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Carbon Storage Declines in Old Boreal Forests Irrespective of Succession Pathway

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ABSTRACT

The boreal forest plays a critical role in regulating global atmospheric carbon dioxide and is highly influenced by wildfire. However, the long-term recovery of forest carbon (C) storage following wildfire remains unclear, especially during late succession. Uncertainty surrounding C storage in old forests largely stems from both a lack of repeated measurements in forest stands older than the longevity of the pioneer cohort and a lack of consideration of multiple succession pathways. In this study, we constructed a replicated chronosequence, which covered a wide range of forest stand age classes (up to 210 years old) following fire in the boreal forest of central Canada. We selected stands of different overstorey types (that is, broadleaf, conifer, or mixedwood) and age classes to account for multiple succession pathways known to occur in our study area. Our results show a strong relationship between total ecosystem C storage and stand age following fire. Broadleaf stands had on average higher total ecosystem C; however, the inferred temporal dynamics of total ecosystem C were similar among all three overstorey types. Importantly, we found that total ecosystem C storage declined from canopy transition to late-succession stages, irrespective of succession pathway, contradicting views that old forests continually accumulate C as they age. Our findings emphasize that further study of stands older than the longevity of the pioneer cohort is critical to better understand the contribution of old forests to the global C cycle.

Key words: boreal forest; carbon storage; fire; forest succession; multiple pathways.

Author Contributions BG and HYHC conceived of or designed study; BG, PK, ZM, and AMH performed research; BG and EBS analyzed data; BG, ART, HYHC, and EBS wrote the paper.

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INTRODUCTION

The world's boreal forests play an important role in regulating atmospheric carbon dioxide through storage of 49% of global forest vegetation and soil carbon (C) (Dixon and others 1994). Wildfire is the predominant form of natural stand-replacing disturbance in the boreal forest and exerts strong impacts on C sequestration and storage (Bond-Lamberty and others 2007). Over the past several decades, fire activity has increased in many regions

to levels unprecedented since the last ice age (Kelly and others 2013), highlighting the importance of understanding its effects on forest C dynamics. Still, the long-term impact and recovery of forest C storage following stand-replacing fire, especially during late succession, remains unclear (Taylor and others 2014). This is especially concerning because boreal forests are expected to experience warming at twice the global average rate over the coming century, increasing the frequency and intensity of fire disturbance (Gauthier and others 2015).

Carbon storage changes as forest stands age. It has long been recognized that forest net ecosystem production (NEP) increases rapidly during early stand development, peaks as stands mature, and then declines as stands age (Ryan and others 1997). During periods of positive NEP, total ecosystem C increases, but during periods of negative NEP (that is, when gross primary production is less than total ecosystem respiration), total ecosystem C decreases. Across diverse forest types, whether forest ecosystems continue to accumulate C, decline, or stabilize as they transition from mature, even-aged stands to structurally complex old-growth stands is unclear, with many studies reporting conflicting results (Bond-Lamberty and others 2004; Harmon and others 2004; Goulden and others 2011; Kashian and others 2013; Taylor and others 2014). One possible explanation for this discrepancy may be lack of consideration of forest canopy transition, from dominance of early- to late-succession species, on C dynamics. Most studies that have examined forest C storage in relation to stand aging in boreal forests have focused on stands that have not yet transitioned from dominance of individuals established immediately after fire and are typically restricted to stands less than 160 years old. The transition from early- to late-succession species in boreal stands generally does not occur until early-succession species have reached their average maximum lifespan, which can be in excess of 150 years (Chen and Popadiouk 2002).

The commonly accepted pathway of forest succession for mesic sites in the North American boreal forest is characterized by the sequential replacement of fast-growing, early-succession colonizers, such as trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.), by slower-growing, shade-tolerant species, such as spruce (*Picea* spp.) and balsam fir (*Abies balsamea* [L.] Mill.) (Chen and Popadiouk 2002). Indeed, it has been postulated that the transition from large, fast-growing, early-succession species to small, slow-growing, late-succession species may contribute to a reduction in NEP and loss of C in old

boreal stands (Taylor and others 2014). Furthermore, depending on predisturbance forest composition, disturbance type and severity, neighboring stands, and the influence of minor disturbances (Johnstone and Chapin 2006; Chen and others 2009), similar site types in the boreal forest may undergo multiple succession pathways (Taylor and Chen 2011). For example, broadleaf stands dominated by shade-intolerant trembling aspen and white birch (*Betula papyrifera* Marsh.) may self-replace in the absence of competition from shade-tolerant conifers (Kneeshaw and Bergeron 1998; Brassard and others 2008). Conifer stands dominated by shade-intolerant jack pine have a high probability of transitioning to shade-tolerant spruce and balsam fir (Taylor and Chen 2011). Minor infestations by spruce budworm (*Choristoneura fumiferana* Clemens) or bark beetle (for example, *Dendroctonus ponderosae* Hopkins) can promote the persistence of broadleaf species in old stands, forming complex mixedwood stands (Kneeshaw and Bergeron 1998). These multiple succession pathways may have diverse effects on forest C storage as species have different growth rates and maximum standing biomass. Furthermore, diverse species mixtures can have positive effects on forest productivity relative to species-poor mixtures, depending on stand age (Zhang and others 2012; Liang and others 2016).

In this study, we used a replicated chronosequence design that covered a wide range of stand age classes (from 8 to 210 years old), following stand-replacing fire, undergoing multiple succession pathways in the boreal forest of central Canada, to examine C storage dynamics. We selected stands of different overstorey types (that is, broadleaf, conifer, or mixedwood) for each age class to address how forest C storage changed in relation to stand aging and succession. Specifically, we sought to address the following questions: (1) Does the direction of forest succession (as represented by different overstorey types at each stand age) influence forest C storage as stands age following stand-replacing fire? and (2) Does C storage increase, decrease, or show no significant change in the late successional stage as stands transition from mature, even-aged stands to structurally complex old-growth stands following different successional trajectories? To understand the age-dependent total C storage dynamics, we determined the dynamics of individual C pools including live biomass, dead wood, forest floor, and mineral soil.

