2.0 Mg C ha⁻¹ year⁻¹ in natural (Bond-Lamberty et al., 2004b; Chen et al., 2002; Goulden et al., 2011; Pregitzer & Euskirchen, 2004) and >3.0 Mg C ha⁻¹ year⁻¹ in managed stands (Peichl et al., 2022). For more productive sites, forest NPP increases rapidly and culminates at an earlier age, and thereafter declines more rapidly (Chen et al., 2002). Many mechanisms have been proposed to explain age-related growth declines in forests (e.g. lower C use efficiency or hydrological limitation), and this notably includes age related declines in N availability in boreal forests (Blasko et al., 2015; DeLuca et al., 2008; Trugman et al., 2016). The hump-shaped temporal NPP pattern can in part explain temporal patterns in soil C accumulation, especially during the first century following disturbance, where a rapid increase in NPP corresponds with a rapid increase in soil C (Table 1; Figure 2).

At present, our knowledge of differences in the NPP dynamics and rates following clear-cutting versus wildfire is limited due to a deficiency of comparative chronosequence studies. Although active stand re-establishment via planting of tree seedlings after clear-cutting could be expected to promote faster NPP recovery rates (Peichl et al., 2023), relatively fast NPP recovery rates following wildfire have also been observed (Hicke et al., 2003; Wirth et al., 2002), possibly due to enhanced soil N availability after burning (DeLuca et al., 2006; Gundale et al., 2005), which sometimes coincides with greater deciduous tree dominance (discussed below). For example, in a study in central Canada, litterfall production was not found to differ between young stands following fire versus logging (Chen et al., 2017). However, the considerable variation within burnt areas due to spatial variability of burning intensity and site conditions complicates such comparisons (Harden et al., 2000; Hicke et al., 2003; Mack et al., 2021; Wang et al., 2001). For instance, for Chinese boreal *Larix* stands, Wang et al. (2001) found that while total NPP did not differ between lightly burned and unburned stands, aboveground NPP of heavily burned stands was up to 92%–95% lower. Further, Mack et al. (2021) showed that severe burning of organic soils shifted tree dominance from slow-growing *Picea mariana* to fast-growing deciduous broadleaf trees in Alaska, which exhibited higher productivity and whole ecosystem C accumulation rates. Further, higher post-fire NPP was reported in wet compared to dry boreal stands in Canada (Bond-Lamberty et al., 2004b), indicating the importance of site characteristics. Recovery of NPP after wildfire can also differ among ecoregions, where climate and soil conditions appear to be important regulators (Amiro et al., 2000, 2003). While it is clear that NPP usually recovers quickly after both wildfire and clear-cutting disturbances, there is a critical need for paired experimental

studies to facilitate direct comparisons of temporal NPP trajectories of wildfire versus management in different environments.

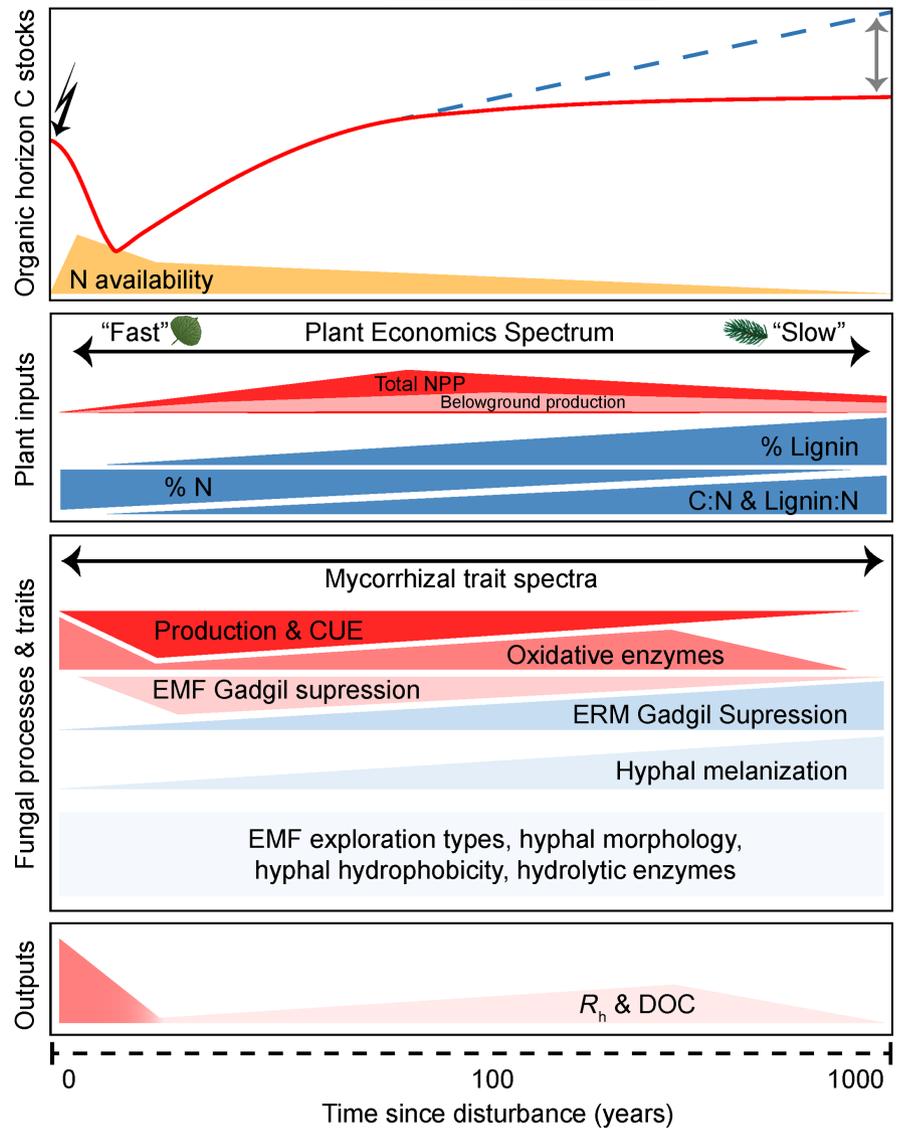
3.2 | Belowground C inputs

As mentioned above, boreal forests allocate as much as 70% of their assimilated C belowground, suggesting that these below-ground inputs are of great importance for soil C accumulation in boreal ecosystems (Ågren et al., 1980; Heinonsalo et al., 2010; Pumpanen et al., 2009; Yuan & Chen, 2010). As such, total belowground C allocation (estimated as the difference between soil C inputs and soil respiration) in boreal conifer forests is around 3 Mg C ha⁻¹ year⁻¹, while total aboveground litterfall is around 0.5 Mg C ha⁻¹ year⁻¹ (Anderson-Teixeira et al., 2021). Live fine roots turnover relatively fast (depending on species), within the range of 0.6 to 1.3 year⁻¹ (Yuan & Chen, 2010). Consequently, to maintain root biomass, a large part of belowground C is directed towards fine roots and associated mycorrhizal fungi, and a smaller portion supports the development of coarse roots. The remaining portion enters the soil in the form of root exudates, which can play a role in soil C accumulation by fostering the development of specific rhizosphere microbial communities but can sometimes also stimulate decomposition of litter and soil organic matter (Chen et al., 2019).

Despite the importance of belowground C inputs to soil C accumulation, how these inputs change through successional time remains little studied (Smyth et al., 2013). In a managed *Pinus sylvestris* chronosequence in Finland, mean annual root production was found to increase with increasing stand age (Makkonen & Helmisaari, 2001). In a Canadian *Picea mariana* chronosequence, fine root production peaked 71 years after fire (Bond-Lamberty et al., 2004a). In another Canadian mixed forest post-fire chronosequence, root production was more than twice as high 48 compared to 232 years post-fire, although these differences were not statistically significant due to very high spatial variability (Finer et al., 1997); whereas, fine root production peaked after 3–11 years in a Canadian mixed-forest post-fire chronosequence, then decreased and remained relatively invariable thereafter (Yuan & Chen, 2012). Differences in sampling depth among studies is a potential source of variation in reported data (Wasyliw & Karst, 2020). Despite the substantial variation among studies, a recent broad meta-analysis by Anderson-Teixeira et al. (2021) concluded that root production generally increased with time in forests up to ca. 100 years age, in line with observed patterns for aboveground biomass growth. Comparable data on root exudates are lacking.

As with other biomass compartments, a key determinant of root contributions to soil C accumulation depend not just on biomass input, but also on the stability of the necromass produced (see “Section 3.3” below). Some studies have found that fine root turnover and necromass production declines in older post-fire stands (Makkonen & Helmisaari, 2001; Yuan & Chen, 2012). In line with this, a long-term chronosequence (ca. 5000 years) in northern Sweden showed that while standing root biomass modestly declined in very

FIGURE 2 A hypothesized depiction of multiple factors controlling the rate and pattern of soil organic horizon C stock accumulation following disturbance in boreal forests, including: net primary productivity (NPP), root production, plant lignin, nitrogen (N), carbon (C) content, and their ratios, N availability, ectomycorrhizal fungi (EMF) production and carbon use efficiency (CUE), oxidative enzymes, Gadgil suppression by EMF and ericoid mycorrhizal fungi (ERM), hyphal melanization, EMF exploration types, hyphal morphology and hydrophobicity, hydrolytic enzymes, heterotrophic respiration, and dissolved organic carbon (DOC) outputs. The red line indicates an asymptotic temporal C accumulation response, whereas the dashed blue line indicates a higher C accumulation trajectory over a longer duration. Controlling factors shaded in red depict factors promote a temporal C accumulation patterns following the red line, whereas factors shaded in blue depict factors that would promote long term C accumulation following the blue line. Shade intensity of each factor indicates the level of certainty and consensus in the literature, with more intense shades indicating greater consensus, and lighter shades indicating more urgent research frontier.



old forest ecosystems, roots and associated fungi contributed more to soil C accumulation in these forests due to slower decomposition of the necromass produced (Clemmensen et al., 2013). Across the few existing studies on fine root biomass and turnover over successional time, there is large variation in tree and understory species composition, type of disturbance, and chronosequence time-span. This, in combination with the high uncertainties inherent in belowground input measurements, make it exceptionally difficult at this point to confidently isolate the influence of various belowground inputs on soil C accumulation.

3.3 | Plant litter quality

Plants vary considerably in their functional traits related to resource acquisition strategies, and the composition of these traits change substantially through forest succession. The primary axis of evolutionary specialization among land plants spans from “acquisitive” or “fast” strategies to “conservative” or “slow” strategies. The former

is characterized by functional traits associated with rapid growth and resource capture (such as high specific leaf area, high leaf N and P), while the latter are characterized by functional traits associated with resource conservation (such as high levels of structural defense; Díaz et al., 2016; Grau-Andres et al., 2022; Reich et al., 1997). Plants with acquisitive traits generally prefer more fertile environments, are more productive, and turn over their tissues faster than do plants with conservative traits (Díaz et al., 2016; Reich et al., 1997). Evidence is also accumulating that plants exhibit some level of trait coordination across the whole plant, such that conservative or acquisitive plants have analogous root, stem, and leaf traits (Weigelt et al., 2021). Functional trait spectra change during forest succession (Harrison & LaForgia, 2019; Lohbeck et al., 2013; Pérez-Ramos et al., 2019; Silva et al., 2015), whereby “fast” strategies usually dominate early in succession when N and light availability is higher, and “slow” strategies gradually become dominant later in succession when nutrient availability declines (Aerts & Chapin, 2000; Bond-Lamberty et al., 2006). This shift in trait spectra during succession can have consequences for decomposition, such

that necromass of early-successional species with acquisitive traits decompose more rapidly, and late-successional conservative species decompose more slowly (Berg et al., 1993; Cornelissen et al., 2004; Cornwell et al., 2008; de la Riva et al., 2019; Freschet et al., 2012; Reich et al., 1997).

Fire severity and frequency serve as important determinants of species-trait transitions. For high-frequency low-severity ground fires, which are typical in Northern Europe and Western Eurasian boreal coniferous forests, tree mortality is often low, and thus changes in forest species composition are more subtle, leaving the quality of litter inputs relatively unchanged between fire intervals. In the case of stand-replacing fire, where mortality is high and a significant portion of the soil organic layer is often consumed, much stronger forest transitions occur, often resulting in deciduous tree dominance early in succession (Mack et al., 2021; Pérez-Izquierdo et al., 2023). Transitions to deciduous species, which exhibit “fast” trait characteristics, have been linked to more rapid recovery of whole ecosystem C stocks, while the impact on soil C recovery remains less clear (Mack et al., 2021). Dominance of “fast” species results in a higher rate of litter production, which may be counteracted by greater decomposability. However, in late successional communities (>100 years), reductions in litter quality (e.g. related to greater abundance of mosses, Ericaceous shrubs, and *Picea* species) could potentially offset the effect that declining NPP may have on soil C, and thereby promote positive soil C accumulation over longer time scales, although this has seldom been tested. In a rare comparison of these two factors, Wardle et al. (2003) and Jonsson and Wardle (2010) used a ca. 5000 year Swedish boreal forest chronosequence to show that a continual decline in NPP was more than offset by a corresponding decline of litter quality and decomposability, leading to a small persistent net positive soil C accumulation rate. These studies therefore suggest that high NPP associated with “fast” species serve as a strong control on the relatively rapid C accumulation observed during the first century of succession, whereas recalcitrant litter traits associated with “slow” species may serve as a stronger control over longer time scales (centuries to millennia).

