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RESEARCH ARTICLE

Early departures and delayed arrivals: Holocene dynamics of temperate tree species in the boreal-temperate ecotone

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Abstract

1. Understanding historical dynamics of peripheral populations over the Holocene provides key insights to anticipate species responses to ongoing global changes. A marginal stand at the leading edge of sugar maple (*Acer saccharum*) range was hereby investigated to infer the Holocene dynamics of sugar maple, red maple (*Acer rubrum*), eastern white pine (*Pinus strobus*), three prominent temperate tree species of the boreal–temperate forest ecotone in eastern Canada.
2. Soil macrofossil charcoal analysis of 25,595 charred wood particles revealed that white pine is detected at this marginal temperate forest site since the early Holocene, red maple since the mid-Holocene and sugar maple since the late-Holocene.
3. The transition from the warmer mid-Holocene to the cooler late-Holocene was marked by a decrease of white pine, which was expected because the environmental envelope of temperate species shifted southward in response to lower mean temperatures of the Neoglacial. In contrast, the abundance of sugar and red maples increased during the cool late-Holocene period.
4. There was a significant lag between the establishment of maples, whereby the hardier red maple was found since the warmer mid-Holocene, while the cold intolerant sugar maple was only detected during the cooler late-Holocene. A shift in the fire regime, a disruption of coniferous priority effects in the soil, as well as the introduction of shared mycorrhizal fungi might tentatively explain the late establishment of maples and the migration lag between the two species.
5. *Synthesis*. As temperate tree species require warmer temperatures than boreal species, some thermophilous species such as white pine increased in abundance at their northern edge during historically warmer periods. Our data reveal that not all temperate species behaved accordingly: maples were scarce during the warm

mid-Holocene, while their abundance increased during the cool late-Holocene. A migration lag suggests that an earlier arrival of generalist species such as red maple might be required to facilitate the later establishment of specialists such as sugar maple. The historic decoupling between macroclimatic trends and temperate species range shift sheds new light on the potential responses of the boreal–temperate ecotone facing modern-day anthropogenic climate change.

KEYWORDS
Acer rubrum (red maple), *Acer saccharum* (sugar maple), boreal-temperate ecotone, forest dynamics, leading edge, marginal populations, *Pinus strobus* (eastern white pine), soil macrofossil charcoal analysis

1 | INTRODUCTION

Species ranges are driven by several factors, including macroclimate, topography, disturbances, soil properties and biotic interactions. Within a geographic range, individuals may vary in the way they interact with their environment (Valladares et al., 2014). For instance, individuals found at the core of the range might have different life-history strategies compared to those in marginal populations at the edges of the range, where populations are typically smaller and more isolated from one another (de Lafontaine et al., 2018; Nadeau & Urban, 2019; Rehm et al., 2015). These differences might reflect local adaptation (including adaptive plasticity) to environmental conditions at the limit of bioclimatic envelopes (Kawecki, 2008), spatial sorting of individuals for increased migration capacity (Shine et al., 2011) or adaptation to contrasted disturbance regimes (Keeley et al., 2011; Pelletier & de Lafontaine, 2023), among others. Peripheral populations at the edge of a species distribution typically experience suboptimal conditions and risk extinction from demographic stochasticity; hence, their resilience is closely tied to changes in their local environment (Antonovics et al., 2006; Lesica & Allendorf, 1995). Thus, while most populations within a species' range can withstand some changes in their environment through adaptation, migration and/or plasticity, the effects of climate change and associated biotic responses should be exacerbated in isolated marginal populations, as they are already at the edge of their bioclimatic envelope. Such sensitivity makes range-edge populations ideal case study models to assess long-term dynamics and population responses to climate change (Saulnier-Talbot et al., 2024). In turn, assessing historical dynamics of peripheral populations over the Holocene has the potential to reveal long-term patterns of interaction with various species, climatic conditions and other environmental variables, which might be useful to anticipate putative species responses to ongoing global changes (de Lafontaine et al., 2018).

The boreal-temperate forest ecotone (BTE) represents the interface between two expansive and cosmopolitan biomes (Goldblum & Rigg, 2010; Saucier et al., 2009). It is characterized by a mixedwood canopy, containing patches of broadleaf-deciduous species, conifers or a combination of both, whose distribution is dictated by topographic and climatic factors, which create patterns of heterogeneous fire regimes whereby coniferous-dominated stands burn more often and with more severity than their deciduous-dominated neighbours (Goldblum & Rigg, 2010). The prevalence of fire in the disturbance regime of the boreal forest and, by extension, within the BTE, implies that the effect of macroclimate on the ecotone's forest mosaic can be indirect or entirely decoupled because forest composition may have a greater proximal effect on fire than climate alone (Carcaillet et al., 2001). Since these variables (fire and climate) are often entangled, research into the dynamics of the BTE on long temporal scales could help isolate some factors that had more bearing on its paleoecological trajectory. Although the BTE is cosmopolitan, the most pristine example of the ecotone is found within eastern Canadian forests, where human activity is present, but to a much lesser extent than in Eurasia, making it a prime location for research on natural ecosystems (Evans & Brown, 2017). As for other ecotones, several tree species reach their range limit within the BTE. For instance, the northern part of the BTE hosts the leading edge (i.e. northern boundary) of eastern white pine (*Pinus strobus*; hereafter white pine), sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*) (Goldblum & Rigg, 2010). Thus, changes in macroclimate and disturbance regimes can induce rapid shifts in the latitude and composition of the BTE. Reconstructing past forest composition and dynamics in marginal stands within the BTE might provide valuable insights about historical changes in the ecotone in response to environmental factors.