MATERIALS AND METHODS

Study Area

Our study was conducted in the boreal forest region, approximately 150 km north of Thunder Bay, Ontario, Canada, between 49°44′–49°65′ N and 89°16′–90°13′ W. This area is characterized by warm summers and cold, snowy winters. Mean annual temperature is 1.9 °C, and mean annual precipitation is 824.8 mm as measured by the closest meteorological station in Cameron Falls, Ontario, Canada (Environment Canada 2017). Soils in our study area were largely deposited by the Wisconsinan glaciation, which ended approximately 9500 years ago in this region (Moran and Clayton 1984). Stand-replacing wildfire is the most common natural disturbance in the study area, with an average fire-return interval of approximately 100 years during the past century, resulting in a mosaic of stand ages across the landscape (Senici and others 2010). We conducted our sampling in the spruce forest, which is approximately a million of hectares. Dominant overstorey tree species in the study area, in order from least to most shade tolerant, include jack pine, trembling aspen, white birch, black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (Burns and Honkala 1990).

Sampling Design

To determine the effect of stand aging and succession on forest C storage, we constructed a chronosequence of postfire stands. Although the use of the chronosequence method has been criticized because it makes the assumption that sample stands along the temporal sequence have followed the same developmental history (Johnson and Miyanishi 2008), given careful site selection, replication, and demonstration of developmental links, the chronosequence method is appropriate for studying patterns of C storage over decadal to centennial time scales (Walker and others 2010). Based on local fire history and the availability of different aged stands in our study area, we were able to sample five different stand age classes, including 8, 34, 99, 147, and 210 years since fire, representing the stand initiation, stem exclusion, early canopy transition, late canopy transition, and gap dynamic stages of boreal forest development, respectively, modified from Chen and Popadiouk (2002).

To account for multiple succession pathways as stands age after fire, we carefully selected different overstorey types for each age class to account for multiple succession pathways. Broadleaf stands or conifer stands had greater than 80% of their total stem density or basal area as broadleaf species or conifer species, respectively, whereas in mixedwood stands, stem density or basal area included relatively equal proportions of both broadleaf and conifer species (Table 1). More specifically, for stands in the stand initiation and stem exclusion stages of development (that is, years 8, 34), we selected broadleaf stands that were dominated by trembling aspen, conifer stands that were dominated by jack pine, and mixedwood stands that contained a mixture of jack pine and trembling aspen. For stands in the canopy transition (that is, years 99, 147) and gap dynamics stages (that is, year 210), we selected broadleaf stands dominated by self-replacing trembling aspen and white birch, conifer stands that were transitioning from jack pine to spruce and balsam fir dominance, and mixedwood stands that were codominated by trembling aspen, white birch, spruce, and balsam fir.

We attempted to select postfire stands that had not been managed, including three replicates for each age class and overstorey type combination; however, two replicate mixedwood stands, each at age 34 and 147 years, were accidentally damaged by harvesting activities between consecutive years of forest inventory, resulting in a total of 43 stands sampled. Sample stands were positioned several kilometers away from each other and selected from different road accesses to minimize the impact of spatial autocorrelation. In order to minimize site variability, all selected stands were located on mesic sites with flat midslope positions, with no slope exceeding 5%. All stands are underlain by moderately deep (≥ 50 cm) glacial tills, belonging to the Brunisolic soil order, according to the Canadian system of soil classification (Soil Classification Working Group 1998). To ensure that each sample stand met the selection criteria, soil pits were dug in each candidate stand to verify whether the site was mesic, following the procedures described in Taylor and others (2000). Soil attribute data for all sites used in this study have been previously reported by Hume and others (2016).

Time since last stand-replacing fire (TSF) for sample stands less than 90 years old was determined from detailed fire records (Senici and others 2010). For stands greater than 90 years old, tree ages were used to estimate minimum TSF following the procedures described in Senici and others (2010). Of all sampled stands, we selected either jack pine or trembling aspen trees to determine minimum TSF. In each stand, three canopy stems

Table 1. Characteristics of the 43 Sample Stands in the Boreal Forests of Ontario, Canada

Age	Overstorey[1]	N	Stand density (stems ha^{-1}) or basal area (m^2 ha^{-1})[2]	Stand composition (%)[3]					
				Trembling aspen	White birch	Jack pine	Spruce spp.	Balsam fir	Others
8	B	3	5933 (581)	95 (5)		5 (5)			
	C	3	7067 (1551)	3 (3)		97 (3)			
	M	3	6933 (926)	45 (9)		55 (9)			
34	B	3	26 (1)	92 (3)	4 (4)	1 (1)	2 (1)		1 (1)
	C	3	28 (2)	4 (2)		95 (3)	1 (1)		
	M	2	19 (3)	52 (6)		35 (1)	11 (7)		2 (2)
99	B	3	51 (7)	91 (2)	3 (2)		1 (1)	1 (1)	4 (1)
	C	3	52 (2)	3 (2)		43 (12)	50 (17)	4 (3)	
	M	3	43 (5)	40 (12)	16 (11)	9 (6)	15 (8)	18 (3)	2 (1)
147	B	3	58 (8)	85 (3)	7 (4)		5 (1)	2 (1)	1 (1)
	C	3	51 (9)	1 (1)	2 (2)	53 (27)	37 (26)	7 (1)	
	M	2	36 (3)	38 (2)	30 (1)		12 (5)	19 (4)	1 (1)
210	B	3	41 (3)	54 (22)	24 (18)		10 (6)	10 (4)	2 (1)
	C	3	40 (8)	5 (5)	7 (4)		36 (18)	50 (17)	2 (1)
	M	3	46 (3)	11 (4)	39 (5)	5 (3)	38 (7)	7 (3)	

Each age–overstorey combination has three replications, except 34- and 147-year-old mixedwood stands (two replicates).
[1]Overstorey types: B = broadleaf, C = conifer, M = mixedwoods.
[2]Values are means with 1 SE in parentheses. Stand density (stems ha^{-1}) was determined for the younger (8-year-old) stands and basal area (m^2 ha^{-1}) for older stands.
[3]The ''Others'' category includes Salix spp., Acer spicatum, Alnus viridis, Sorbus decora, Corylus cornuta, Prunus pensylvanica, and Larix laricina.

were sampled by extracting a core or stem disk at breast height (1.3 m above root collar). The cores and disks were transported to our laboratory, where the cores were mounted on constructed core strips and sanded to make rings visible. Stem disks were cut transversely, then mounted on constructed core strips, and sanded to make rings visible. Rings were counted using a handheld magnifier or a microscope until the same count was obtained three successive times. Based on a locally derived age correction model developed by Vasiliauskas and Chen (2002), 7 years were added to ring counts to determine minimum TSF.