In managed boreal forests, which typically experience rotation periods of 100 years or less, natural regeneration of deciduous tree species can quickly dominate stands opened up by clear-cutting (Harvey & Bergeron, 1989; Ilintsev et al., 2020), similar to stand replacing wildfire. However, management often prioritizes specific tree species through active planting and multiple thinning events over the stand rotation. Here, the productivity and litter traits of the prioritized tree species have a greater potential to influence soil C accumulation than successional turnover of species through time. Vesterdal et al. (2013) summarized soil C stock data from published boreal and temperate forest common garden experiments that allows direct comparison of effects of different species while holding environmental and historical legacies constant. They found that the total amount of accumulated soil C did not consistently differ among tree species, but deciduous trees tended to accumulate more C in the mineral soil, while evergreen species promoted C accumulation in the organic horizon. Updating the approach of Vesterdal

et al. (2013) for boreal forests specifically, we compiled data from 17 boreal tree species experiments (Table 2; Supporting Information). These studies covered major boreal genera, *Picea*, *Pinus*, *Betula*, and to a lesser extent *Populus* and *Larix*. In contrast to the conclusion by Vesterdal et al. (2013), a majority of these studies showed that *Picea* promoted greater soil C accumulation in both the organic and mineral soil horizons, although with several exceptions. A generally higher C accumulation associated with *Picea* in Table 2 seemingly contradicts the chronosequence study by Mack et al. (2021), where soil C stocks appeared unaffected by dominant tree species, and no clear differences in soil C accumulation trajectories were found between deciduous versus *Picea* successional trajectories. This suggests that species by site fertility interactions are likely important in driving soil C accumulation. More specifically, species with “slow” traits may promote soil C accumulation to a greater extent in lower-fertility environments where they are most competitive.

3.4 | Mycorrhizal mycelial production and necromass

As mycorrhizal fungi have numerous influences on soil C cycling processes in boreal forests, their community compositional dynamics following clear-cutting or wildfire has important implications for understanding soil C stock recovery patterns. Most boreal tree species form symbioses with ectomycorrhizal fungi (EMF), whereas many understory shrubs form symbioses with ericoid mycorrhizal (ERM) fungi. Mycorrhizal fungi are important in regulating the fate of soil C inputs in boreal forests via their mycelial production and necromass stability (Ekblad et al., 2013). Globally, it has been estimated that approximately 7%–10% of NPP supports mycorrhizal fungal growth (Ekblad et al., 2013; Hobbie, 2006; Mäkelä et al., 2022). Peak EMF mycelial production has been found to coincide with canopy closure, after which production declines (Hagenbo et al., 2017). Biomass production of EMF has often been assumed to correlate with mycelial exploration types, which categorizes fungal species according to the presence, length, and branching patterns of hyphae emanating from root tips (Agerer, 2001). Taxa classified as “contact” or “short-distance” exploration types have less visible mycelia emanating from root tips than do those classified as “medium-distance” or “long-distance” exploration types. It is often assumed that long-distance and medium-distance “fringed” exploration types have higher rates of biomass production than do contact or medium distance types (Weigt et al., 2012), but this assumption has been questioned (Jørgensen et al., 2021).

Necromass production and differences in necromass stability among mycorrhizal taxa are important determinants of soil C accumulation. Some EMF fungi produce hydrophobic mycelium, which is considered to promote more stable necromass than hydrophilic mycelium (Ekblad et al., 2013; Rillig et al., 2007). Further, small-diameter hyphae have been found to decompose more slowly than large diameter hyphae (McCormack et al., 2010). Previous work suggests that medium- and long-distance exploration hyphal types are more often

TABLE 2 Summary of studies evaluating tree species effects on soil organic carbon in boreal forests. Three experiment types were considered, common garden (CG), paired stand (PS), and single-tree plot (ST) designs. Genera are ranked according to C stock size in humus and mineral soil. Search methods and references are reported in the [Supporting Information](#).

Reference	Location	Design	Site age (year)	Organic horizon C stock size	Mineral soil C stock size
Smolander and Kitunen (2021)	Finland	CG	45	<i>Picea</i> > <i>Betula</i>	NA
Blasko (2020)	Sweden	CG	63	<i>Pinus</i> > <i>Picea</i>	<i>Pinus</i> = <i>Picea</i>
Segura et al. (2019)	Sweden	CG	51	<i>Betula</i> = <i>Picea</i> = <i>Larix</i> = <i>Pinus</i>	Forest floor and mineral soil together
Olsson et al. (2012)	Finland	CG	79	<i>Picea</i> > <i>Pinus</i> > <i>Betula</i>	Forest floor and mineral soil together
Smolander et al. (2005)	Finland	CG	35	<i>Picea</i> > <i>Betula</i>	NA
Alriksson (1998)	Sweden	CG	27	<i>Betula</i> = <i>Pinus</i> = <i>Larix</i> = <i>Picea</i>	<i>Betula</i> = <i>Pinus</i> = <i>Larix</i> = <i>Picea</i>
Alban (1982)	Minnesota, USA	CG	50–60	<i>Pinus</i> = <i>Picea</i> > <i>Populus</i>	<i>Pinus</i> = <i>Picea</i> > <i>Populus</i>
Paré et al. (2022)	Québec, Canada	PS	50–120	<i>Picea</i> = <i>Abies</i>	<i>Picea</i> = <i>Abies</i>
Kjønaas et al. (2021)	Norway	PS	45–103	<i>Picea</i> > <i>Betula</i>	<i>Picea</i> = <i>Betula</i>
Laganiere et al. (2015)	Ontario, Canada	PS	92	<i>Pinus</i> = <i>Populus</i>	<i>Populus</i> > <i>Pinus</i>
Laganiere et al. (2015)	Québec, Canada	PS	99	<i>Picea</i> > <i>Populus</i>	<i>Picea</i> > <i>Populus</i>
Laganiere et al. (2015)	Québec, Canada	PS	96	<i>Picea</i> > <i>Populus</i>	<i>Picea</i> > <i>Populus</i>
Bjarnadottir (2009)	Iceland	PS		NA	<i>Picea</i> > <i>Pinus</i> > <i>Larix</i>
Ritter (2007)	Iceland	PS	14–97	NA	<i>Betula</i> = <i>Larix</i>
Snorasson et al. (2002)	Iceland	PS	16–54	Very little C stock in humus	<i>Picea</i> > <i>Larix</i> > <i>Betula</i>
Sigurðardóttir (2000)	Iceland	PS	43–65	<i>Pinus</i> > <i>Betula</i> = <i>Larix</i>	<i>Pinus</i> = <i>Betula</i> = <i>Larix</i>
Legaré et al. (2005)	Québec, Canada	ST	139	<i>Picea</i> > <i>Populus</i>	NA

hydrophobic, while contact and short-distance types are more often hydrophilic (Lilleskov et al., 2011). A growing body of evidence also suggests that hyphal content of the pigment melanin plays a central role in necromass stability and soil C accumulation (Fernandez et al., 2016, 2019). Several studies have demonstrated that highly melanized necromass persists longer than less melanized necromass (Certano et al., 2018; Fernandez & Kennedy, 2018). In boreal forests, the widespread ascomycetous EMF species *Cenococcum geophilum* and *Hyaloscypha finlandica*, as well as most ERM, are known to possess high melanin content (Fernandez et al., 2019), and may therefore disproportionately contribute to soil C accumulation.

Potential trait trade-offs across EMF species regarding their mycelial production rates, and necromass stability will influence EMF contribution to soil C following wildfire and harvesting disturbances, but our knowledge regarding the presence or strength of such trade-offs is currently limited (Figure 2). Ectomycorrhizal fungal communities in young secondary forests have low diversity and are dominated by the Atheliaceae family, including the genera *Tylospora*, *Amphinema*, as well as for example *Suillus brevipes* and *Tomentella/Thelephora* species (Kyaschenko et al., 2017; Twieg et al., 2007; Wallander et al., 2010). These “early stage” EMF fungal taxa tend to be more tolerant to high levels of inorganic N (Jørgensen et al., 2024; Lilleskov et al., 2019) with faster mycelial growth (Jørgensen et al., 2023) and higher biomass turnover (Hagenbo et al., 2018) relative to “late stage” taxa. The gradual development of N limitation during stand development appears to favor the genera *Cortinarius* and *Russula*, which

possess key traits (discussed later) for N acquisition in older forests (Hagenbo et al., 2018; Kyaschenko et al., 2017). Shifts in EMF composition toward these late-stage taxa appear to correspond with reduced mycelial production rates, but mycelial biomass is maintained at high levels by slow turnover (Hagenbo et al., 2018). Declining mycelial production and turnover in older N-limited forests may be coordinated with declining needle production and turnover (Reich et al., 2014). Differences in hyphal traits between early and late successional EMF communities (e.g. melanin content, hyphal diameter, hydrophobicity) may influence necromass stability, but data on how these traits change through time are limited.

The effects of wildfire versus clear-cut harvesting on mycelial production and stability remain poorly understood, but differences are likely related to tree and understory plant species composition. Cord-forming EMF species may initially increase with stand age before declining as stands approach old-growth characteristics, and ERM fungi become more dominant (Clemmensen et al., 2015; Fanin et al., 2022). As Ericaceous shrubs become more dominant over time, studies have demonstrated that ERM necromass favors soil C accumulation, in part due to its higher melanin content (Clemmensen et al., 2015). Because broadleaf-dominated boreal forests are less often associated with ericaceous understories than conifer-dominated forests (Hart & Chen, 2008), owing to their “fast” trait characteristics (as previously discussed), severely burned stands that become dominated by broadleaf species may exhibit prolonged shifts toward ERM dominance. In contrast, clear-cut harvesting and

conifer tree planting may favor earlier dominance of Ericaceous understories in some situations, which could result in more stable necromass production via ERM fungi. Understanding the temporal dynamics of fungal necromass production and stability during forest development clearly remains a research frontier.

4 | CARBON OUTPUT

4.1 | Heterotrophic respiration

Total soil respiration (R_s) is typically divided into two main components. The first component consists of autotrophic respiration of belowground plant parts plus associated mycorrhizal fungi (usually referred collectively as autotrophic respiration, R_a , due to impracticality of separating roots and mycorrhizal mycelium). The second component consists of heterotrophic respiration (R_h) of free-living microorganisms that decompose litter and existing soil organic matter. In boreal forests, the ratio of autotrophic to heterotrophic soil respiration can vary widely over the succession of a developing forest (Martinez-Garcia et al., 2022) but has been shown to be nearly even in mid-rotational managed forests (Högberg et al., 2001). Carbon respired through R_a has a very short residence time, and its large signal can obscure measurement of heterotrophic efflux from microbial breakdown of organic matter, which is much more relevant for understanding the dynamics of soil C stock changes through time. Partitioning these different soil CO₂ sources is difficult in practice, and various experimental techniques such as tree girdling (Högberg et al., 2001), trenching, incubations, and ¹⁴C signature analysis have been used to attempt this (e.g. Czimczik et al., 2006). Because it is so difficult to measure, variation in R_h remains one of the most enigmatic controls of soil C stock changes following disturbance. This has led to controversy regarding the degree to which soil C loss following clear-cutting influences the break-even point of net ecosystem production (Lindroth, 2023; Peichl et al., 2023). Further, there are a wide range of environmental controls on R_h , (e.g. temperature, moisture, nutrient availability, substrate chemistry, rate of detrital inputs, and soil community composition; Harmon et al., 2011) that are known to vary from site to site and through time, which can make temporal trends difficult to describe.