Global temperatures progressed through three main stages during the Holocene: a cool early-Holocene, a warm mid-Holocene, with temperatures higher than today and a final cool late-Holocene (Marcott et al., 2013). Although this broad pattern was global, there were substantial regional differences in the exact timing of each period. For example, within North America's BTE, the warm mid-Holocene was somewhat delayed due to the presence of the Laurentide ice sheet (Bajolle et al., 2018). Still, the warm temperatures of the mid-Holocene Climatic Optimum (Hypsithermal interval) were beneficial to some North American temperate tree species. For instance, white pine (Terasmae & Anderson, 1970), American beech (*Fagus grandifolia*) (Bennett, 1988; Cogbill, 2005), yellow birch (*Betula alleghaniensis*) (Larochelle et al., 2018) and possibly eastern white cedar (Jules et al., 2018) readily tracked their optimal climatic conditions and extended towards their northern limit, starting *c.*

8000 calibrated years before present (cal year BP). It is generally assumed, though not empirically tested, that most temperate tree species followed a similar pattern, which led to the assertion that this was a period of increased species biodiversity in the northern part of the BTE (Richard et al., 2020). The end of the mid-Holocene and beginning of the late-Holocene Neoglacial cooling period, *c.* 4000 cal year BP, led to a general decline in temperature and thus a putative degradation of environmental conditions for temperate species, potentially triggering their collapse in the boreal forest and a southward shrinkage of their distribution (Liu, 1990; Richard et al., 2020). Along with decreased temperatures, the cool late-Holocene was marked by an increase of fire size and severity, as well as a reduction in air mass stability, leading to an increase in the abundance of boreal conifer species adapted to stand-replacing wildfires (Ali et al., 2012; Blarquez et al., 2015). Some temperate species then retreated from the northern parts of the BTE, such as white pine (Terasmae & Anderson, 1970), which is a relatively thermophilous species better adapted to repeated low-intensity surface fires. The Holocene dynamics were likely instrumental in shaping the northern BTE continuum, that is, a relatively homogeneous boreal forest matrix with scattered inclusions of northern hardwood stands whose abundance decreases along the latitudinal gradient. However, it is still unknown whether all temperate species responded similarly, or whether other ecological constraints have shaped contrasted historical trajectories.

Leading-edge tree populations can either originate from long-distance dispersal events during range expansion or represent relict populations following the collapse of a once more extensive distribution (de Lafontaine et al., 2018). Although small and isolated, these stands are located at the geographical vanguard and might thus serve as predispersed outposts, fostering species' capacity to track climate change velocity through the rapid colonization of the local landscape following an improvement of environmental conditions (Davis & Shaw, 2001). Their presence plays a crucial role in mitigating constraints on migration potential, including limited seed dispersal distances (McLachlan et al., 2005), preferential browsing (Brown & Vellend, 2014) and long generation time (Petit & Hampe, 2006). For instance, leading-edge populations have already been instrumental for the contemporary northern expansions of some species (Solarik et al., 2018). Yet, marginal populations are typically limited by conditions at the limit of species' bioclimatic envelope as well as other biotic (Brown & Vellend, 2014) and abiotic (Boisvert-Marsh & de Blois, 2021; Carteron et al., 2020) factors. To overcome these limitations, tree species might alter their environments by establishing soil priority effects through leaf litter and phenol diffusion (Solarik et al., 2020), by modifying disturbance regimes through canopy structure and humidity (Hély et al., 2000) and by introducing beneficial companion species, such as mycorrhizae (Collin et al., 2018). For instance, warmer temperatures can foster the establishment of some generalist temperate tree species in boreal environments that are otherwise inhospitable to other temperate species. More specialist temperate species may thus lag behind climate improvement as they require the initial presence of generalist broadleaf species to break the ecological inertia of conifer-dominated stand dynamics and alter the boreal forest environment enough to allow their establishment. Based on regional-scale paleopollen reconstructions from lake sediments, Paillard et al. (2023) suggested that early establishment of broadleaf species, such as white birch (*Betula papyrifera*) and/or yellow birch, facilitated later establishment of sugar maple at the northern limit of the BTE. Furthermore, Dumont et al. (2024) analysed local-scale soil macrofossil charcoal particles in a marginal stand at the northern limit of both red and sugar maple. They reported a 3000-year lag between the generalist red maple and the specialist sugar maple, which they ascribed either to the facilitation process or a dispersal limitation of the later colonist. However, their study relied on relatively few fossil remains; thus, further efforts are required to elucidate the origin and population dynamics at the leading edge of temperate species within the northern part of the BTE.

Soil macrofossil charcoal analysis (SMCA) relies on botanically identifying and radiocarbon dating wood charcoal particles >2 mm recovered from inorganic soils. The approach has proved to be a valuable paleoecological tool to infer past dynamics of small marginal forest stands (de Lafontaine et al., 2014). When a fire consumes forest trees, charcoal particles are produced because of incomplete combustion of woody material (Bird et al., 2015). Although deciduous stands are less fire-prone compared to conifer-dominated stands, the trees within both stands are equally susceptible to produce such charred fragments during a given fire event (Fréjaville et al., 2013; Hély et al., 2000). Once generated, charcoal particles >2 mm are deposited and buried in situ and are thus seldom remobilized extra-locally (a few meters at most; Ohlson & Tryterud, 2000). Additionally, once charcoal particles are integrated into the mineral component, they remain mostly recalcitrant to physical, chemical and biological degradation in the soil environment for several millennia (de Lafontaine et al., 2011; de Lafontaine & Asselin, 2011). Microanatomical features of macrofossil wood charcoal particles enable taxonomic identification of the trees that were consumed (Vernet et al., 2002). Wood charcoal particles are amenable to direct and reliable radiocarbon dating due to their high carbon content and low risk of contamination (Libby & Johnson, 1955). Their short dispersal distance enables stand-scale reconstructions (Payette et al., 2012; Talon et al., 2005) and comparisons of past forest dynamics at a fine spatial scale (de Lafontaine & Payette, 2011, 2012). Interpreting such high-resolution inferences in light of regional-scale reconstructions, such as from lake sediment paleopalynological analyses, represents a robust approach to decipher historical responses of tree species to past climate change (Minchev & de Lafontaine, 2024; Remy et al., 2018).