Data Collection

Aboveground Live Biomass Carbon

In each selected stand, we randomly established a 400-m^2 (11.28 m radius) circular sampling plot. Within each plot, diameters at breast height (DBH; 1.3 m above the root collar) of all overstorey trees (DBH ≥ 9 cm) were measured. Trees with a DBH in the range of 3–9 cm were measured within a 50-m^2 circular subplot (3.99 m radius; shared plot center with the 400-m^2 plot). Aboveground biomass of all trees at least 3 cm in DBH was estimated as the sum of bark, stem, branch, and foliage biomass calculated by using published Canadian allometric equations (Lambert and others 2005). For tree

saplings (DBH < 3 cm) and large shrubs (height ≥ 50 cm), the base diameter of each individual was measured in three randomly selected 2 × 2 m plots within each 400-m^2 main plot. Aboveground biomass of tree saplings and large shrubs was estimated by using allometric equations developed for small trees and large shrubs (Smith and Brand 1983; Bond-Lamberty and others 2002).

Aboveground biomass of understorey vegetation, including short shrubs (height < 50 cm), forbs, graminoids (grass, sedge), bryophytes (mosses), ferns, and lichens, was estimated by two stages of sampling during July 2014, when annual plant cover was at or near its maximum (MacDonald and others 2012). Firstly, the percent cover of each understorey species was estimated within each 400-m^2 plot. Secondly, the percent cover of each understorey species was visually estimated again within twenty-one 2 × 2 m subplots, which were randomly located in the larger 400-m^2 main plot. All understorey plants in the subplots were then harvested by species, stored in paper bags, and transported to the laboratory for biomass determination. Samples were oven-dried at 68 °C for 48 h and weighed. Data of all harvested samples were pooled together, and linear regression was used to develop allometric relationships between understorey biomass and percent coverage for each growth form (MacDonald and others 2012). The

whole plot biomass was then estimated based on percent cover of each species from the first step by using developed regressions from the second step.

Belowground Live Biomass Carbon

Coarse root (> 10 mm diameter) biomass was calculated for the individual tree and large shrub species using published allometric equations. When a species-specific coarse root biomass equation was not available, we used the equation corresponding to the species with the most similar lifeform characteristics (Burns and Honkala 1990). For jack pine, aspen, black spruce, and balsam fir at least 10 cm DBH, we used locally developed, species-specific equations (Brassard and others 2011). For white spruce and white birch at least 10 cm DBH, equations developed by Brassard and others (2011) for black spruce and aspen were used, respectively. There was no shrub at least 10 cm DBH present in any of our plots. For jack pine, aspen, black spruce, and white birch less than 10 cm DBH and *Salix* spp., we used the species-specific equations developed by Bond-Lamberty and others (2002) for central Canadian boreal forests. For white spruce and balsam fir less than 10 cm DBH, we used the equation for black spruce, whereas the equation for trembling aspen was used for *Acer spicatum*, *Alnus* spp., *Prunus pensylvanica*, *Castanea* spp., *Corylus cornuta*, and *Sorbus* spp.

For medium (2–10 mm in diameter) and fine root (≤ 2 mm in diameter) biomass data, we used the medium and fine root biomass data from a similar chronosequence study conducted close to our study area (Yuan and Chen 2012) due to time and resource limitations. As Yuan and Chen (2012) only focused on mixedwood stands, we measured fine root biomass in the 8- and 34-year-old stands across all overstorey types and developed linear regressions to estimate medium and fine root biomass for broadleaf and conifer stands.

In each 400-m² plot, seven soil cores (6.6 cm in diameter) were randomly selected to collect fine roots using a power auger. Cores were collected monthly from June–October 2014 and in May 2015, with six sampling times in total (we reported the average of six measurements). The extracted soils were separated into a forest floor layer and two mineral soil layers (0–15 and 15–30 cm) and transported in an ice-filled cooler to the laboratory, where they were stored in a freezer until processing. In the laboratory, samples were soaked in water to separate roots from the soil and then sieved (0.2-mm mesh). Fine roots were sorted according to vitality (live or dead). Live roots were

pale-colored on the exterior, elastic and flexible, free of decay, and had a whitish cortex, whereas dead roots were brown or black, rigid, and inflexible, in various stages of decay, and had a darker cortex. The ''live'' and ''dead'' components were then oven-dried separately to a constant mass at 65 °C and weighed.

We segregated the measured fine root biomass data according to overstorey type (that is, broadleaf, conifer, and mixedwood) and built linear regressions between fine root biomass in mixedwood stands and in conifer stands, and between fine root biomass in mixedwood stands and in broadleaf stands, respectively (see Figure S1). For each stand's age, medium and fine root biomass in broadleaf and conifer stands were then estimated by using mixedwood data from Yuan and Chen (2012) and locally developed regressions.

Aboveground Deadwood Carbon

Aboveground deadwood included downed woody debris (DWD) and aboveground snags. Downed woody debris was defined as all dead wood lying or standing (with a zenith angle ≤ 45°) with a mid-length diameter at least 2 cm and was measured using the line intercept method (Husch and others 2002). Two 30-m transects were established in each sample stand, radiating out from the center of each 400-m² circular plot. The first transect was oriented randomly, whereas the second was at a 90° angle to the first. The diameter at transect, species, and decay class, according to Seedre and others (2013), of all DWD pieces at least 2 cm occurring along the transect were recorded. The volume of DWD on an area basis (m³/ha) was calculated using the formula described by (Husch and others 2002):

$$\mathrm{DWD} = \frac{\pi^2 \sum d^2}{8L} \qquad (1)$$

where d is the piece intercept diameter (cm) and L is the length (m) of the transect. The volume of DWD was converted to necromass using site-specific deadwood density values developed by Seedre and others (2013).