In one of the first studies to describe temporal patterns of R_h in boreal forests, Pregitzer and Euskirchen (2004) employed a meta-analysis approach of studies conducted in forests of different ages and disturbance types. While not distinguishing between disturbance types, their meta-analysis indicated that R_h in boreal forests was substantially less variable through time than was NPP, a key finding reinforced by later studies (Peichl et al., 2022; Uri et al., 2022). In a recent comprehensive meta-analysis, Anderson-Teixeira et al. (2021) found no clear change in R_h with stand age up to 100 years. By contrast, Pregitzer and Euskirchen (2004) found that R_h ranged between 1.5 and 3.5 Mg C ha⁻¹, with highest rates observed in the intermediate age class (71–120 years since disturbance), lowest in the oldest age class (>200 years since disturbance),

and intermediate in recently disturbed forests; however, R_h was much less variable than NPP.

There are several reasons to expect that temporal change in R_h may differ in response to fire versus clear-cutting disturbances. While both disturbance types can reduce vegetation cover and thus increase soil temperatures (promoting R_h), they also differ substantially in the amount and quality of soil organic matter available for decomposition. Fire often consumes a substantial portion of surface soil organic matter, leaving behind a smaller C stock for saprotrophic organisms to respire. Further, fire can convert organic matter into pyrogenic C (i.e. “black C”), which is substantially more resistant to decomposition following disturbance. In a Canadian *Pinus banksiana* forest, Santin et al. (2015) estimated that as much as 28% of biomass affected by fire was converted to pyrogenic C. Pyrogenic C stocks have been estimated in the range of 3–10 Mg C ha⁻¹ (Ohlson et al., 2009; Preston et al., 2017; Santin et al., 2015), which, due to its recalcitrance, can slow down site level R_h rates. Numerous studies have demonstrated short-term reductions in R_s after wildfire, with high-intensity or high-frequency fires causing more severe reductions, coinciding with tree death, loss of soil organic matter, and production of pyrogenic C (Kelly et al., 2021; Sawamoto et al., 2000; Singh et al., 2008). Many such studies have not actually determined the contribution of R_h to R_s following fire; however, those that have generally showed reduced R_h (Gui et al., 2023; Song et al., 2019). Utilizing longer-term chronosequences, Bond-Lamberty et al. (2004a) showed that R_h decreased sharply 7 years after wildfire in a well-drained forest chronosequence, but increased in a poorly drained chronosequence, indicating that the short-term R_h response can be influenced by site characteristics. However, over a longer duration, they found that both chronosequences exhibited relatively constant R_h . Similarly, using a long-term Canadian wildfire chronosequence, Goulden et al. (2011) found that R_h was relatively invariable through time, even as NPP strongly recovered. In another chronosequence in central Canada, Czimczik et al. (2006) found that R_h remained relatively low for decades after fire (<20% of R_s), but then increased substantially in mid-successional stands (>40 years following fire). Collectively, these studies suggest that fire initially reduces R_h , which eventually rebounds, and then remains relatively invariable over longer time scales in the absence of another disturbance.

In contrast to fire, clear-cutting typically does not involve direct removal of soil C, and instead often involves a large input of fresh logging residues (e.g. branches, leaves, and dead roots) that have the potential to stimulate short term R_h . Further, clear-cutting eliminates mycorrhizal fungi through loss of host trees, which can further impact decomposition (discussed in the following section). It is clear that clear-cut forests act as C sources for years to decades following cutting due to R_h exceeding NPP; however, the issue of whether R_h increases or remains constant following clear-cutting remains unresolved, even though it has important implications for understanding net forest C balance and is the source of much debate (Lindroth, 2023; Peichl et al., 2023). Few studies have actually partitioned R_h along post-clear-cut chronosequences. Some

studies employing chronosequence approaches have shown that R_h does in fact temporarily increase following clear-cutting (Howard et al., 2004; Uri et al., 2022), while other studies have shown that R_h is not markedly stimulated by clear-cutting (Mäkiranata et al., 2010; Martinez-Garcia et al., 2022).

In addition to the common practice of clear-cutting in boreal forests, even-aged management systems typically include some form of mechanical scarification or “site preparation” to improve regeneration of seedlings (Figure 1). This can include practices such as disc trenching, mounding, soil inversion, or harrowing, which serve as major disturbances to soils (Cardoso et al., 2020). The effect of these practices on R_h or decomposition are highly variable, with some studies reporting significant reductions (Maillard et al., 2010; Simola, 2018; Strömngren et al., 2017), some indicating minimal or no impact on soil C stocks (Mjöfors et al., 2015, 2017; Strömngren et al., 2013), and yet others indicating that decomposition accelerates (Lundmark-Thelin & Johansson, 1997; Mallik & Hu, 1997; Mjöfors et al., 2015). Given the highly variable patterns of R_h and decomposition following clear-cutting and site preparation, and substantial debate surrounding this topic, a clear research priority is to determine fundamental factors that explain temporal variation in R_h among studies, such as climate, hydrology, or fertility.

4.2 | Influence of mycorrhiza on heterotrophic respiration

After stand death, EMF generally disappear, regardless of whether the disturbance agent is forestry (Kyaschenko et al., 2017), severe fire (Pérez-Izquierdo et al., 2023) or insect outbreaks (Stursová et al., 2014). This loss may be partially mitigated by tree retention in managed stands (Sterkenburg et al., 2019) or by tree survival following fire (Pérez-Izquierdo et al., 2021). Because symbiotic fungi receive C from host plants, they are generally expected to have a more positive influence on soil C build-up than saprotrophs, which instead rely on organic matter breakdown as their energy source. However, root-associated fungi not only contribute to organic matter accumulation through their own necromass production, but can also influence existing soil C and nutrient dynamics through two opposing mechanisms (Frey, 2019), specifically by acting as strong competitors for soil N, or via production of oxidative enzymes that can destabilize soil organic matter.

It is recognized that EMF are strong competitors for nutrients by efficiently occupying soil space (Bödeker et al., 2016), and by selectively removing and immobilizing N from soil organic matter (Kyaschenko et al., 2019; Näsholm et al., 2013). As a result, they restrict N availability for other organisms, including saprotrophic Agaricomycetes (Sterkenburg et al., 2018), thus limiting saprotrophic activity. This phenomenon is referred to as the “Gadgil effect” (Gadgil & Gadgil, 1971). Direct measurements in boreal forests have found that a significant but small Gadgil effect impairs litter decomposition. Sterkenburg et al. (2018) showed that *Pinus* litter decomposition was

11% slower when mycorrhizal fungi and roots were present, compared to when they were excluded. Likewise, Maaroufi et al. (2019) showed an approximately 10% decrease in litter decomposition in the presence of mycorrhizal roots compared to inside trenched plots that lacked roots, and that trenching significantly reduced N export from decomposing litter substrates. Given the control that EMF have on saprotrophic activity, disturbance-induced death of EMF is usually followed by proliferation of opportunistic fungi, which decompose recently dead roots, mycorrhizal mycelium, and soil C (Kim et al., 2021; Kohout et al., 2018; Lindahl et al., 2010; Sterkenburg et al., 2018) (Kim et al., 2021) (Kim et al., 2021) (Kim et al., 2021) (Kim et al., 2021). These opportunistic saprotrophs appear to have a low capacity to decompose recalcitrant C pools, but nonetheless may contribute modestly to increased R_h following disturbance (Kyaschenko et al., 2017).

In addition to the “Gadgil effect” that impairs organic matter decomposition, some EMF taxa have the ability to produce enzymes that carry out extracellular oxidation. Pronounced capacity to decompose large aromatic complexes, such as lignin, has evolved exclusively in the fungal class Agaricomycetes (Floudas et al., 2012). A majority of EMF belong to the Agaricomycetes, where most EMF lineages have lost their capacity to decompose lignocellulose, and instead obtain more easily available sugars directly from their host trees (Kohler et al., 2015). However, some EMF genera have retained their ancestral capacity for oxidative depolymerization of aromatic soil compounds (Bödeker et al., 2014; Nicolás et al., 2019). These may be referred to as “EMF decomposers”, as they combine oxidative decomposition with symbiotic C acquisition. They generally lack enzymes to hydrolyse cellulose and primarily forage organic matter for N rather than metabolically useful C (Forsmark et al., 2024; Lindahl & Tunlid, 2015; Maillard et al., 2023).

Ectomycorrhizal decomposers in the species-rich genus *Cortinarius* are a diverse and often dominant group in older N poor forests (>50 years) where they appear to be actively involved in organic matter decomposition (Bödeker et al., 2014). The presence of certain common *Cortinarius* species has been linked to a 33% reduction in local C storage in the organic horizon (Lindahl et al., 2021). Ectomycorrhizal fungal communities substantially change following disturbance, and remain altered for at least 50 years after clear-cutting (Kyaschenko et al., 2017; Varenus et al., 2017). Many *Cortinarius* species in particular are sensitive to forestry-related disturbance (Kyaschenko et al., 2017; Twieg et al., 2007; Varenus et al., 2017), potentially due to their slow mycelial growth and high demand of host C (Jørgensen et al., 2021). Their decline after disturbance has been linked to an almost complete loss of oxidative enzyme activity in the more recalcitrant deeper parts of the organic horizon (Pérez-Izquierdo et al., 2021; Sterkenburg et al., 2018). Thus, whereas losses of EMF after disturbance may stimulate short-term (0–10 years) C losses via the Gadgil effect, rapid growth of EMF (Hagenbo et al., 2017; Wallander et al., 2010) may hamper decomposition in developing stands (10–50 years old) if the community is depleted in species with decomposer capacity (Kyaschenko et al., 2017). At later successional stages (>50 years), proliferation

TABLE 3 A description of major fungal groups, and their capacity to decompose organic matter, suppress saprotrophs (i.e. Gadgil effect), and their expected net effect on soil organic matter accumulation.

Description	Principal taxonomy	Root association	Decomposer capacity	Gadgil effect	Effect on organic matter
Ericoid mycorrhizal fungi and other root-associates	Ascomycota	Symbiotic, melanin rich	Hydrolytic	Strong	Strongly positive
Ectomycorrhizal non-decomposers; early stage	Agaricomycetes	Symbiotic	Low	Strong	Positive
Opportunistic moulds and yeasts	Ascomycota and others	Free-living	Hydrolytic		Neutral
Ectomycorrhizal decomposers; late stage	Agaricomycetes (e.g. <i>Cortinarius</i>)	Symbiotic	Oxidative	Weak	Negative
Saprotrophic Agaricomycetes	Agaricomycetes	Free-living	Hydrolytic and oxidative		Strongly negative

of EMF decomposers may maintain organic matter turnover and nutrient cycling under intensifying N-limitation (Forsmark et al., 2020; Lindahl et al., 2021; Figure 2; Table 3).

In a longer time perspective (>100 year time-scales), changing vegetation composition and increasing N-limitation (Gundale et al., 2011) are commonly linked to increasing abundance of root-associated ascomycetes, including those that form mycorrhizal association with ericoid shrubs (Clemmensen et al., 2015). Ericoid roots and their associated mycorrhizal fungi are efficient in immobilizing N (Mielke et al., 2022), which may lead to competitive suppression of both EMF and saprotrophic decomposers, analogous to Gadgil suppression for EMF (Fanin et al., 2022). Although ERM have a wide repertoire of hydrolytic enzymes that should provide them some flexibility to persist as saprotrophs, they lack the oxidative systems required to be efficient decomposers (Martino et al., 2018). Low activity of EMF decomposers relative to ERM can lead to continued long-term soil C accumulation (Ward et al., 2022). These studies indicate that the trajectory of soil C accumulation is influenced by the shifting balance between fungal functional groups during succession, with sequential dominance of saprotrophs (ca. 0–15 years), EMF taxa incapable of decomposition (ca. 15–50 years), EMF decomposers (ca. 50–100+ years), and finally ericoid dominance (100+ years; Figure 2; Table 3).

4.3 | Dissolved organic carbon

Exports of dissolved organic carbon (DOC) from boreal soils are generally considered small compared to heterotrophic respiration fluxes. For example, a recent C budget in a boreal forest in northern Sweden found negligible DOC in lysimeters (Marshall et al., 2023). Further, in three 40-year old *Picea abies* stands in Sweden, 95% of the DOC flux from the organic horizon to the mineral layer (9.3 to 28 g C m⁻² year⁻¹) was captured through sorption in the top 50 cm of the mineral soil (Kleja et al., 2008). Since there are a variety of methods for measuring DOC fluxes, such as lysimeters and sampling wells, and also variation among studies in which soil layers and depths are measured, direct comparison among studies and

models predicting DOC pools and fluxes can be challenging (e.g. Kleja et al., 2008; Neff & Asner, 2001). Nevertheless, there is an increasing amount of literature highlighting the importance of including DOC export in boreal C budgets (Cole et al., 2007; Öquist et al., 2014; Regnier et al., 2013). For example, a recent global and biome level modelling study by Nakhavali et al. (2021) estimated that of the total net ecosystem production of boreal forests (0.23 Pg C year⁻¹), approximately 10.4% is lost through DOC export, suggesting that DOC is not a trivial flux that can be overlooked. Further, it is now well documented that DOC exports in boreal streams has been steadily increasing over decades (leading to “stream brownification”), suggesting these exports are becoming increasingly important (e.g. Fork et al., 2020; Kritzberg et al., 2020).