Elucidating long-term dynamics of temperate species in response to past climate change could provide key insights about the present and future trajectory of the BTE. To this end, we hereby focus on white pine, red maple and sugar maple, three prominent temperate species whose leading-edge stands reach the northern part of the BTE. White pine is a coniferous tree species that appears to have readily tracked past climate changes and was dominant in the study region during a large part of the Holocene

(Bajolle et al., 2018; Bussières et al., 2023; Paillard et al., 2023; Richard et al., 2020). Red maple is a generalist temperate broadleaf tree species that is seldom dominant in the canopy, but whose abundance appears to be closely tied to shifts in climate and fire regime (Mondou Laperrière et al., 2024). The species thrives in a variety of environmental conditions, ranging from dry uplands to wetlands and tolerates a wide range of soil types, moisture levels and pH conditions. Red maple is also well adapted to disturbances such as fire, logging and land-use changes (Abrams, 1998; Ostrowsky & Ashton, 2022). Finally, sugar maple is a specialist temperate broadleaf tree species that is dominant in the deciduous forest south of the BTE, and whose increase in abundance within the ecotone could eventually lead to a biome shift. The species is among the most shade-tolerant tree species in Eastern North America, which fosters its establishment in forest understory conditions and small canopy gaps (Ashton et al., 1999; Canham, 1988). Nevertheless, sugar maple requires well-drained, mesic soils rich in nutrients (Collin, Messier, Côté, et al., 2016).

This study relies on SMCA to reconstruct stand-scale Holocene dynamics at the leading edge of the three focal temperate taxa reaching the northern limit of the BTE in eastern North America. Our null working hypothesis posits that the limit of the northern temperate forest assemblage closely tracked Holocene climate shifts, with temperate tree species migrating northward in sync with warmer periods and retreating during colder phases. However, based on previous paleoecological reconstructions from lake sediments within the study site (lake Labelle; Paillard et al., 2023) and SMCA reconstructions from various sites elsewhere within the northern part of the BTE (Dumont et al., 2024; Mondou Laperrière et al., 2024), we rather predict individual species responses. Specifically, we hypothesize that white pine and red maple have readily tracked past climate changes, while sugar maple has lagged behind, as it might depend on the earlier establishment of other broadleaf species to break legacy effects (Dumont et al., 2024; Paillard et al., 2023).

2 | METHODS

2.1 | Sampling site and study species

The Ruisseau-Clinchamp forest (RC forest; 48.18° N, −79.46° E) is located within the balsam fir-white birch bioclimatic domain, which represents the northern part of the BTE in the province of Québec, Canada (Figure 1). Climate is subpolar with mean January and July temperatures of −17.5°C and 17.3°C, respectively. Mean annual precipitation amounts to 805 mm, with 29% falling as snow (Montbeillard station 1973–1996; Environment and natural resources Canada). RC forest surrounds Lake Labelle, where a thorough paleoecological analysis of lake sediments was recently conducted (Paillard et al., 2023). The forest includes a few isolated stands of the target temperate tree species interspersed within the regional matrix dominated by balsam fir (*Abies balsamea*) along with various amounts of aspen, white birch, white spruce (*Picea glauca*) and black spruce (*P. mariana*). Low-altitude stands are mainly on clayey soil, while higher altitude soil is mostly till. Sugar and red maple are among the most widespread temperate broadleaf species of the deciduous forest in northeastern North America. In Canada, sugar maple distribution reaches the Canadian Maritimes in the east and southern Québec and Ontario in the west (Godman et al., 1990; Figure 1a), whereas red maple extends slightly further north (Figure 1b). Marginal populations of both maple species are mainly found atop hills (red maple) or midway down the slopes (sugar maple) but are scarce to non-existent at lower elevations (Gosselin et al., 1998). White pine is a temperate conifer whose distribution broadly overlaps that of sugar maple (Figure 1c). While it can grow alongside maple in mesic, nutrient-rich sites, white pine is more tolerant of dry, nutrient-poor soils and is well adapted to a regime of frequent, low-severity surface fires (Wendel & Smith, 1990). All three species reach their northern limit within the BTE, where they form isolated stands.

2.2 | Fieldwork

A grid of 4 km^2 (2 km × 2 km) with a 200-m spacing was centred on a sugar maple stand located at the core of the RC forest (Figure 1d). Within this grid, two sampling methods were used: grid- and plot-based. For the grid-based method, observation points were placed at 50-m intervals along the 10 east–west transects forming the 4-km^2 grid, excluding impassable areas, such as over bodies of water (total $n = 390$ observation points; Figure 1d). At each point, forest composition was inventoried by recording the presence and estimated abundance of each tree species within a 360° field of vision centred on the point, with ranges reaching *c.* 25 m, although this was variable according to stem density (Saucier et al., 1994). This procedure allowed us to more comprehensively assess the local presence and relative abundance of all temperate tree species within the RC forest: sugar maple, red maple, yellow birch, eastern white cedar and white pine. Furthermore, every 200 m along the same transects, the inorganic soil was sampled for SMCA. At each sampling microsite, care was taken to remove the organic soil and clean the interface layer between the organic and inorganic soil compartments, thus reducing the risk of contamination of samples by charcoal particles from the last fire that may be overrepresented in the organic topsoil due to insufficient pedoturbation. The inorganic soil was then sampled using a 750 cm^3 root auger (Eijkelkamp, Netherlands) and kept in plastic bags at room temperature until laboratory analyses. Lakes, ponds or mires hindered sampling at 5 of the 100 microsites (total $n = 95$ soil samples within the grid).