Snags consisted of standing dead trees, with both intact tops and broken tops, and stumps, which consisted of broken top snags with heights less than 1.3 m. Standing dead trees included all trees that appeared dead with no green foliage remaining and stood with a zenith angle of greater than 45° and were at least 1.3 m in height. The DBH of all standing dead trees (> 2 cm DBH) was measured in each 400-m² plot. Aboveground necromass of standing dead trees was estimated similarly to live

tree biomass, using collected DBH data and species-specific allometric equations (Lambert and others 2005); however, to account for loss of bark and branches that accompany decay after death, all standing dead trees were grouped into one of the following three categories developed by Seedre and others (2014), and their biomasses were reduced accordingly: (1) all bark and branches remained intact (no reduction); (2) only 50% of bark and 70% of branches remained intact (thus, a 50% bark and 30% branch biomass reduction was applied); and (3) only 20% of bark and 50% of branches remained intact (thus, an 80% bark and 50% branch biomass reduction was applied).

For each snag with a broken top, diameters both at the top and at the stem base, as well as the height, were measured in each 400-m^2 plot. Each snag or stump was assigned a locally derived deadwood decay class (Seedre and others 2013). Snag and stump volume was estimated using a truncated cone formula (Husch and others 2002) and was converted to necromass using the site-specific deadwood density values locally developed by Seedre and others (2013).

Belowground Deadwood Carbon

Belowground deadwood consists of root necromass of snags and stumps. The coarse root necromass of snags and stumps was calculated similarly to live coarse roots. However, because the equations of Bond-Lamberty and others (2002) and Brassard and others (2011) were developed for live trees, dead coarse root necromass estimates have to be adjusted to reflect decay class (Seedre and others 2013). For example, an individual tree that has been dead a long time would have a more decayed coarse root system and less root necromass than an individual with a shorter time since death. To calculate dead coarse root necromass and account for mass losses due to decay, we used the following equation, which takes advantage of the strong correlation between coarse root necromass and density during decay (Olajuyigbe and others 2011):

$$CRB_{adj} = \left(\frac{DW}{LW}\right) \times CRB_{unadj} \qquad (2)$$

where CRB_{adj} is the coarse root necromass of a snag or stump after correcting for losses associated with decay, LW is the density of the individual assuming it was still alive, DW is the density of the individual in its current state of decay, and CRB_{unadj} is the calculated coarse root biomass using the equations of Bond-Lamberty and others (2002) or Brassard and others (2011) as if the individual were still alive. LW values were taken from Alemdag (1984), who reports average stem wood density values for live jack pine, aspen, white birch, black spruce, white spruce, and balsam fir from samples collected in the boreal forest of Ontario, Canada. DW values were calculated using local equations from Seedre and others (2013), derived from the same study area.

Dead medium and fine root necromass was estimated using the same method mentioned above for live medium and fine root biomass. Simple linear regressions were developed between fine root necromass in mixedwood stands and in conifer stands, and between fine root necromass in mixedwood stands and in broadleaf stands, respectively (see Figure S2). Dead medium and fine root necromass data for all mixedwood stands of our chronosequence were derived from the chronosequence study of Yuan and Chen (2012), and then, we used locally developed fine root necromass equations (see Figure S2) to calculate medium and fine root necromass data in broadleaf and conifer stands for each stand age.

Total aboveground tree biomass and tree coarse root biomass were converted to C using locally developed C concentrations estimated by Gao and others (2016). The C content of aboveground understorey vegetation was calculated as 45% of dry biomass (IPCC 2013). Belowground medium and fine root C content was similarly assumed to be 45% of dry biomass. The C content of aboveground deadwood and belowground deadwood was assumed to be 50% of dry necromass, whereas C content of dead medium and fine roots was assumed as 45% of dry necromass (Garrett and others 2012). All live biomass and deadwood C pools were scaled up to Mg C ha^{-1}.

Forest Floor and Mineral Soil Carbon

Forest floor C and mineral soil C for all sites in this study have been previously reported (Hume and others 2016). In brief, ten soil cores were randomly collected per 400-m^2 main plot using a Dutch soil auger. Soil cores were separated by forest floor (that is, the fibric and humus layers) and two mineral soil layers according to mineral soil depth, that is, M1 (0–15 cm) and M2 (15–30 cm). Soil samples were stored in a cooler and immediately transported to the laboratory for chemical analysis. Soil samples were air-dried to constant weight and sieved (2-mm mesh) to remove coarse fragments and then ground to pass through a 100-mesh (0.15 mm) sieve to ensure a uniform sample. Total C for each sample was determined by the flash

dynamic combustion method and converted to Mg C ha^{-1} following the method described by Wairiu and Lal (2003).

We did not collect mineral soil samples greater than 30 cm depth as C storage in the deep mineral soil was expected to change little over the temporal range of our chronosequence (Harden and others 1997; Wirth and others 2002; Goulden and others 2011). Nonetheless, to provide a more realistic estimate of total mineral soil C storage at each site, we used the average value of deep (30–100 cm) mineral soil C mass derived by Laganière and others (2012) from six local 92-year-old stands from our study area to approximate mineral soil C deeper than 30 cm in each of our study stands.

Data Analysis

To address our first research question of whether the direction of forest succession influences forest C storage as stands age following stand-replacing fire, we used a two-way analysis of variance (ANOVA) to test the effects of stand age and overstorey type on total ecosystem C storage. Specifically, we tested whether age-related changes in forest C storage differed among three overstorey types through examination of the interaction term as shown in the following statistical model.

$$Y_{ijk} = \mu + A_i + T_j + A \times T_{ij} + \varepsilon_{(ij)k} \qquad (3)$$

where Y_{ijk} is forest C storage, μ is the overall mean, A_i ($i = 1, 2, \ldots, 5$) represents stand age, T_j ($j = 1, 2, 3$) is the overstorey type, and $\varepsilon_{(ij)k}$ is random sampling error within stand age class and overstorey type.

For our second question, we used Tukey's honest significant difference (HSD) test to examine whether C storage increased, decreased, or showed no significant change as postfire boreal stands transitioned from mature, even-aged stands to structurally complex old-growth stands (that is, from

147- to 210-year-old stands), and whether this change in C storage was influenced by successional pathways, characterized by overstory types. Furthermore, as individual C pools transfer C among each other and have potentially different age-dependent C dynamics (Seedre and others 2011), we also performed the two-way ANOVA (equation 3) on each C pool component to test the influence of succession pathways on individual C pools to help understand underlying changes in total ecosystem C storage. We verified the ANOVA assumptions of normality and homogeneity of variance using the Shapiro–Wilk test and Levene's test, respectively. The tests revealed the assumptions of normality and homogeneity were met for all analyses without data transformation. All data analyses were performed in R 3.4.2 (R Development Core Team 2017).