The effect of disturbances such as wildfire and clear-cutting can have varying and sometimes large impacts on DOC outputs from terrestrial boreal forest systems. For example, immediate effects of wildfire on DOC concentrations in stream water can vary greatly, and be both positive, negative, or neutral (see reviews by Betts & Jones, 2009; Granath et al., 2021; Rodríguez-Cardona et al., 2020; Smith et al., 2011). In contrast to fire, DOC exports directly following clear-cutting are more consistently reported to increase (see review by Kreuzweiser et al., 2008). For example, in *Picea abies* forests in Sweden, DOC in headwater streams has been shown to increase immediately after clear-cutting (Schelker et al., 2012), resulting in a 70% increase in terrestrial DOC exports (Laudon et al., 2009). France et al. (2000) studied 116 lakes across Canada and found that DOC concentrations increased in relation to past disturbances (4–13 years prior), including forest fire and partial and full forest harvesting, with the greatest effects following clear-cutting. Following this increase immediately after clear-cutting, several studies have suggested that DOC exports decrease during initial stand development. For example, Clarke et al. (2007) showed that DOC concentrations beneath the organic horizon decreased to a minimum 10–30 years after harvest, when stand development is very rapid. Further, Fork et al. (2020) suggested that older conifer forests in northern Sweden are a relatively large source of DOC exports to streams.

While there is clearly a scarcity of studies that allow thorough evaluation of how time since disturbance in natural versus managed

boreal forest systems influences DOC outputs, available literature suggests that DOC exports are highest directly after clear-cutting, and potentially also later in forest succession as forests reach maturity. Factors affecting temporal change in DOC export may include precipitation, changing NPP and soil respiration (Pumpanen et al., 2014; Zhu et al., 2022), and changes in NPP and soil respiration. Further, mycorrhizal processes discussed in the previous section may play an important role on DOC production in boreal forests. Specifically, the higher oxidative activities associated with saprotrophs early in succession (i.e. due to the loss of Gadgil suppression), as well as the higher oxidative enzyme activities associated with EMF decomposers later in succession, could help to explain patterns of DOC production and export during succession (Figure 2). Such relationships, while currently speculative, may not only be useful to understand patterns of soil C accumulation but also boreal stream-water brownification trends.

5 | CONCLUSIONS

Soil C accumulation in boreal forests is highly dynamic following disturbance, with evidence suggesting that asymptotic relationships are not necessarily universal, but nonetheless appear common. Our literature search also highlighted that soil C accumulation data from other types of disturbances (e.g. insect outbreaks) are urgently needed to complement the larger body of literature from chronosequences after wildfire and clear-cutting. Our review also highlights several key drivers of these temporal patterns. High rates of soil C accumulation early in succession appear to be driven by high NPP, mycorrhizal mycelial production, associated Gadgil suppression of saprotrophs, and the disappearance of disturbance-sensitive mycorrhizal decomposers. As forests mature, N availability declines, and the abundance of EMF decomposers increases, which together act to slow C accumulation rates. However, the soil C recovery dynamics of mature forests can depend on the balance between EMF decomposers, which promote carbon loss, versus key traits associated with ericaceous shrubs that promote C accumulation. Our review suggests that soil communities dominated by EMF decomposers will greatly limit C accumulation, whereas communities dominated by ERM will promote long-term soil C accumulation due to their highly melanized hyphae, and their suppression of saprotrophic and EMF decomposers.

Further, some key differences in soil C development after fire and clear-cutting are clear. Firstly, while fire is generally characterized by high loss rates during the actual disturbance, followed by low short-term heterotrophic respiration (R_h), clear-cutting sometimes appears to promote early successional (<10 years) soil C losses in some forests via higher R_h . However, the magnitude and consistency of this response appears to be highly variable among studies. Over longer time scales, median C accumulation rates appears to be relatively similar between these disturbance types (Table 1). Our review also identified major knowledge gaps regarding the biological controls on soil C accumulation following

disturbance (Figure 2). Notably, while studies measuring total soil respiration (R_s) are numerous, few studies have directly compared the short- and long-term response of R_h to fire and management. In particular, there is a need for robust temporal data on the contribution of R_h to net ecosystem production, to better inform ongoing scientific and policy debate about C balances following clear-cutting. Regardless of these knowledge gaps, the temporal pattern of soil C accumulation has implications for understanding the importance of disturbance intervals for the landscape-level soil C balance (Flannigan et al., 2009). Our literature search implies that shortening of disturbance intervals to under 100 years may result in a reduction in landscape-level soil organic C stocks, because soil C accumulation has not yet reached an asymptotic inflection point by that time. While important for all disturbance types, the consequence of shortened disturbance intervals may be especially important when disturbance causes severe initial soil carbon losses, for example in response to severe wildfire or specific management practices (e.g. organic horizon removal).

Finally, while it is clear that soil fungal communities can change substantially during stand development, much remains unknown about how relationships and trade-offs between key fungal traits (e.g. mycorrhizal exploration types, hyphal morphology, melanization, necromass stability and decomposer capacities) shift as fungal communities change. Further, the competitive controls between EMF decomposers versus ERM are crucial for understanding long-term soil C accumulation rates with increasing time since disturbance, given that the literature currently emphasizes the C destabilizing and stabilizing mechanisms of these functional group, respectively. An improved understanding of these key frontiers will facilitate better representation of boreal forest C dynamics in soil organic C and Earth system models as well as guide land use decisions. This is urgently needed given the clear role of boreal soils in the global C cycle, and the changes they are experiencing from natural and anthropogenic disturbance.

AUTHOR CONTRIBUTIONS

Michael J. Gundale: Writing – review and editing. **E. Petter Axelsson:** Writing – review and editing. **Vincent Buness:** Writing – review and editing. **Timon Callebaut:** Writing – review and editing. **Thomas H. DeLuca:** Writing – review and editing. **Stefan F. Hupperts:** Writing – review and editing. **Theresa S. Ibáñez:** Writing – review and editing. **Daniel B. Metcalfe:** Writing – review and editing. **Marie-Charlotte Nilsson:** Writing – review and editing. **Matthias Pechl:** Writing – review and editing. **Clydecia M. Spitzer:** Writing – review and editing. **Zsofia R. Stangl:** Writing – review and editing. **Joachim Strengbom:** Writing – review and editing. **Maja K. Sundqvist:** Writing – review and editing. **David A. Wardle:** Writing – review and editing. **Björn D. Lindahl:** Writing – review and editing.

ACKNOWLEDGEMENTS

This project was initiated from research grants awarded to MJG (Project 2021-02116) and BL (Project 2021-02121) by Swedish FORMAS. All authors contributed to the ideas and development of

the manuscript. We thank two reviewers for constructive feedback on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Michael J. Gundale  <https://orcid.org/0000-0003-2447-609X>
 E. Petter Axelsson  <https://orcid.org/0000-0002-0906-8365>
 Vincent Buness  <https://orcid.org/0000-0003-0428-2669>
 Timon Callebaut  <https://orcid.org/0009-0008-3161-1855>
 Thomas H. DeLuca  <https://orcid.org/0000-0003-1561-9597>
 Stefan F. Hupperts  <https://orcid.org/0000-0002-9498-5183>
 Theresa S. Ibáñez  <https://orcid.org/0000-0003-2459-5945>
 Daniel B. Metcalfe  <https://orcid.org/0000-0001-8325-9269>
 Marie-Charlotte Nilsson  <https://orcid.org/0000-0002-9254-2223>
 Matthias Peichl  <https://orcid.org/0000-0002-9940-5846>
 Clydecia M. Spitzer  <https://orcid.org/0000-0002-0766-4518>
 Zsófia R. Stangl  <https://orcid.org/0000-0002-0119-747X>
 Joachim Strengbom  <https://orcid.org/0000-0002-1720-5016>
 Maja K. Sundqvist  <https://orcid.org/0000-0001-5947-839X>
 David A. Wardle  <https://orcid.org/0000-0002-0476-7335>
 Björn D. Lindahl  <https://orcid.org/0000-0002-3384-4547>

REFERENCES

- Aerts, R., & Chapin, F. S. (2000). The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. In A. H. Fitter & D. G. Raffaelli (Eds.), *Advances in ecological research* (Vol. 30, pp. 1–67). Elsevier.
- Agerer, R. (2001). Exploration types of ectomycorrhizae—A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. *Mycorrhiza*, 11, 107–114.
- Ågren, G. I., Axelsson, B., Flower-Ellis, J. G. K., Linder, S., Persson, H., Staaf, H., & Troeng, E. (1980). Annual Carbon Budget for a Young Scots Pine. *Ecological Bulletins*, 32, 307–313.
- Amiro, B. D., Chen, J. M., & Liu, J. (2000). Net primary productivity following forest fire for Canadian ecoregions. *Canadian Journal of Forest Research*, 30, 939–947.
- Amiro, B. D., MacPherson, J. I., Desjardins, R. L., Chen, J. M., & Liu, J. (2003). Post-fire carbon dioxide fluxes in the western Canadian boreal forest: Evidence from towers, aircraft and remote sensing. *Agricultural and Forest Meteorology*, 115, 91–107.
- Anderson, J. M. (1991). The effects of climate change on decomposition processes in grassland and coniferous forests. *Ecological Applications*, 1, 326–347.
- Anderson-Teixeira, K. J., Herrmann, V., Morgan, R. B., Bond-Lamberty, B., Cook-Patton, S. C., Ferson, A. E., Muller-Landau, H. C., & Wang, M. M. H. (2021). Carbon cycling in mature and regrowth forests globally. *Environmental Research Letters*, 16(5), 053009. <https://doi.org/10.1088/1748-9326/abed01>
- Balshi, M. S., McGuire, A. D., Duffy, P., Flannigan, M., Walsh, J., & Melillo, J. (2009). Assessing the response of area burned to changing climate in western boreal North America using a Multivariate Adaptive Regression Splines (MARS) approach. *Global Change Biology*, 15, 578–600.
- Bellassen, V., & Luyssaert, S. (2014). Managing forests in uncertain times. *Nature*, 506, 153–155.
- Berg, B., Berg, M., Bottner, P., Box, E., Breymeyer, A., De Anta, R. C., Couteaux, M., Escudero, A., Gallardo, A., & Kratz, W. (1993). Litter mass loss rates in pine forests of Europe and Eastern United States: Some relationships with climate and litter quality. *Biogeochemistry*, 20, 127–159.
- Betts, E. F., & Jones, J. B. (2009). Impact of wildfire on stream nutrient chemistry and ecosystem metabolism in boreal Forest catchments of interior Alaska. *Arctic Antarctic and Alpine Research*, 41, 407–417.
- Bill, K. E., Dieleman, C. M., Baltzer, J. L., Degré-Timmons, G., Mack, M. C., Day, N. J., Cumming, S. G., Walker, X. J., & Turetsky, M. R. (2023). Post-fire recovery of soil organic layer carbon in Canadian Boreal Forests. *Ecosystems*, 26, 1623–1639. <https://doi.org/10.1007/s10021-023-00854-0>
- Blasko, R., Bach, L. H., Yarwood, S. A., Trumbore, S. E., Högberg, P., & Högberg, M. N. (2015). Shifts in soil microbial community structure, nitrogen cycling and the concomitant declining N availability in ageing primary boreal forest ecosystems. *Soil Biology & Biochemistry*, 91, 200–211.
- Blaško, R., Forsmark, B., Gundale, M. J., Lundmark, T., & Nordin, A. (2020). Impacts of tree species identity and species mixing on ecosystem carbon and nitrogen stocks in a boreal forest. *Forest Ecology and Management*, 458, 117783. <https://doi.org/10.1016/j.foreco.2019.117783>
- Bödeker, I. T. M., Clemmensen, K. E., de Boer, W., Martin, F., Olson, A., & Lindahl, B. D. (2014). Ectomycorrhizal Cortinari species participate in enzymatic oxidation of humus in northern forest ecosystems. *New Phytologist*, 203, 245–256.
- Bödeker, I. T. M., Lindahl, B. D., Olson, Å., & Clemmensen, K. E. (2016). Mycorrhizal and saprotrophic fungal guilds compete for the same organic substrates but affect decomposition differently. *Functional Ecology*, 30, 1967–1978.
- Bond-Lamberty, B., Gower, S. T., Wang, C., Cyr, P., & Veldhuis, H. (2006). Nitrogen dynamics of a boreal black spruce wildfire chronosequence. *Biogeochemistry*, 81, 1–16.
- Bond-Lamberty, B., Wang, C. K., & Gower, S. T. (2004a). Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence. *Tree Physiology*, 24, 1387–1395.
- Bond-Lamberty, B., Wang, C. K., & Gower, S. T. (2004b). Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. *Global Change Biology*, 10, 473–487.
- Bradshaw, C. J. A., & Warkentin, I. G. (2015). Global estimates of boreal forest carbon stocks and flux. *Global and Planetary Change*, 128, 24–30.
- Cardoso, J. C., Burton, P. J., & Elkin, C. M. (2020). A disturbance ecology perspective on silvicultural site preparation. *Forests*, 11, 1278. <https://doi.org/10.3390/f11121278>
- Certano, A. K., Fernandez, C. W., Heckman, K. A., & Kennedy, P. G. (2018). The afterlife effects of fungal morphology: Contrasting decomposition rates between diffuse and rhizomorphic necromass. *Soil Biology & Biochemistry*, 126, 76–81.
- Chen, H. Y. H., Brant, A. N., Seedre, M., Brassard, B. W., & Taylor, A. R. (2017). The contribution of litterfall to net primary production during secondary succession in the boreal forest. *Ecosystems*, 20, 830–844.
- Chen, L. Y., Liu, L., Qin, S. Q., Yang, G. B., Fang, K., Zhu, B., Kuzyakov, Y., Chen, P. D., Xu, Y. P., & Yang, Y. H. (2019). Regulation of priming effect by soil organic matter stability over a broad geographic scale. *Nature Communications*, 10, 5112. <https://doi.org/10.1038/s41467-019-13119-z>
- Chen, W. J., Chen, J. M., Price, D. T., & Cihlar, J. (2002). Effects of stand age on net primary productivity of boreal black spruce