Based on identification data and species abundance from the grid sampling method, three stand types were selected for the plot-based method: (1) balsam fir and white birch stands (WBF) representative of the regional conifer-dominated forest matrix of the northern BTE, (2) sugar and red maple stands (SRM) representative of leading-edge marginal populations of these two target species and (3) eastern white cedar and yellow birch stands (YBC) representative of other temperate species. Two stands of each type were

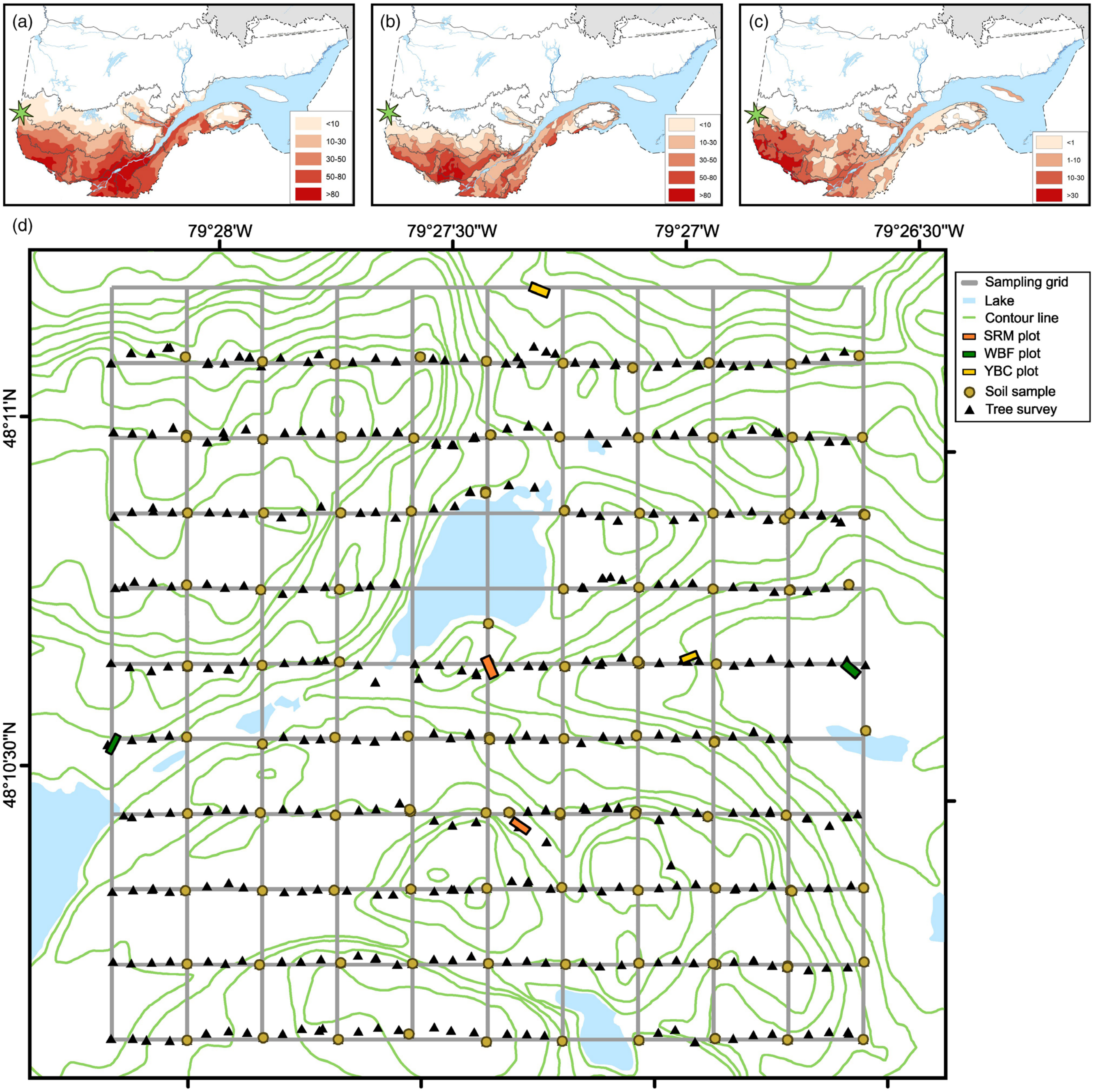

FIGURE 1 Distribution and abundance of *Acer saccharum* (a), *Acer rubrum* (b), and *Pinus strobus* (c) in the province of Québec, Canada. The green stars indicate the location of the Ruisseau-Clinchamp forest, and the different shades of red represent the relative abundance of each target temperate tree species in Québec's Ministry of Natural Resources and Forests inventory plots (Morneau et al., 2022). Sampling design within the 4 km^2 study area (d).

sampled ($n = 6$ sampling plots; Figure 1d). Within each 1000-m^2 plot (50 m × 20 m), all trees were botanically identified and measured (diameter at breast height, DBH; 1.3 m height). Additionally, regeneration was estimated by tallying seedlings and saplings ($DBH < 2$ cm) using ten 4 m^2-subplots spaced every 5 m along the 50-m length of the plot. Finally, inorganic soil was sampled at 25 microsites (located at 5 m intervals along the periphery and in the centre of the plot) following the approach described for the grid-based method (total $n = 150$ soil samples in the plots).