RESULTS

Following stand-replacing fire, total ecosystem C changed significantly with stand age. Broadleaf stands on average had higher total ecosystem C than conifer and mixedwood stands, but age-related trends of total ecosystem C storage were similar for all three overstorey types (Table 2). Averaged across all overstorey types, total ecosystem C increased rapidly from 96.5 ± 5.1 (Mean $\pm$ S.E.) Mg C ha^{-1} in 8-year-old stands to 300.4 ± 9.4 Mg C ha^{-1} in 99-year-old stands, peaking at 327.9 ± 11.9 Mg C ha^{-1} in 147-year-old stands and then significantly decreasing to 271.1 ± 13.6 Mg C ha^{-1} in 210-year-old stands (Figure 1A).

Among all C pools, the live biomass C pool had the strongest temporal dynamics (Figure 1B). Total live biomass C was significantly influenced by stand age, overstorey type, and their interaction (Table 2, Figure 2A). Similar to changes in total ecosystem C storage, live biomass C, averaged over all over-

Table 2. Results of Stand Age (A_i) and Overstorey Type (T_j) on Total Ecosystem C and Individual C Pools Following Fire

C pools	A_i (d.f. = 4)		T_j (d.f. = 2)		$A \times T_{ij}$ (d.f. = 8)	
	F	P	F	P	F	P
Total ecosystem C	124.5	< **0.001**	6.1	**0.006**	1.5	0.202
Total live biomass	50.8	< **0.001**	4.7	**0.017**	1.8	0.112
Total deadwood	1.9	0.144	0.7	0.516	1.4	0.259
Forest floor	8.8	< **0.001**	0.5	0.591	4.0	**0.003**
Mineral soil	5.5	**0.002**	1.6	0.215	1.9	0.102

The columns give the degrees of freedom (d.f.), F value, and P value. Statistically significant terms (p < 0.05) are in bold.
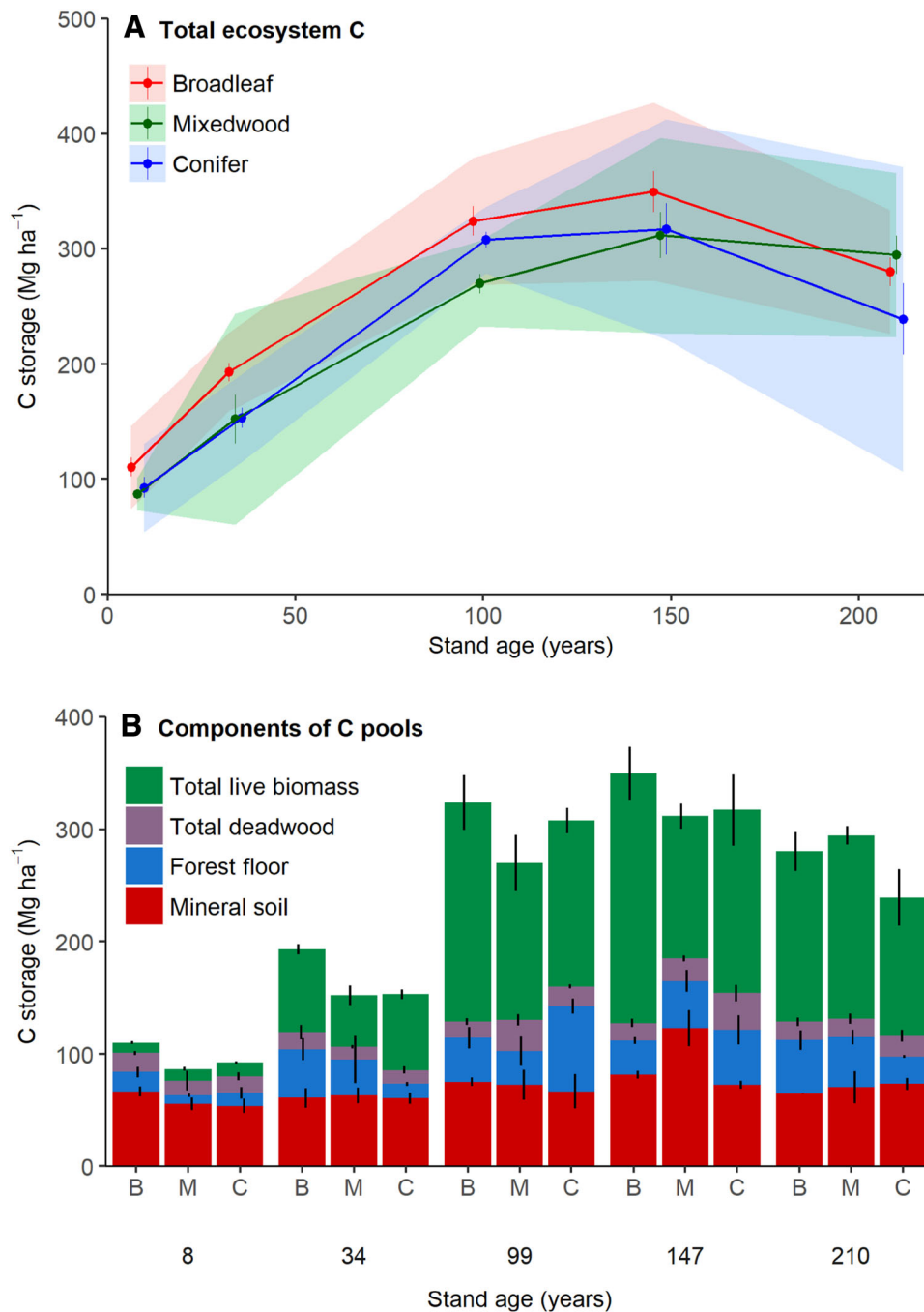
Figure 1. Carbon storage in relation to time since stand-replacing fire and overstorey type for **A** total ecosystem and **B** components of the four individual pools. Symbols and vertical lines represent sample means and standard errors, respectively, and ribbons represent the 95% confidence interval of sample means.