- forests in Ontario, Canada. *Canadian Journal of Forest Research*, 32, 833–842.
- Clark, D. A., Brown, S., Kicklighter, D. W., Chambers, J. Q., Thomlinson, J. R., & Ni, J. (2001). Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, 11, 356–370.
- Clarke, N., Wu, Y. J., & Strand, L. T. (2007). Dissolved organic carbon concentrations in four Norway spruce stands of different ages. *Plant and Soil*, 299, 275–285.
- Clemmensen, K. E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R. D., Wardle, D. A., & Lindahl, B. D. (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science*, 339, 1615–1618.
- Clemmensen, K. E., Finlay, R. D., Dahlberg, A., Stenlid, J., Wardle, D. A., & Lindahl, B. D. (2015). Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. *New Phytologist*, 205, 1525–1536.
- Cole, J. J., Prairie, Y. T., Caraco, N. F., McDowell, W. H., Tranvik, L. J., Striegl, R. G., Duarte, C. M., Kortelainen, P., Downing, J. A., Middelburg, J. J., & Melack, J. (2007). Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. *Ecosystems*, 10, 171–184.
- Cornelissen, J. H. C., Quedsted, H., Gwynn-Jones, D., Van Logtestijn, R., De Beus, M., Kondratyuk, A., Callaghan, T. V., & Aerts, R. (2004). Leaf digestibility and litter decomposability are related in a wide range of subarctic plant species and types. *Functional Ecology*, 18, 779–786.
- Cornwell, W. K., Cornelissen, J. H., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quedsted, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., ... Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, 11, 1065–1071.
- Czimczik, C. I., Trumbore, S. E., Carbone, M. S., & Winston, G. C. (2006). Changing sources of soil respiration with time since fire in a boreal forest. *Global Change Biology*, 12, 957–971.
- de Groot, W. J., Flannigan, M. D., & Cantin, A. S. (2013). Climate change impacts on future boreal fire regimes. *Forest Ecology and Management*, 294, 35–44.
- de la Riva, E. G., Prieto, I., & Villar, R. (2019). The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. *Plant and Soil*, 435, 353–366.
- DeLuca, T. H., & Boisvenue, C. (2012). Boreal forest soil carbon: Distribution, function and modelling. *Forestry*, 85, 161–184.
- DeLuca, T. H., MacKenzie, M. D., Gundale, M. J., & Holben, W. E. (2006). Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Science Society of America Journal*, 70, 448–453.
- DeLuca, T. H., Zackrisson, O., Gundale, M. J., & Nilsson, M. C. (2008). Ecosystem feedbacks and nitrogen fixation in boreal forests. *Science*, 320, 1181.
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A. T., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167.
- Ekblad, A., Wallander, H., Godbold, D. L., Cruz, C., Johnson, D., Baldrian, P., Björk, R. G., Epron, D., Kieliszewska-Rokicka, B., Kjeller, R., Kraigher, H., Matzner, E., Neumann, J., & Plassard, C. (2013). The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: Role in carbon cycling. *Plant and Soil*, 366, 1–27.
- Fanin, N., Clemmensen, K. E., Lindahl, B. D., Farrell, M., Nilsson, M. C., Gundale, M. J., Kardol, P., & Wardle, D. A. (2022). Ericoid shrubs shape fungal communities and suppress organic matter decomposition in boreal forests. *New Phytologist*, 236, 684–697.
- Fernandez, C. W., Heckman, K., Kolka, R., & Kennedy, P. G. (2019). Melanin mitigates the accelerated decay of mycorrhizal necromass with peatland warming. *Ecology Letters*, 22, 498–505.
- Fernandez, C. W., & Kennedy, P. G. (2015). Moving beyond the black-box: Fungal traits, community structure, and carbon sequestration in forest soils. *New Phytologist*, 205, 1378–1380.
- Fernandez, C. W., & Kennedy, P. G. (2018). Melanization of mycorrhizal fungal necromass structures microbial decomposer communities. *Journal of Ecology*, 106, 468–479.
- Fernandez, C. W., Langley, J. A., Chapman, S., McCormack, M. L., & Koide, R. T. (2016). The decomposition of ectomycorrhizal fungal necromass. *Soil Biology & Biochemistry*, 93, 38–49.
- Finer, L., Messier, C., & De Grandpre, L. (1997). Fine-root dynamics in mixed boreal conifer – Broad-leaved forest stands at different successional stages after fire. *Canadian Journal of Forest Research*, 27, 304–314.
- Flannigan, M., Stocks, B., Turetsky, M., & Wotton, M. (2009). Impacts of climate change on fire activity and fire management in the circum-boreal forest. *Global Change Biology*, 15, 549–560.
- Floudas, D., Binder, M., Riley, R., Barry, K., Blanchette, R. A., Henrissat, B., Martínez, A. T., Otillar, R., Spatafora, J. W., Yadav, J. S., Aerts, A., Benoit, I., Boyd, A., Carlson, A., Copeland, A., Coutinho, P. M., de Vries, R. P., Ferreira, P., Findley, K., ... Hobbie, D. S. (2012). The Paleozoic origin of enzymatic lignin decomposition reconstructed from 31 fungal genomes. *Science*, 336, 1715–1719.
- Fork, M. L., Sponseller, R. A., & Laudon, H. (2020). Changing source-transport dynamics drive differential browning trends in a boreal stream network. *Water Resources Research*, 56, e2019WR026336. <https://doi.org/10.1029/2019WR026336>
- Forsmark, B., Bizjak, T., Nordin, A., Rosenstock, N. P., Wallander, H., & Gundale, M. J. (2024). Shifts in microbial community composition and metabolism correspond with rapid soil carbon accumulation in response to 20 years of simulated nitrogen deposition. *Science of the Total Environment*, 918, 170741.
- Forsmark, B., Nordin, A., Maaroufi, N. I., Lundmark, T., & Gundale, M. J. (2020). Low and high nitrogen deposition rates in northern coniferous forests have different impacts on aboveground litter production, soil respiration, and soil carbon Stocks. *Ecosystems*, 23, 1423–1436.
- France, R., Steedman, R., Lehmann, R., & Peters, R. (2000). Landscape modification of DOC concentration in boreal lakes: Implications for UV-B Sensitivity. *Water, Air, and Soil Pollution*, 122, 153–162.
- Freschet, G. T., Aerts, R., & Cornelissen, J. H. C. (2012). A plant economics spectrum of litter decomposability. *Functional Ecology*, 26, 56–65.
- Frey, S. D. (2019). Mycorrhizal fungi as mediators of soil organic matter dynamics. *Annual review of ecology, evolution, and systematics*, 50, 237–259.
- Gadgil, R. L., & Gadgil, P. D. (1971). Mycorrhiza and litter decomposition. *Nature*, 233, 133.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. (2015). Boreal forest health and global change. *Science*, 349, 819–822.
- Goulden, M. L., McMillan, A. M. S., Winston, G. C., Rocha, A. V., Manies, K. L., Harden, J. W., & Bond-Lamberty, B. P. (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, 17(2), 855–871. <https://doi.org/10.1111/j.1365-2486.2010.02274.x>
- Gower, S. T., Krankina, O., Olson, R. J., Apps, M., Linder, S., & Wang, C. (2001). Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecological Applications*, 11, 1395–1411.
- Granath, G., Evans, C. D., Strengbom, J., Fölster, J., Grelle, A., Strömqvist, J., & Köhler, S. J. (2021). The impact of wildfire on biogeochemical fluxes and water quality in boreal catchments. *Biogeosciences*, 18, 3243–3261.
- Grau-Andres, R., Kardol, P., & Gundale, M. (2022). Trait coordination in boreal mosses reveals a bryophyte economics spectrum. *Dryad*.