2.3 | Laboratory

All soil samples ($n = 245$ samples) were immersed 12–24 h in a 1% sodium hydroxide (NaOH) or 2.5% sodium hexametaphosphate ($(NaPO_3)_6$) solution for sandy or clayey samples, respectively. This step dispersed soil aggregates, which helped release charcoal particles. The material was then washed under running water for 10 min in a sieve column of 4 mm and 2 mm mesh sizes on an automatic vibratory wet sieve shaker (Retsch, Germany). Charcoal fragments were manually extracted from the sieved debris under a stereomicroscope (Olympus, Japan), dried at room temperature and weighed to the nearest 0.1 mg using an analytical scale (Sartorius, Germany). Charcoal particles ≥2.5 mg were identified to the lowest taxonomic level possible under an optical microscope mounted with an episcopic light source (Olympus, Japan) at magnifications between 25× and 500×. To optimize the taxonomic identification effort, a maximum of 20 particles per soil sample were assayed. Taxonomic identification relied on wood microanatomical criteria following botanical keys (IAWA Committee, 1989, 2004; Hoadley, 1990; Schoch et al., 2004; Vernet et al., 2002), and a charred wood reference collection (Université du Québec à Rimouski, Rimouski, Canada). Maples were identified by helical thickenings on vessel elements, with sugar maples having large (>8 seriate) rays as well as uniseriate rays, thus being heterogeneous, whereas soft maples have either 1–3 seriate or 4–8 seriate rays but are always homogeneous. In the study area, soft maples can include red maple and mountain maple (*Acer spicatum*), which are virtually indistinguishable based on the microscopic anatomy of their wood. However, in practice, we will hereby interpret soft maple identifications as red maple because mountain maple is a shrub species with far less wood biomass compared to red maple. This difference in relative abundance of available fuel is further compounded by the probability that the smaller shrub stems are more likely to fully combust during a fire, thus leaving no charcoal fragments, as illustrated by the scarcity of shrub taxa in our (and other) mineral soil charcoal records (see Section 3; Talon et al., 2005). White pine was identified using the presence of 1–2 large fenestriform pits in cross-fields. Although not strictly impossible, it would be quite time-consuming to attempt distinguishing white pine from red pine (*Pinus resinosa*) based on microscopic wood anatomy. Because lacustrine pollen reconstruction does not indicate the presence of red pine in our study area during the Holocene (Paillard et al., 2023), and since this species is currently absent in the RC forest, it is safe to assume that these charcoal particles are white pine.

2.4 | Radiocarbon dating

Maple (*Acer saccharum*, *A. rubrum* and *Acer* sp.) and white pine charcoal fragments were radiocarbon dated by Accelerator Mass Spectrometry (^{14}C-AMS) at the Radiochronology Laboratory of the Centre for Northern Studies (Université Laval, Québec, Canada) and the Keck Carbon Cycle AMS Facility (University of California, Irvine, USA). Selection of charcoal fragments to be radiocarbon dated focused on the three target temperate species. For each soil sample (grid and plot) containing maple charcoal, one charred maple particle was dated ($n=9$ *Acer saccharum*, 25 *A. rubrum* and 14 *Acer* sp.). White pine greatly outnumbered maple in the charcoal record (see Section 3), hence only charred white pine particles from soil samples (plot) containing maple charcoal were dated ($n=11$ *Pinus strobus*). Wherever more than one charcoal fragment met these criteria, the charred particle to be dated was randomly selected.

2.5 | Statistical analyses

Radiocarbon ages ($n=59$ dates; ^{14}C year BP) were calibrated (cal year BP; 2σ range) using the IntCal20 curve (Reimer et al., 2020) implemented in the *calibrate* function of the *rcarbon* R package (Crema & Bevan, 2021). Stand-scale histories were compiled using the *spd* function of the *rcarbon* package to create summed probability graphs and detect individual fire events. All calibrated dates, grid- and plot-based, were then pooled together using the *spd* function and composite kernel density estimates (CKDE; Brown, 2017) were generated for each target species from 10,000 sampling repetitions and a 100-year kernel bandwidth using the *sampleDates* and *ckde* functions of the *rcarbon* package. The aim of this procedure was to infer target species' historical demographic trajectories from time-frequency changes of radiocarbon dates (Crema, 2022). Statistical analyses were carried out in R 4.1.3 statistical software (R Core Team, 2021).

3 | RESULTS

3.1 | Forest composition and structure

Assessment of forest composition based on the grid-based method allowed us to identify three stand types that were further investigated with a plot-based method. For each stand type, two locations deemed representative were selected to establish sampling plots ($n=6$ plots). Tree-size distribution of the six sampled stands shows that, while there are clear differences between the three stand types, replicates for each forest type were similar (Figure 2). All three stand types displayed a reverse J-shape tree-size structure, indicative of old-growth forests with continuous regeneration (Pach & Podlaski, 2015) and dominant individuals reaching over 54 cm DBH (Figure 2). SRM stands were dominated by red and sugar maples, the latter representing the largest trees in both replicates, along with white birch (Figure 2a,b). Red maple, not sugar maple, was also found in the other stand types (WBF, YBC), but was sparser and mostly limited to smaller size classes. WBF stands were dominated by large white spruces and white birches, whereas balsam fir was most abundant in smaller size classes and the regeneration stratum (Figure 2c,d). In fact, coniferous species such as balsam fir and white spruce were generally present in all stand types, though white spruce only achieved dominance in coniferous WBF stands, while fir was ubiquitous, but only in the smaller size classes (<20 cm DBH). YBC stands were most diverse, but only yellow birch and eastern white cedar were found in all size classes, from the regeneration stratum up to the largest trees (Figure 2e,f). Although white pine is scant in the RC forest, it is worth noting that it was entirely absent from the inventoried plots; hence, it does not appear as a major component of the most common stand types.