storey types, increased rapidly from 9.4 ± 1.3–12.6 ± 1.1 Mg C ha^{-1} in 8-year-old stands to 139.5 ± 25.1–195.1 ± 24.5 Mg C ha^{-1} in 99-year-old stands. However, age-related changes in live biomass C marginally differed among overstorey types thereafter (Table 2, Figure 2A). Conifer and broadleaf stands continued to increase to a peak of

163.1 ± 8.3 and 221.9 ± 23.4 Mg ha^{-1} in the 147-year-old stands, respectively, and then declined. In comparison, the mixedwood stands showed a slight decrease and then increased to a peak of 163.4 ± 8.3 Mg ha^{-1} in the 210-year-old stands. Total deadwood C only demonstrated a marginally significant change with stand age (Table 2,
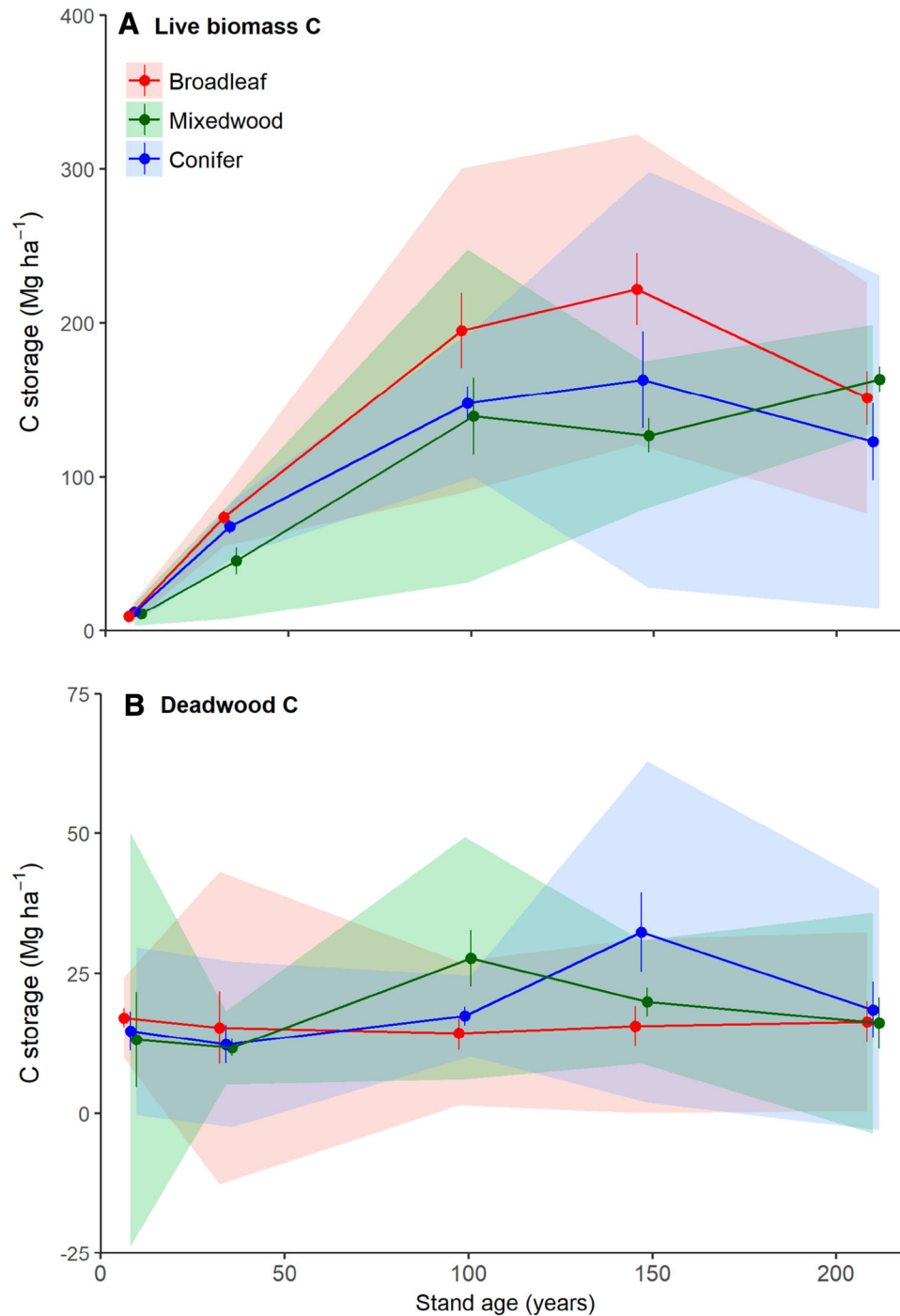
Figure 2. Carbon storage in relation to time since stand-replacing fire and overstorey type for **A** live biomass and **B** deadwood. Symbols and vertical lines represent sample means and standard errors, respectively, and ribbons represent the 95% confidence interval of sample means.

$P < 0.15$), and it did not change notably until 147 years old (Figure 2B).