- Gui, H. R., Wang, J. L., Hu, M. J., Zhou, Z. X., & Wan, S. Q. (2023). Impacts of fire on soil respiration and its components: a global meta-analysis. *Agricultural and Forest Meteorology*, 336, 109496.
- Gundale, M. J., DeLuca, T. H., Fiedler, C. E., Ramsey, P. W., Harrington, M. G., & Gannon, J. E. (2005). Restoration treatments in a Montana ponderosa pine forest: Effects on soil physical, chemical and biological properties. *Forest Ecology and Management*, 213, 25–38.
- Gundale, M. J., Fajardo, A., Lucas, R. W., Nilsson, M. C., & Wardle, D. A. (2011). Resource heterogeneity does not explain the diversity-productivity relationship across a boreal island fertility gradient. *Ecography*, 34, 887–896.
- Hagenbo, A., Clemmensen, K. E., Finlay, R. D., Kyaschenko, J., Lindahl, B. D., Fransson, P., & Ekblad, A. (2017). Changes in turnover rather than production regulate biomass of ectomycorrhizal fungal mycelium across a *Pinus sylvestris* chronosequence. *New Phytologist*, 214, 424–431.
- Hagenbo, A., Kyaschenko, J., Clemmensen, K. E., Lindahl, B. D., & Fransson, P. (2018). Fungal community shifts underpin declining mycelial production and turnover across a *Pinus sylvestris* chronosequence. *Journal of Ecology*, 106, 490–501.
- Harden, J. W., Trumbore, S. E., Stocks, B. J., Hirsch, A., Gower, S. T., O'Neill, K. P., & Kasichke, E. S. (2000). The role of fire in the boreal carbon budget. *Global Change Biology*, 6, 174–184. <https://doi.org/10.1046/j.1365-2486.2000.06019.x>
- Harmon, M. E., Bond-Lamberty, B., Tang, J. W., & Vargas, R. (2011). Heterotrophic respiration in disturbed forests: A review with examples from North America. *Journal of Geophysical Research – Biogeosciences*, 116, G00K04.
- Harrison, S., & LaForgia, M. (2019). Seedling traits predict drought-induced mortality linked to diversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 5576–5581.
- Hart, S. A., & Chen, H. Y. H. (2008). Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. *Ecological Monographs*, 78, 123–140.
- Harvey, B. D., & Bergeron, Y. (1989). Site patterns of natural regeneration following clear-cutting in northwestern Quebec. *Canadian Journal of Forest Research*, 19, 1458–1469.
- Heinonsalo, J., Pumpanen, J., Rasilo, T., Hurme, K.-R., & Ilvesniemi, H. (2010). Carbon partitioning in ectomycorrhizal Scots pine seedlings. *Soil Biology and Biochemistry*, 42, 1614–1623.
- Hicke, J. A., Asner, G. P., Kasichke, E. S., French, N. H. F., Randerson, J. T., Collatz, G. J., Stocks, B. J., Tucker, C. J., Los, S. O., & Field, C. B. (2003). Postfire response of North American boreal forest net primary productivity analyzed with satellite observations. *Global Change Biology*, 9(8), 1145–1157. <https://doi.org/10.1046/j.1365-2486.2003.00658.x>
- Hobbie, E. A. (2006). Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. *Ecology*, 87, 563–569.
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A. F. S., Ekblad, A., Högberg, M. N., Nyberg, G., Ottosson-Löfvenius, M., & Read, D. J. (2001). Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, 411, 789–792.
- Howard, E. A., Gower, S. T., Foley, J. A., & Kucharik, C. J. (2004). Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biology*, 10, 1267–1284.
- Ilintsev, A., Bogdanov, A., Nakvasina, E., Amosova, I., Koptev, S., & Tretyakov, S. (2020). The natural recovery of disturbed soil, plant cover and trees after clear-cutting in the boreal forests, Russia. *Forest-Biogeosciences and Forestry*, 13, 531–540.
- Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D. W., Minkinen, K., & Byrne, K. A. (2007). How strongly can forest management influence soil carbon sequestration? *Geoderma*, 137, 253–268.
- Jenny, H. (1994). *Factors of soil formation*. Dover Publications, Inc.
- Jonsson, M., & Wardle, D. A. (2010). Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems. *Biology Letters*, 6, 116–119.
- Jørgensen, K., Clemmensen, K. E., Wallander, H., & Lindahl, B. D. (2023). Do ectomycorrhizal exploration types reflect mycelial foraging strategies? *New Phytologist*, 237, 576–584.
- Jørgensen, K., Clemmensen, K. E., Wallander, H., & Lindahl, B. D. (2024). Ectomycorrhizal fungi are more sensitive to high soil nitrogen levels in forests exposed to nitrogen deposition. *New Phytologist*. <https://doi.org/10.1111/nph.19509>
- Jørgensen, K., Granath, G., Strengbom, J., & Lindahl, B. (2021). Links between boreal forest management, soil fungal communities and belowground carbon sequestration. *Zenodo*.
- Kalyn, A. L., & Van Rees, K. C. J. (2006). Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. *Agricultural and Forest Meteorology*, 140, 236–243.
- Kasichke, E. S., & Turetsky, M. R. (2006). Recent changes in the fire regime across the North American boreal region—Spatial and temporal patterns of burning across Canada and Alaska. *Geophysical Research Letters*, 33, L09703.
- Kelly, J., Ibáñez, T. S., Santín, C., Doerr, S. H., Nilsson, M. C., Holst, T., Lindroth, A., & Kljun, N. (2021). Boreal forest soil carbon fluxes one year after a wildfire: Effects of burn severity and management. *Global Change Biology*, 27, 4181–4195.
- Kim, S., Axelsson, E. P., Girona, M. M., & Senior, J. K. (2021). Continuous-cover forestry maintains soil fungal communities in Norway spruce dominated boreal forests. *Forest Ecology and Management*, 480, 118659.
- Kleja, D. B., Svensson, M., Majdi, H., Jansson, P. E., Langvall, O., Bergkvist, B., Johansson, M. B., Weslien, P., Truusb, L., Lindroth, A., & Ågren, G. I. (2008). Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden. *Biogeochemistry*, 89, 7–25.
- Kohler, A., Kuo, A., Nagy, L. G., Morin, E., Barry, K. W., Buscot, F., Canbäck, B., Choi, C., Cichocki, N., Clum, A., Colpaert, J., Copeland, A., Costa, M. D., Doré, J., Floudas, D., Gay, G., Girlanda, M., Henriessat, B., Herrmann, S., ... Mycorrhizal Genomics Initiative Consortium. (2015). Convergent losses of decay mechanisms and rapid turnover of symbiosis genes in mycorrhizal mutualists. *Nature Genetics*, 47(4), 410–U176. <https://doi.org/10.1038/ng.3223>
- Kohout, P., Charvátová, M., Stursová, M., Masínová, T., Tomsovsky, M., & Baldrian, P. (2018). Clearcutting alters decomposition processes and initiates complex restructuring of fungal communities in soil and tree roots. *ISME Journal*, 12, 692–703.
- Kreutzweiser, D. P., Hazlett, P. W., & Gunn, J. M. (2008). Logging impacts on the biogeochemistry of boreal forest soils and nutrient export to aquatic systems: A review. *Environmental Reviews*, 16, 157–179.
- Kritzberg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L. A., & Laudon, H. (2020). Browning of freshwaters: Consequences to ecosystem services, underlying drivers, and potential mitigation measures. *Ambio*, 49, 375–390.
- Kyaschenko, J., Clemmensen, K. E., Hagenbo, A., Karlton, E., & Lindahl, B. D. (2017). Shift in fungal communities and associated enzyme activities along an age gradient of managed *Pinus sylvestris* stands. *ISME Journal*, 11, 863–874.
- Kyaschenko, J., Ovaskainen, O., Ekblad, A., Hagenbo, A., Karlton, E., Clemmensen, K. E., & Lindahl, B. D. (2019). Soil fertility in boreal forest relates to root-driven nitrogen retention and carbon sequestration in the mor layer. *New Phytologist*, 221, 1492–1502.
- Langanieri, J., Cavard, X., Brassard, B. W., Pare, D., Bergeron, Y., & Chen, H. Y. H. (2015). The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes. *Forest Ecology and Management*, 354, 119–129.

- Laudon, H., Hedtj rn, J., Schelker, J., Bishop, K., Sorensen, R., &  gren, A. (2009). Response of dissolved organic carbon following forest harvesting in a boreal forest. *Ambio*, 38, 381–386.
- Lilleskov, E. A., Hobbie, E. A., & Horton, T. R. (2011). Conservation of ectomycorrhizal fungi: Exploring the linkages between functional and taxonomic responses to anthropogenic N deposition. *Fungal Ecology*, 4, 174–183.
- Lilleskov, E. A., Kuyper, T. W., Bidartondo, M. I., & Hobbie, E. A. (2019). Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: A review. *Environmental Pollution*, 246, 148–162.
- Lindahl, B. D., de Boer, W., & Finlay, R. D. (2010). Disruption of root carbon transport into forest humus stimulates fungal opportunists at the expense of mycorrhizal fungi. *ISME Journal*, 4, 872–881.
- Lindahl, B. D., Kyaschenko, J., Varenus, K., Clemmensen, K. E., Dahlberg, A., Karlton, E., & Stendahl, J. (2021). A group of ectomycorrhizal fungi restricts organic matter accumulation in boreal forest. *Ecology Letters*, 24, 1341–1351.
- Lindahl, B. D., & Tunlid, A. (2015). Ectomycorrhizal fungi—Potential organic matter decomposers, yet not saprotrophs. *New Phytologist*, 205, 1443–1447.
- Lindroth, A. (2023). Clarifying the carbon balance recovery time after clear-cutting. *Global Change Biology*, 29, 4178–4179.
- Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Mart nez-Ramos, M., Meave, J. A., Paz, H., P rez-Garc a, E. A., Romero-P rez, I. E., Tauro, A., & Bongers, F. (2013). Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*, 94, 1211–1216.
- Lorenz, K., Lal, R., Lorenz, K., & Lal, R. (2010). *Carbon sequestration in Forest ecosystems introduction*. Springer.
- Lundmark-Thelin, A., & Johansson, M. B. (1997). Influence of mechanical site preparation on decomposition and nutrient dynamics of Norway spruce (*Picea abies* (L) Karst) needle litter and slash needles. *Forest Ecology and Management*, 96, 101–110.
- Luyssaert, S., Inglima, I., Jung, M., Richardson, A. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E. D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J. M., Chambers, J., Ciais, P., & Janssens, I. A. (2007). CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, 13, 2509–2537.
- Maaroufi, N. I., Nordin, A., Palmqvist, K., Hasselquist, N. J., Forsmark, B., Rosenstock, N. P., Wallander, H., & Gundale, M. J. (2019). Anthropogenic nitrogen enrichment enhances soil carbon accumulation by impacting saprotrophs rather than ectomycorrhizal fungal activity. *Global Change Biology*, 25, 2900–2914.
- Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., & Miller, S. N. (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. *Science*, 372, 280–283.
- Maillard,  ., Par , D., & Munson, A. D. (2010). Soil carbon stocks and carbon stability in a twenty-year-old temperate plantation. *Soil Science Society of America Journal*, 74, 1775–1785.
- Maillard, F., Kohler, A., Morin, E., Hossann, C., Miyauchi, S., Ziegler-Devin, I., G rant, D., Angeli, N., Lipzen, A., Keymanesh, K., Johnson, J., Barry, K., Grigoriev, I. V., Martin, F. M., & Bu e, M. (2023). Functional genomics gives new insights into the ectomycorrhizal degradation of chitin. *New Phytologist*, 238, 845–858.
- M kel , A., Tian, X. L., Repo, A., Ilvesniemi, H., Marshall, J., Minunno, F., N sholm, T., Schiestl-Aalto, P., & Lehtonen, A. (2022). Do mycorrhizal symbionts drive latitudinal trends in photosynthetic carbon use efficiency and carbon sequestration in boreal forests? *Forest Ecology and Management*, 520, 120355. <https://doi.org/10.1016/j.foreco.2022.120355>
- M kiranta, P., Riutta, T., Penttil , T., & Minkinen, K. (2010). Dynamics of net ecosystem CO₂ exchange and heterotrophic soil respiration following clearfelling in a drained peatland forest. *Agricultural and Forest Meteorology*, 150, 1585–1596.
- Makkonen, K., & Helmisaari, H. S. (2001). Fine root biomass and production in Scots pine stands in relation to stand age. *Tree Physiology*, 21, 193–198.
- Mallik, A. U., & Hu, D. (1997). Soil respiration following site preparation treatments in boreal mixedwood forest. *Forest Ecology and Management*, 97, 265–275.
- Marshall, J. D., Tarvainen, L., Zhao, P., Lim, H., Wallin, G., N sholm, T., Lundmark, T., Linder, S., & Peichl, M. (2023). Components explain, but do eddy fluxes constrain? Carbon budget of a nitrogen-fertilized boreal Scots pine forest. *New Phytologist*, 239, 2166–2179.
- Martinez-Garcia, E., Nilsson, M. B., Laudon, H., Lundmark, T., Fransson, J. E. S., Wallerman, J., & Peichl, M. (2022). Overstory dynamics regulate the spatial variability in forest-floor CO₂ fluxes across a managed boreal forest landscape. *Agricultural and Forest Meteorology*, 318, 108916.
- Martino, E., Morin, E., Grelet, G. A., Kuo, A., Kohler, A., Daghino, S., Barry, K. W., Cichocki, N., Clum, A., Dockter, R. B., Hainaut, M., Kuo, R. C., LaButti, K., Lindahl, B. D., Lindquist, E. A., Lipzen, A., Khouja, H. R., Magnuson, J., Murat, C., ... Perotto, S. (2018). Comparative genomics and transcriptomics depict ericoid mycorrhizal fungi as versatile saprotrophs and plant mutualists. *New Phytologist*, 217, 1213–1229.
- McCormack, M. L., Pritchard, S. G., Breland, S., Davis, M. A., Prior, S. A., Runion, G. B., Mitchell, R. J., & Rogers, H. H. (2010). Soil fungi respond more strongly than fine roots to elevated CO₂ in a model regenerating longleaf pine-wiregrass ecosystem. *Ecosystems*, 13, 901–916.
- Mielke, L. A., Ekblad, A., Finlay, R. D., Fransson, P., Lindahl, B. D., & Clemmensen, K. E. (2022). Ericaceous dwarf shrubs contribute a significant but drought-sensitive fraction of soil respiration in a boreal pine forest. *Journal of Ecology*, 110, 1928–1941.
- Mj fors, K., Str mgren, M., Nohrstedt, H., Johansson, M. B., & G rden s, A. I. (2017). Indications that site preparation increases forest ecosystem carbon stocks in the long term. *Scandinavian Journal of Forest Research*, 32, 717–725.
- Mj fors, K., Stromgren, M., Nohrstedt, H. O., & Gardenas, A. I. (2015). Impact of site-preparation on soil-surface CO₂ fluxes and litter decomposition in a clear-cut in Sweden. *Silva Fennica*, 49, 1403.
- Nakhavali, M., Lauerwald, R., Regnier, P., Guenet, B., Chadburn, S., & Friedlingstein, P. (2021). Leaching of dissolved organic carbon from mineral soils plays a significant role in the terrestrial carbon balance. *Global Change Biology*, 27, 1083–1096.
- N sholm, T., H gberg, P., Franklin, O., Metcalfe, D., Keel, S. G., Campbell, C., Hurry, V., Linder, S., & H gberg, M. N. (2013). Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytologist*, 198, 214–221.
- Neff, J. C., & Asner, G. P. (2001). Dissolved organic carbon in terrestrial ecosystems: Synthesis and a model. *Ecosystems*, 4, 29–48.
- Nicol s, C., Martin-Bertelsen, T., Floudas, D., Bentzer, J., Smits, M., Johansson, T., Troein, C., Persson, P., & Tunlid, A. (2019). The soil organic matter decomposition mechanisms in ectomycorrhizal fungi are tuned for liberating soil organic nitrogen. *ISME Journal*, 13, 977–988.
- Nilsson, M. C., & Wardle, D. A. (2005). Understorey vegetation as a forest ecosystem driver: Evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment*, 3, 421–428.
- Odum, E. P. (1969). Strategy of ecosystem development. *Science*, 164, 262.
- Ohlson, M., Dahlberg, B., Okland, T., Brown, K. J., & Halvorsen, R. (2009). The charcoal carbon pool in boreal forest soils. *Nature Geoscience*, 2, 692–695.
-  quist, M. G., Bishop, K., Grelle, A., Klemedtsson, L., K hler, S. J., Laudon, H., Lindroth, A., Ottosson L fvenius, M., Wallin, M. B., & Nilsson, M. B. (2014). The full annual carbon balance of boreal forests is highly sensitive to precipitation. *Environmental Science & Technology Letters*, 1, 315–319.