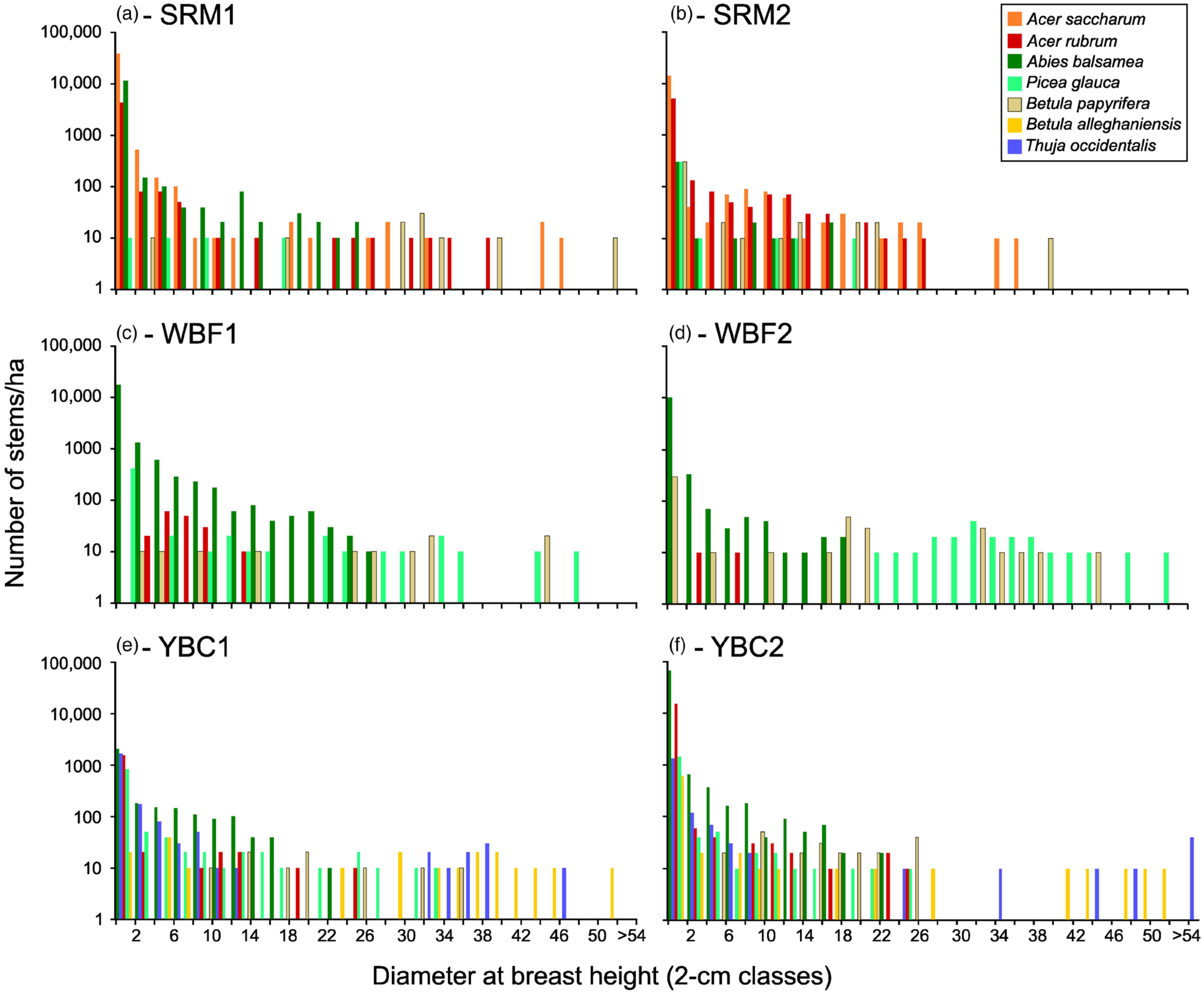

FIGURE 2 Tree-size structure of sugar maple-red maple (SRM) stands (a and b), balsam fir-white birch (WBF) stands (c and d) and eastern white cedar-yellow birch (YBC) stands (e and f) representative of the Ruisseau-Clinchamp forest. Note logarithmic scale of the number of stems ha^{-1} on the *y* axis.

3.2 | Past and present occurrences of the three target temperate species

Relative abundance of the three target temperate tree species within the RC forest was estimated from 390 observation points distributed across the 4 km^2 grid. Red maple was found throughout the sampling grid, at 312 out of 390 (80%) observation points, whereas sugar maple (40/390; 10%) and white pine (48/390; 12%) were more sporadic (Figure 3). The presence of macrofossil charcoal particles in the soil samples gathered from 95 microsites across the grid was used to estimate historical occurrences of each target species. Red maple and sugar maple charcoal particles were recovered in 15 and 4 of the 95 soil samples (16% and 4%), respectively. Hence, the two maple species were relatively less abundant in the fossil record compared to modern-day observations. By contrast, white pine charcoal particles indicative of past occurrence were relatively more abundant (34/95; 36%) than their contemporary distribution would suggest, with numerous charcoal fragments being found far from living individuals (Figure 3). Living sugar maple and white pine trees were seldom found together at observation points, with sugar maple mostly in the centre and northwest quadrant of the grid, whereas white pine was chiefly restricted to the northeast and southeast corners.

3.3 | Stand-scale Holocene dynamics of the three target temperate species

A total of 25,595 macrofossil charcoal particles were extracted from all soil samples, of which 9365 were recovered from the grid and 16,230 from the six sampling plots. A total of 1598 and 1931 fragments were partially or successfully identified from the grid and the plots, respectively. The number of macrofossil charcoal particles