Carbon storage in the forest floor changed significantly with stand age and showed a significant interaction effect between stand age and overstorey type (Table 2, Figure 3A). The forest floor C pool increased rapidly in the broadleaf and mixedwood from 8 to 34 years old, but fluctuated thereafter. It remained relatively low in the conifer stands until it peaked in the 99-year-old stands and then significantly declined in the 210-year-old stands (Figure 3A). Similar to forest floor C storage, our
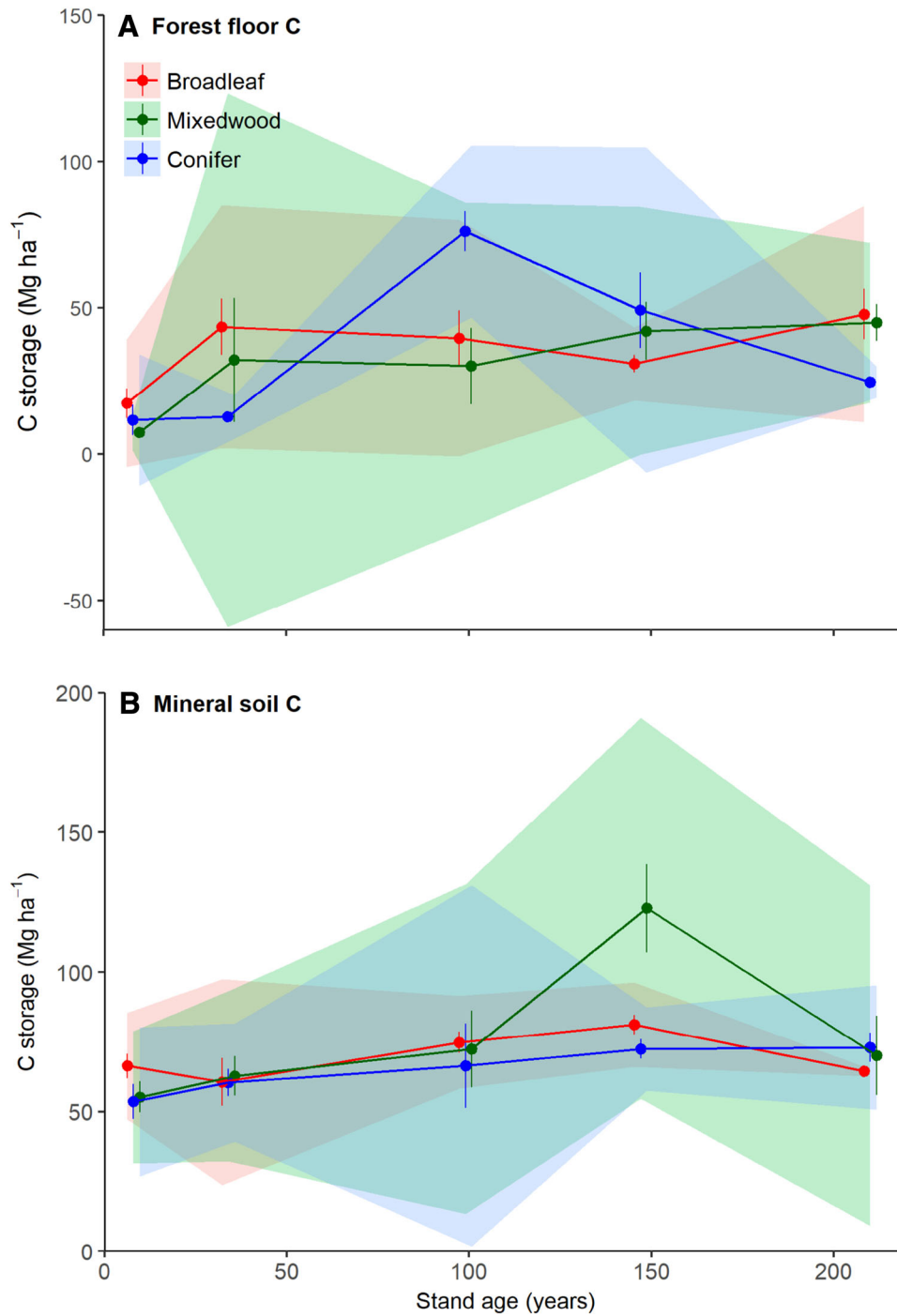
Figure 3. Carbon storage in relation to time since stand-replacing fire and overstorey type for **A** forest floor and **B** mineral soil. Symbols and vertical lines represent sample means and standard errors, respectively, and ribbons represent the 95% confidence interval of sample means.

ANOVA test indicated a significant age effect on mineral soil C storage; however, age-related changes in mineral soil C marginally differed among the three overstorey types (Table 2). Our data suggest that mineral soil C storage remained relatively stable throughout succession and that the age-re-lated effect was mainly caused by the peak in mineral soil C observed in the 147-year-old mixedwood stands. During late succession, mixed-woods had a steeper decline in mineral soil C than other types from 147- to 210-year-old stands (Figure 3B).

DISCUSSION

Carbon Dynamics Among Overstory Types

Overall, our results show a strong relationship between total ecosystem C and stand age following fire, similar to previous studies (Pregitzer and Euskirchen 2004; Goulden and others 2011; Taylor and others 2014). We found broadleaf stands had, on average, higher total ecosystem C and live biomass C than the other types, supporting a previous hypothesis that suggests aspen abundance is a key driver of ecosystem C storage in Canadian boreal forest (Pare and Bergeron 1995; Laganière and others 2015). However, despite that boreal forest stands may follow multiple succession pathways as they age, our study did not detect any significant difference in total ecosystem C dynamics between the three overstorey types over the span of our chronosequence (that is., 210 years). This suggests that succession trajectory may have little effect on total ecosystem C storage as forests age and that succession only accounts for minor variations in total ecosystem C storage dynamics as forest stands transition from mature, even-aged stands to structurally complex old-growth stands.

Although total ecosystem C storage had similar age-dependent trends among the three overstorey types, we did observe significant differences among stand types in the dynamics of individual C pools that comprise total ecosystem C, corroborating previous reports (Pregitzer and Euskirchen 2004; Seedre and others 2011). The live biomass C pool increased sharply from age 8 to age 99 years for all stand types, driving the rapid recovery of total ecosystem C storage (90% within 99 years) relative to the mean fire interval of 100 years, which agrees with a previous chronosequence study of *Pinus contorta*-dominated forests (Kashian and others 2013). However, during the late successional stage, the live biomass C pool declined substantially from age 147 to 210 years in the broadleaf and conifer-dominated overstorey types, whereas the mixedwoods continued to accumulate live biomass C, peaking in the oldest measured stands. This divergent pattern may be attributable to differences in tree mortality rates experienced among stand types. For instance, the negative effects of conspecific neighbors have been reported to increase tree mortality rates, especially for trembling aspen, white birch, and spruce (Luo and Chen 2011), which dominated our broadleaf and conifer stand types, potentially causing higher tree mortality in old broadleaf and conifer stands compared with mixedwood stands. Furthermore, due to the potential effects of resource partitioning and niche complementary, mixtures of fast-growing, shade-intolerant species (for example, trembling aspen and white birch) and slower-growing, shade-tolerant species (for example, spruce and fir) may have a positive effect on the long-term productivity of old mixedwood stands compared with less diverse broadleaf and conifer-dominated stands (Zhang and others 2012).