- Palviainen, M., Lauren, A., Pumpanen, J., Bergeron, Y., Bond-Lamberty, B., Larjavaara, M., Kashian, D. M., Koster, K., Prokushkin, A., Chen, H. Y. H., Seedre, M., Wardle, D. A., Gundale, M. J., Nilsson, M.-C., Wang, C., & Berninger, F. (2020). Decadal-scale recovery of carbon stocks after wildfires throughout the Boreal Forests. *Global Biogeochemical Cycles*, 34(8), e2020GB006612. <https://doi.org/10.1029/2020gb006612>
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., & Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, 333(6045), 988–993. <https://doi.org/10.1126/science.1201609>
- Pappas, C., Maillet, J., Rakowski, S., Baltzer, J. L., Barr, A. G., Black, T. A., Faticchi, S., Laroque, C. P., Matheny, A. M., Roy, A., Sonnentag, O., & Zha, T. (2020). Aboveground tree growth is a minor and decoupled fraction of boreal forest carbon input. *Agricultural and Forest Meteorology*, 290, 108030.
- Peichl, M., Martínez-García, E., Fransson, J. E. S., Wallerman, J., Laudon, H., Lundmark, T., & Nilsson, M. B. (2023). On the uncertainty in estimates of the carbon balance recovery time after forest clear-cutting. *Global Change Biology*, 29, E1–E3.
- Peichl, M., Martínez-García, E., Fransson, J. E. S., Wallerman, J., Laudon, H., Lundmark, T., & Nilsson, M. B. (2022). Landscape-variability of the carbon balance across managed boreal forests. *Global Change Biology*, 29, 1119–1132. <https://doi.org/10.1111/gcb.16534>
- Pérez-Izquierdo, L., Bengtsson, J., Clemmensen, K. E., Granath, G., Gundale, M. J., Ibáñez, T. S., Lindahl, B. D., Strengbom, J., Taylor, A., Viketoft, M., Wardle, D. A., & Nilsson, M. C. (2023). Fire severity as a key determinant of aboveground and belowground biological community recovery in managed even-aged boreal forests. *Ecology and Evolution*, 13, 1–19.
- Pérez-Izquierdo, L., Clemmensen, K. E., Strengbom, J., Granath, G., Wardle, D. A., Nilsson, M. C., & Lindahl, B. D. (2021). Crown-fire severity is more important than ground-fire severity in determining soil fungal community development in the boreal forest. *Journal of Ecology*, 109, 504–518.
- Pérez-Ramos, I. M., Matías, L., Gómez-Aparicio, L., & Godoy, Ó. (2019). Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications*, 10, 2555.
- Pregitzer, K. S., & Euskirchen, E. S. (2004). Carbon cycling and storage in world forests: Biome patterns related to forest age. *Global Change Biology*, 10, 2052–2077.
- Preston, C. M., Simard, M., Bergeron, Y., Bernard, G. M., & Wasylyshen, R. E. (2017). Charcoal in organic horizon and surface mineral soil in a boreal forest fire chronosequence of western Quebec: Stocks, depth distribution, chemical properties and a synthesis of related studies. *Frontiers in Earth Science*, 5. <https://doi.org/10.3389/feart.2017.00098>
- Pumpanen, J., Lindén, A., Miettinen, H., Kolari, P., Ilvesniemi, H., Mammarella, I., Hari, P., Nikinmaa, E., Heinonsalo, J., Bäck, J., Ojala, A., Berninger, F., & Vesala, T. (2014). Precipitation and net ecosystem exchange are the most important drivers of DOC flux in upland boreal catchments. *Journal of Geophysical Research - Biogeosciences*, 119, 1861–1878.
- Pumpanen, J. S., Heinonsalo, J., Rasilo, T., Hurme, K.-R., & Ilvesniemi, H. (2009). Carbon balance and allocation of assimilated CO₂ in Scots pine, Norway spruce, and silver birch seedlings determined with gas exchange measurements and ¹⁴C pulse labelling. *Trees*, 23, 611–621.
- Regnier, P., Friedlingstein, P., Ciais, P., Mackenzie, F. T., Gruber, N., Janssens, I. A., Laruelle, G. G., Lauerwald, R., Luysaert, S., Andersson, A. J., Arndt, S., Arnosti, C., Borges, A. V., Dale, A. W., Gallego-Sala, A., Goddéris, Y., Goossens, N., Hartmann, J., Heinze, C., ... Thullner, M. (2013). Anthropogenic perturbation of the carbon fluxes from land to ocean. *Nature Geoscience*, 6, 597–607.
- Reich, P. B., Rich, R. L., Lu, X. J., Wang, Y. P., & Oleksyn, J. (2014). Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 13703–13708.
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: Global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America*, 94, 13730–13734.
- Rillig, M. C., Caldwell, B. A., Wösten, H. A. B., & Sollins, P. (2007). Role of proteins in soil carbon and nitrogen storage: Controls on persistence. *Biogeochemistry*, 85, 25–44.
- Rodríguez-Cardona, B. M., Coble, A. A., Wymore, A. S., Kolosov, R., Podgorski, D. C., Zito, P., Spencer, R. G. M., Prokushkin, A. S., & McDowell, W. H. (2020). Wildfires lead to decreased carbon and increased nitrogen concentrations in upland arctic streams. *Scientific Reports*, 10, 8722.
- Santín, C., Doerr, S. H., Preston, C. M., & González-Rodríguez, G. (2015). Pyrogenic organic matter production from wildfires: A missing sink in the global carbon cycle. *Global Change Biology*, 21, 1621–1633.
- Sawamoto, T., Hatano, R., Yajima, T., Takahashi, K., & Iseae, A. P. (2000). Soil respiration in Siberian taiga ecosystems with different histories of forest fire. *Soil Science and Plant Nutrition*, 46, 31–42.
- Schelker, J., Eklöf, K., Bishop, K., & Laudon, H. (2012). Effects of forestry operations on dissolved organic carbon concentrations and export in boreal first-order streams. *Journal of Geophysical Research - Biogeosciences*, 117, G01011.
- Schulze, E. D., Lloyd, J., Kelliher, F. M., Wirth, C., Reibmann, C., Lühker, B., Mund, M., Knohl, A., Milyukova, I. M., Schulze, W., Ziegler, W., Varlagin, A. B., Sogachev, A. F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M. I., Tchebakova, N., & Vygodskaya, N. N. (1999). Productivity of forests in the Euro Siberian Boreal region and their potential to act as a carbon sink -: A synthesis. *Global Change Biology*, 5(6), 703–722. <https://doi.org/10.1046/j.1365-2486.1999.00266.x>
- Shao, P. S., Han, H. Y., Sun, J. K., & Xie, H. T. (2023). Effects of global change and human disturbance on soil carbon cycling in boreal forest: A review. *Pedosphere*, 33, 194–211.
- Silva, M. A. M., Pinto, A. d. V. F., do Nascimento, L. M., Lins-e-Silva, A. C. B., de Lima, A. L. A., & Rodal, M. J. N. (2015). Does the plant economics spectrum change with secondary succession in the forest? *Trees*, 29, 1521–1531.
- Simola, H. (2018). Persistent carbon loss from the humus layer of tilled boreal forest soil. *European Journal of Soil Science*, 69, 303–314.
- Singh, S., Amiro, B. D., & Quideau, S. A. (2008). Effects of forest floor organic layer and root biomass on soil respiration following boreal forest fire. *Canadian Journal of Forest Research*, 38, 647–655.
- Smith, H. G., Sheridan, G. J., Lane, P. N. J., Nyman, P., & Haydon, S. (2011). Wildfire effects on water quality in forest catchments: A review with implications for water supply. *Journal of Hydrology*, 396, 170–192.
- Smyth, C. E., Kurz, W. A., Neilson, E. T., & Stinson, G. (2013). National-scale estimates of forest root biomass carbon stocks and associated carbon fluxes in Canada. *Global Biogeochemical Cycles*, 27, 1262–1273.
- Song, J., Liu, Z., Zhang, Y., Yan, T., Shen, Z. H., & Piao, S. L. (2019). Effects of wildfire on soil respiration and its heterotrophic and autotrophic components in a montane coniferous forest. *Journal of Plant Ecology*, 12, 336–345.
- Sothe, C., Gonsamo, A., Arabian, J., Kurz, W. A., Finkelstein, S. A., & Snider, J. (2022). Large soil carbon storage in terrestrial ecosystems of Canada. *Global Biogeochemical Cycles*, 36, e2021GB007213.