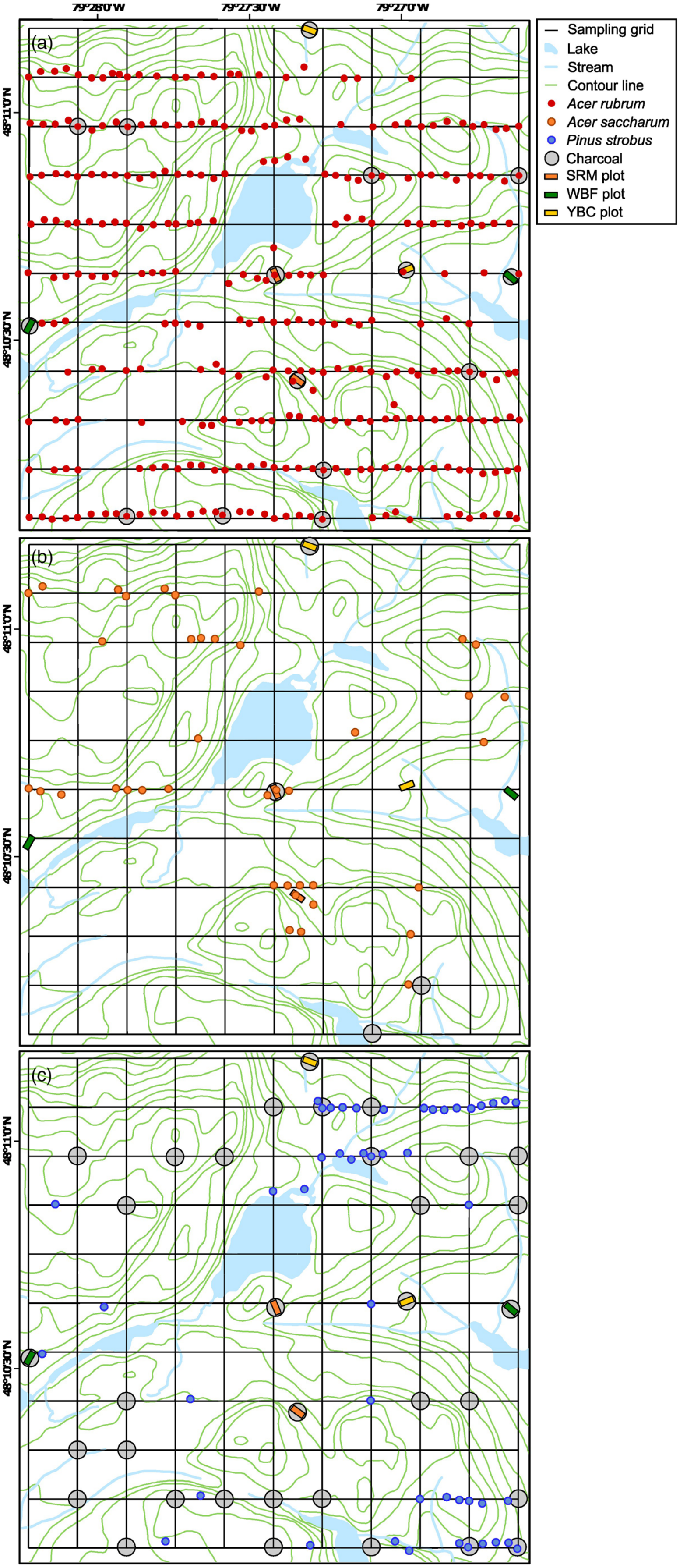

FIGURE 3 Modern-day distribution (coloured dots) and historical occurrences of (open circles) *Acer rubrum* (a), *Acer saccharum* (b), and *Pinus strobus* (c) on a 4 km^2 study site at the Ruisseau-Clinchamp forest. Tree composition was surveyed at 390 observation points, and the presence of macrofossil charcoal particles was assessed from 95 soil samples across the sampling grid.

differed between the different stand types ($F_{2,144} = 7.3$, $p < 0.001$), with significantly more fragments recovered from YBC stands compared to SRM and WBF stands (Figure 4A). Modern-day forest stand composition differed from soil macrofossil charcoal spectra (Figure 4B,C). For instance, maple stands (SRM) are currently dominated by broadleaf species, while the charcoal assemblage is mostly represented by conifers. Indeed, maple species represent a low proportion of the charcoal record compared to their modern-day relative abundance within the stands. By contrast, charcoal particles identified as *Abies* sp./*Thuja* sp. (likely balsam fir) dominate the fossil record, although balsam fir is currently a minor component in SRM stands. Past reconstruction at WBF and YBC stands is somewhat closer to present forest composition, but there are still some discrepancies, namely the larger proportions of fir or spruce in modern-day stands compared to the fossil record. Fossil evidence of sugar maple was recovered in two stands (SRM1 and YBC2) whereas red maple macrofossil charcoal was found in all sampled plots. Interestingly, white pine charcoal was readily found in the soil of all sampled plots, despite the species being currently absent from these six plots.

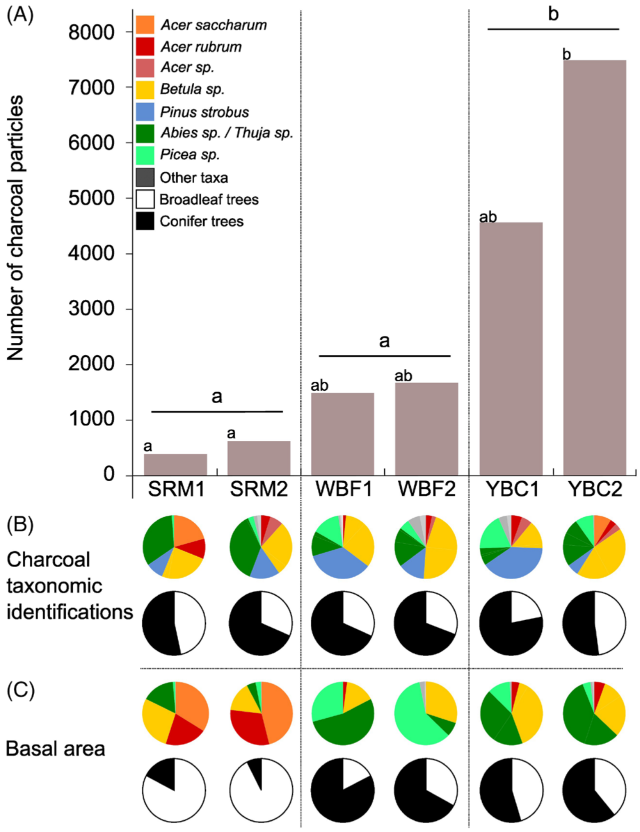

FIGURE 4 Soil macrofossil charcoal record (A, B) and relative basal area of tree species (C) at sugar maple-red maple (SRM) stands, balsam fir-white birch (WBF) stands and eastern white cedar-yellow birch (YBC) stands representative of the Ruisseau-Clinchamp forest. Bars represent the total number of charcoal particles extracted from soil samples. Different letters indicate statistically significant differences between sampling plots or stand types (A). Pie-charts indicate the relative abundance of the various taxa identified (top row) as well as the relative amount of broadleaf and coniferous species (lower row) expressed as a percentage of the fossil record (B) or as the relative basal area of living trees (C).