We also found conifer stands differ from broadleaf and mixedwood stands in the way they accumulate forest floor C, in agreement with previous reports of tree species composition effects on forest floor C storage (Laganière and others 2012, 2013). During early stand development (that is, 8 and 34 years), conifer stands contained less forest floor C than broadleaf or mixedwood stands. This may be because in young conifer stands, the main input of C to the forest floor is slow-decomposing needle leaf litter. Conversely, young mixedwood and broadleaf stands support a higher density and diversity of understory shrub and herb species (Hart and Chen 2008). The contribution of the understory vegetation combined with higher annual turnover of broadleaf litterfall (Chen and others 2017) may lead to higher C accumulation in the forest floor. However, as conifer stands age, their understory becomes increasingly dominated by shade-tolerant, bryophyte species (Hart and Chen 2008). Furthermore, cool, damp conditions, typical of conifer understory environments, impede decomposition and contribute to the accumulation of dead organic matter (Lang and others 2009). This is supported in Figure 3A by the large hump in forest floor C in the conifer stands during the intermediate stages of stand development (that is, the 99-year-old stands). Eventually, as conifer stands undergo canopy breakup and transition to structurally complex old-growth stands, increased light to the forest floor can enhance forest floor decomposition and alter understorey vegetation composition (Laganière and others 2012; Kumar and others 2017).

Correspondingly, we observed marginal differences in mineral soil C dynamics among the three overstorey types. Mixedwood stands had higher mineral soil C in 147-year-old stands, but then declined more sharply, thereafter, compared with the other overstorey types. High mineral soil C storage in the 147-year-old mixedwood stands may relate to the positive contribution of species diversity on fine root productivity and mortality (Jacob and others 2014; Ma and Chen 2016), which is the major input of C to the mineral soil layer in boreal

forests (Clemmensen and others 2013). The potential increase in soil organic matter decomposition in the oldest mixedwood stands (> 147 years old) may be attributable to the effects of the litter mixture on local decomposers, relative to broadleaf and conifer stands. For instance, chemically divergent litter quality combined with increased surface temperature, due to late-succession canopy breakup, can promote the abundance and activities of decomposers (Gartner and Cardon 2004) and thus accelerate decomposition in late succession.

Despite that other similar chronosequence studies have observed ''U'' shaped trends in deadwood abundance over time, with high deadwood abundance immediately following disturbance and again during late succession (for example, Kashian and others 2013; Taylor and others 2014), we observed only marginal age-related changes in total deadwood C for all three overstorey types over the span of our chronosequence. The abundance of deadwood in younger forests is largely dependent on the intensity and severity of fire as well as prefire site condition such as stand density (Flannigan and others 2000; Wang and others 2003). The low deadwood C we observed in the 8-year-old stands may have resulted from high intensity and severity fire and/or prefire stands were dominated by small-sized, young trees, thus leading to low postfire deadwood abundance on our sites (see Figure S3). Further, we observed relatively stable deadwood C throughout late succession, consistent with previous studies in our area (Brassard and Chen 2008). Despite the potential for high inputs of mortality originated deadwood during the canopy transition stage of stand development (that is, the 99- to 147-year age cohorts), most of this deadwood would decompose over 60 years (Angers and others 2010), leading to low deadwood abundance between in the 210-year-old stands. Further, the oldest stands were also dominated by faster decomposing balsam fir and white birch stems, which may also have contributed to low observed deadwood.

Carbon Dynamics During Late Succession

Overall, within the timeframe of our chronosequence, our results showed a significant decline in total ecosystem C storage (that is, negative NEP) as stands transitioned into late succession. Our findings conflict with the view, based largely on chronosequence studies that do not consider forest succession, that old forests may slow in their rate of C accumulation, but still continually accumulate C (Odum 1969; Luyssaert and others 2008; Goulden and others 2011; Kashian and others 2013; Gough and others 2016). Our observed decline in total ecosystem C storage during late succession was previously reported by Taylor and others (2014) in the same study area, but this study only considered a single succession pathway, with limited sample plots. By expanding the sample size to include different forest overstorey types to account for multiple succession pathways, our study adds further support for the hypothesis that as boreal forests age and transition into late succession, they undergo a decline in total ecosystem C storage. Of course, it is reasonable to point out that old stands cannot decline in perpetuity, or else they would disappear. Thus, it remains to be observed how long this decline phase persists and at what point do old boreal forests achieve a steady C state balance (if ever) since plant diversity is expected to increase after canopy transition (Roberts and Gilliam 1995), likely promoting C uptake and storage in forests (Liang and others 2016; Zhang and others 2017).

It is worth noting, however, that forest companies in our study area preferentially harvest mature, ''productive'' stands. Consequently, this may induce bias in our sample of old stands since it is conceivable that the old, 210-year stands (ca. 3000 ha of our study area, which is approximately one million ha) represent less desirable, low-productivity stands left unharvested, which could have artificially driven the decline in C storage we observed in late succession. However, commercial forestry in our study area did not begin until the mid-1970s and targeted mostly pure jack pine stands less than 120 years old. Our oldest stands, which were almost 160 years old in the 1970s, were beyond the preferred age for harvesting in the area at that time and, consequently, were left unharvested. Thus, the possibility of ''cherry-picking'' low-productivity, 210-year-old stands is low and confirmed from our personal communications with the long-term District Forester in this area, Paul Poschmann, who has been working as the area forester since the mid-1970s.

Although our results show an overall decline in total ecosystem C storage, the mechanisms that drive this decline seemed to differ according to overstorey type. For instance, a reduction in live biomass C, mainly resulting from increased tree mortality during canopy transition, led to total ecosystem C decline after year 147 in broadleaf and conifer stands. However, the decrease in total ecosystem C observed in mixedwood stands was

largely driven by decreases in mineral soil C, suggesting that an increase in decomposition may be an important driver of total C decline. Nonetheless, the generality of these hypotheses needs further investigation that explicitly examines C flux (for example, forest production, tree mortality rate, and decomposition) while also considering multiple succession pathways.

By accounting for multiple succession pathways, our results show a strong relationship between total ecosystem C storage and stand age following fire. Broadleaf stands had on average higher total ecosystem C; however, temporal dynamics of total ecosystem C were similar among all three overstorey types. Moreover, we show that total ecosystem C storage declines during canopy transition to late-succession forests, irrespective of successional pathway, conflicting traditional views that old forests continually accumulate C as they age. However, further studies that include stands older than 200 years must be conducted to determine how long this decline phase persists and at what point do old boreal forests achieve a steady C state.

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