- Sterkenburg, E., Clemmensen, K. E., Ekblad, A., Finlay, R. D., & Lindahl, B. D. (2018). Contrasting effects of ectomycorrhizal fungi on early and late stage decomposition in a boreal forest. *ISME Journal*, *12*, 2187–2197.
- Sterkenburg, E., Clemmensen, K. E., Lindahl, B. D., & Dahlberg, A. (2019). The significance of retention trees for survival of ectomycorrhizal fungi in clear-cut Scots pine forests. *Journal of Applied Ecology*, *56*, 1367–1378.
- Strömberg, M., Egnell, G., & Olsson, B. A. (2013). Carbon stocks in four forest stands in Sweden 25 years after harvesting of slash and stumps. *Forest Ecology and Management*, *290*, 59–66.
- Strömberg, M., Mjöfors, K., & Olsson, B. A. (2017). Soil-surface CO₂ flux during the first 2 years after stump harvesting and site preparation in 14 Swedish forests. *Scandinavian Journal of Forest Research*, *32*, 213–221.
- Stursová, M., Snajdr, J., Cajthaml, T., Bárta, J., Santrucková, H., & Baldrian, P. (2014). When the forest dies: The response of forest soil fungi to a bark beetle-induced tree dieback. *ISME Journal*, *8*, 1920–1931.
- Tarnocai, C., Canadell, J. G., Schuur, E. A. G., Kuhry, P., Mazhitova, G., & Zimov, S. (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, *23*, GB2023.
- Trugman, A. T., Fenton, N. J., Bergeron, Y., Xu, X., Welp, L. R., & Medvigy, D. (2016). Climate, soil organic layer, and nitrogen jointly drive forest development after fire in the North American boreal zone. *Journal of Advances in Modeling Earth Systems*, *8*, 1180–1209.
- Turetsky, M. R., Kane, E. S., Harden, J. W., Ottmar, R. D., Manies, K. L., Hoy, E., & Kasischke, E. S. (2011). Recent acceleration of biomass burning and carbon losses in Alaskan forests and peatlands. *Nature Geoscience*, *4*, 27–31.
- Twieg, B. D., Durall, D. M., & Simard, S. W. (2007). Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytologist*, *176*, 437–447.
- Uri, V., Kukumägi, M., Aosaar, J., Varik, M., Becker, H., Aun, K., Lõhmus, K., Soosaar, K., Astover, A., Uri, M., Buht, M., Sepaste, A., & Padari, A. (2022). The dynamics of the carbon storage and fluxes in Scots pine (*Pinus sylvestris*) chronosequence. *Science of the Total Environment*, *817*, 152973.
- Varenus, K., Lindahl, B. D., & Dahlberg, A. (2017). Retention of seed trees fails to lifeboat ectomycorrhizal fungal diversity in harvested Scots pine forests. *FEMS Microbiology Ecology*, *93*, fix105. <https://doi.org/10.1093/femsec/fix105>
- Vesterdal, L. N., Sigurdsson, B. D., & Gundersen, P. (2013). Do tree species influence soil carbon stocks in temperate and boreal forests? *Forest Ecology and Management*, *309*, 4–18.
- Walker, X. J., Baltzer, J. L., Cumming, S. G., Day, N. J., Ebert, C., Goetz, S., Johnstone, J. F., Potter, S., Rogers, B. M., Schuur, E. A. G., Turetsky, M. R., & Mack, M. C. (2019). Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature*, *572*, 520.
- Wallander, H., Johansson, U., Sterkenburg, E., Durling, M. B., & Lindahl, B. D. (2010). Production of ectomycorrhizal mycelium peaks during canopy closure in Norway spruce forests. *New Phytologist*, *187*, 1124–1134.
- Wang, C. K., Gower, S. T., Wang, Y. H., Zhao, H. X., Yan, P., & Bond-Lamberty, B. P. (2001). The influence of fire on carbon distribution and net primary production of boreal *Larix gmelinii* forests in north-eastern China. *Global Change Biology*, *7*, 719–730.
- Ward, E. B., Duguid, M. C., Kuebbing, S. E., Lendemer, J. C., & Bradford, M. A. (2022). The functional role of ericoid mycorrhizal plants and fungi on carbon and nitrogen dynamics in forests. *New Phytologist*, *235*, 1701–1718.
- Wardle, D. A., Hornberg, G., Zackrisson, O., Kalela-Brundin, M., & Coomes, D. A. (2003). Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science*, *300*, 972–975.
- Wasyliw, J., & Karst, J. (2020). Shifts in ectomycorrhizal exploration types parallel leaf and fine root area with forest age. *Journal of Ecology*, *108*, 2270–2282.
- Watts, J. D., Farina, M., Kimball, J. S., Schiferl, L. D., Liu, Z. H., Arndt, K. A., Zona, D., Ballantyne, A., Euskirchen, E. S., Parmentier, F. J. W., Helbig, M., Sonntag, O., Tagesson, T., Rinne, J., Ikawa, H., Ueyama, M., Kobayashi, H., Sachs, T., Nadeau, D. F., ... Oechel, W. C. (2023). Carbon uptake in Eurasian boreal forests dominates the high-latitude net ecosystem carbon budget. *Global Change Biology*, *29*(7), 1870–1889. <https://doi.org/10.1111/gcb.16553>
- Weigelt, A., Mommer, L., Andrzejczak, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C., Meier, I. C., van der Plas, F., Poorter, H., Roumet, C., van Ruijven, J., Sabatini, F. M., Semchenko, M., ... McCormack, M. L. (2021). An integrated framework of plant form and function: The belowground perspective. *New Phytologist*, *232*, 42–59.
- Weigt, R. B., Raidl, S., Verma, R., & Agerer, R. (2012). Exploration type-specific standard values of extramatrical mycelium—A step towards quantifying ectomycorrhizal space occupation and biomass in natural soil. *Mycological Progress*, *11*, 287–297.
- Wirth, C., Czimeczik, C. I., & Schulze, E. D. (2002). Beyond annual budgets: Carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. *Tellus Series B: Chemical and Physical Meteorology*, *54*, 611–630.
- Wooster, M. J., & Zhang, Y. H. (2004). Boreal forest fires burn less intensely in Russia than in North America. *Geophysical Research Letters*, *31*, L20505.
- Yuan, Z. Y., & Chen, H. Y. H. (2010). Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. *Critical Reviews in Plant Sciences*, *29*, 204–221.
- Yuan, Z. Y., & Chen, H. Y. H. (2012). Fine root dynamics with stand development in the boreal forest. *Functional Ecology*, *26*, 991–998.
- Zheng, D., Prince, S., & Hame, T. (2004). Estimating net primary production of boreal forests in Finland and Sweden from field data and remote sensing. *Journal of Vegetation Science*, *15*, 161–170.
- Zhu, X. D., Chen, L., Pumpanen, J., Ojala, A., Zobitz, J., Zhou, X., Laudon, H., Palviainen, M., Neitola, K., & Berninger, F. (2022). The role of terrestrial productivity and hydrology in regulating aquatic dissolved organic carbon concentrations in boreal catchments. *Global Change Biology*, *28*(8), 2764–2778. <https://doi.org/10.1111/gcb.16094>

DATA SOURCES

- Alban, D. H. (1982). Effects of nutrient accumulation by Aspen, spruce, and pine on soil properties. *Soil Science Society of America Journal*, *46*, 853–861.
- Alriksson, A. E., & Hillevi, M. (1998). Variations in mineral nutrient and C distribution in the soil and vegetation compartments of five temperate tree species in NE Sweden. *Forest Ecology and Management*, *108*, 261–273.
- Andrieux, B., Beguin, J., Bergeron, Y., Grondin, P., & Paré, D. (2018). Drivers of postfire soil organic carbon accumulation in the boreal forest. *Global Change Biology*, *24*, 4797–4815.
- Bill, K. E., Dieleman, C. M., Baltzer, J. L., Degré-Timmons, G., Mack, M. C., Day, N. J., Cumming, S. G., Walker, X. J., & Turetsky, M. R. (2023). Post-fire recovery of soil organic layer carbon in Canadian boreal forests. *Ecosystems*, *26*, 1623–1639.
- Bjarnadóttir, B. (2009). *Carbon stocks and fluxes in a young Siberian larch (*Larix sibirica*) plantation in Iceland*. Physical Geography and Ecosystem Science, University of Lund.
- Blaško, R., Forsmark, B., Gundale, M. J., Lundmark, T., & Nordin, A. (2020). Impacts of tree species identity and species mixing on ecosystem carbon and nitrogen stocks in a boreal forest. *Forest Ecology and Management*, *458*, 117783. <https://doi.org/10.1016/j.foreco.2019.117783>
- Goulden, M. L., McMillan, A. M. S., Winston, G. C., Rocha, A. V., Manies, K. L., Harden, J. W., & Bond-Lamberty, B. P. (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, *17*(2), 855–871. <https://doi.org/10.1111/j.1365-2486.2010.02274.x>
- Harden, J. W., Manies, K. L., O'Donnell, J., Johnson, K., Frolking, S., & Fan, Z. S. (2012). Spatiotemporal analysis of black spruce forest soils and implications

- for the fate of C. *Journal of Geophysical Research - Biogeosciences*, 117, G01012.
- Howard, E. A., Gower, S. T., Foley, J. A., & Kucharik, C. J. (2004). Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biology*, 10, 1267–1284.
- Kjønaas, O. J., Bárcena, T. G., Hysten, G., Nordbakken, J. F., & Økland, T. (2021). Boreal tree species change as a climate mitigation strategy: Impact on ecosystem C and N stocks and soil nutrient levels. *Ecosphere*, 12(11), e03826.
- Laganière, J., Paré, D., Bergeron, Y., & Chen, H. Y. N. (2012). The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. *Soil Biology and Biochemistry*, 53, 18–27.
- Laganière, J., Laganière, J., Cavard, X., Brassard, B. W., Paré, D., Bergeron, Y., & Chen, H. Y. H. (2015). The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes. *Forest Ecology and Management*, 354, 119–129.
- Larjavaara, M., Berninger, F., Palviainen, M., Prokushkin, A., & Wallenius, T. (2017). Post-fire carbon and nitrogen accumulation and succession in Central Siberia. *Scientific Reports*, 7, 12776.
- Lecomte, N., Simard, M., Fenton, N., & Bergeron, Y. (2006). Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. *Ecosystems*, 9, 1215–1230.
- Légaré, S., Paré, D., & Bergeron, Y. (2005). Influence of Aspen on Forest floor properties in Black spruce-dominated stands. *Plant and Soil*, 275(1–2), 207–220.
- Mack, M. C., Walker, X. J., Johnstone, J. F., Alexander, H. D., Melvin, A. M., Jean, M., & Miller, S. M. (2021). Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. *Science*, 372, 280–283.
- Martin, J. L., Gower, S. T., Plaut, J., & Holmes, B. (2005). Carbon pools in a boreal mixedwood logging chronosequence. *Global Change Biology*, 11, 1883–1894.
- Martinez-Garcia, E., Nilsson, M. B., Laudon, H., Lundmark, T., Fransson, J. E. S., Wallerman, J., & Peichle, M. (2022). Overstory dynamics regulate the spatial variability in forest-floor CO₂ fluxes across a managed boreal forest landscape. *Agricultural and Forest Meteorology*, 318, 108916.
- Moroni, M. T., Shaw, C. H., & Otahal, P. (2010). Forest carbon stocks in Newfoundland boreal forests of harvest and natural disturbance origin I: Field study. *Canadian Journal of Forest Research*, 40, 2135–2145.
- Olsson, B. A., Hansson, K., Persson, T., Beuker, E., & Helmisaari, H. S. (2012). Heterotrophic respiration and nitrogen mineralisation in soils of Norway spruce, Scots pine and silver birch stands in contrasting climates. *Forest Ecology and Management*, 269, 197–205.
- O'Neill, K. P., Kasischke, E. S., & Richter, D. D. (2003). Seasonal and decadal patterns of soil carbon uptake and emission along an age sequence of burned black spruce stands in interior Alaska. *Journal of Geophysical Research-Atmospheres*, 108, FFR-11.
- Palviainen, M., Lauren, A., Pumpanen, J., Bergeron, Y., Bond-Lamberty, B., Larjavaara, M., Kashian, D. M., Köster, K., Prokushkin, A., Chen, H. Y. H., Seedre, M., Wardle, D. A., Gundale, M. J., Nilsson, M.-C., Wang, C., & Berninger, F. (2020). Decadal-scale recovery of carbon stocks after wildfires throughout the boreal forests. *Global Biogeochemical Cycles*, 34, 17.
- Paré, D., Laganière, J., Larocque, G. R., & Boutin, R. (2022). Effects of climate and forest composition on soil carbon cycling, soil organic matter stability and stocks in a humid boreal region. *EGU sphere*, 2022, 1–30.
- Pregitzer, K. S., & Euskirchen, E. S. (2004). Carbon cycling and storage in world forests: Biome patterns related to forest age. *Global Change Biology*, 10, 2052–2077.
- Rapalee, G., Trumbore, S. E., Davidson, E. A., Harden, J. W., & Veldhuis, H. (1998). Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. *Global Biogeochemical Cycles*, 12, 687–701.
- Ritter, E. (2007). Carbon, nitrogen and phosphorus in volcanic soils following afforestation with native birch (*Betula pubescens*) and introduced larch (*Larix sibirica*) in Iceland. *Plant and Soil*, 295, 239–251.
- Seedre, M., Taylor, A. R., Brassard, B. W., Chen, H. Y. H., & Jogiste, K. (2014). Recovery of ecosystem carbon Stocks in Young boreal forests: A comparison of harvesting and wildfire disturbance. *Ecosystems*, 17, 851–863.
- Segura, J. H., Nilsson, M. B., Sparrman, T., Serk, H., Schleucher, J., Tolu, J., & Öquist, M. G. (2019). Boreal tree species affect soil organic matter composition and saprotrophic mineralization rates. *Plant and Soil*, 441(1–2), 173–190.
- Sigurðardóttir, R. (2000). *Effects of different forest types on total ecosystem carbon sequestration in Hallormsstaður forest*. Eastern Iceland Yale University.
- Smolander, A., & Kitunen, V. (2021). Soil organic matter properties and C and N cycling processes: Interactions in mixed-species stands of silver birch and conifers. *Applied Soil Ecology*, 160, 103841.
- Smolander, A., Loponen, J., Suominen, K., & Kitunen, V. (2005). Organic matter characteristics and C and N transformations in the humus layer under two tree species, *Betula pendula* and *Picea abies*. *Soil Biology and Biochemistry*, 37(7), 1309–1318.
- Snorrason, A., Sigurdsson, B. D., Gudbergsson, G., Svavarsdóttir, K., & Jónsson, T. H. (2002). Carbon sequestration in forest plantations in Iceland. *Icelandic Agricultural Sciences*, 15, 81–93.
- Trumbore, S. E., & Harden, J. W. (1997). Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area. *Journal of Geophysical Research-Atmospheres*, 102, 28817–28830.
- Wardle, D. A., Hornberg, G., Zackrisson, O., Kalela-Brundin, M., & Coomes, D. A. (2003). Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science*, 300, 972–975.
- Wirth, C., Czimczik, C. I., & Schulze, E. D. (2002). Beyond annual budgets: Carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. *Tellus Series B: Chemical and Physical Meteorology*, 54, 611–630.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gundale, M. J., Axelsson, E. P., Buness, V., Callebaut, T., DeLuca, T. H., Hupperts, S. F., Ibáñez, T. S., Metcalfe, D. B., Nilsson, M.-C., Peichl, M., Spitzer, C. M., Stangl, Z. R., Strengbom, J., Sundqvist, M. K., Wardle, D. A., & Lindahl, B. D. (2024). The biological controls of soil carbon accumulation following wildfire and harvest in boreal forests: A review. *Global Change Biology*, 30, e17276. <https://doi.org/10.1111/gcb.17276>