A total of 13 charcoal particles were radiocarbon dated between 6000 and 285 cal year BP at SRM1 (Table S1; Figure S1). Two fragments of white pine dated back to the mid-Holocene, while all other particles (4 white pine, 5 sugar maple and 2 red maple) were from the late Holocene. At SRM2, 8 of the 9 dated maple charcoal fragments were dated between 3585 and 300 cal year BP (5 red maple and 3 *Acer* sp.), while one *Acer* sp. particle was found at 4830 cal year BP. A single red maple macrofossil dated to 1410 cal year BP was recovered from WBF1, whereas three red maple and one *Acer* sp. particles from WBF2 were dated between 4200 and 2240 cal year BP. At YBC1, two red maple and two *Acer* sp. fragments were dated between 1620 and 490 cal year BP. A total of 15 charcoal particles from YBC2 were dated between 6920 and 390 cal year BP. White pine was the only taxon dating back to the mid-Holocene, and the youngest pine fragment was from 1780 cal year BP. By contrast, maple fragments (*Acer saccharum*, *Acer rubrum* and *Acer* sp.) were no older than 2740 cal year BP (Table S1; Figure S1). A total of 59 charcoal particles of the three targeted temperate tree species were radiocarbon dated from the entire RC forest (grid and plots). The historical reconstruction spanned the last *c*. 7000 years and showed a time-transgressive transition of the forest composition (Figure 5a,b). The composite kernel density estimate (CKDE) of the changing frequency of white pine radiocarbon dates indicates a high radiocarbon frequency of white pine between 6500 and 4500 cal year BP, decreasing to null values until erratic peaks at 3000 and 1800 cal year BP, followed by a null frequency for the last millennium (Figure 5c). For red maple, CKDE distribution shows a seemingly null radiocarbon frequency before 4000 cal year BP and a steady increase between 4000 and 1800 cal year BP, followed by a gradual decline during the last millennium, albeit never reaching null values. Sugar maple radiocarbon frequency is null before reaching a sudden peak at 1800 cal year BP, which remained relatively high up to present day.

4 | DISCUSSION

In this study, we relied on SMCA to reconstruct the Holocene history of leading-edge populations of three temperate tree species from RC forest, a northern outpost of temperate forest found within eastern Canadian BTE. We reject the null hypothesis because our results indicate that temperate tree species did not share a joint ecological history, merely tracking Holocene climate as a constant forest assemblage. Instead, temperate species display idiosyncratic trajectories with different timing of population expansion or regression at their leading edge within the northern part of the BTE. The RC forest underwent a time-transgressive transition of temperate tree species composition during the last 7000 years. The mid-Holocene Climatic Optimum (Hypsithermal interval) was exclusively represented by white pine (*c*. 7000–4000 cal year BP), followed by a transitional period whereby red maple established at the onset of the Neoglacial cooling (*c*. 4000–2000 cal year BP), and finally a period of

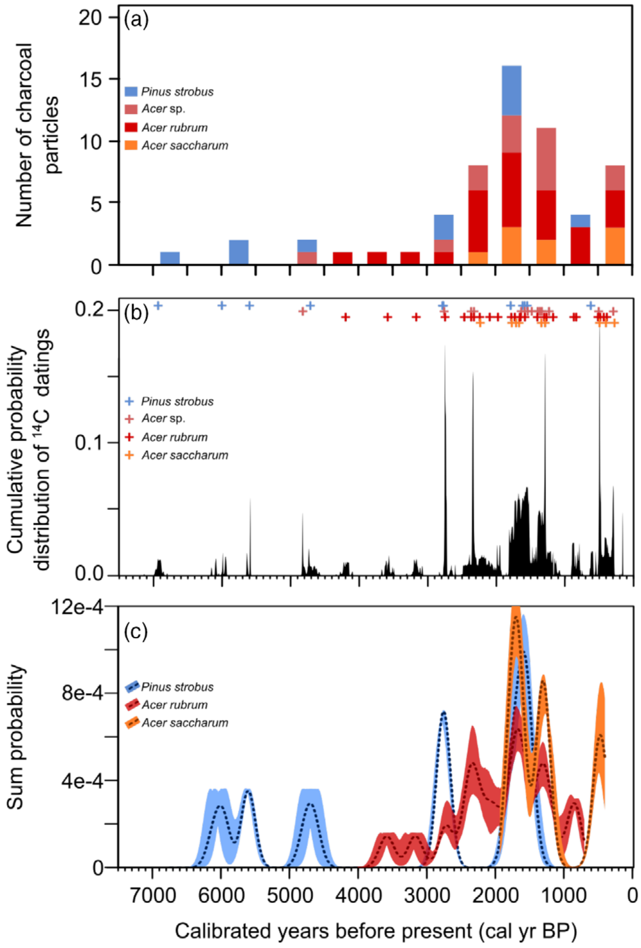

FIGURE 5 Long-term dynamics of three temperate tree species (*Acer rubrum*, *Acer saccharum* and *Pinus strobus*) at their leading edge of distribution, within the Ruisseau-Clinchamp forest. (a) Number of charcoal particles per taxon in each 500-year interval. (b) Summed probability distribution of 59 calibrated ^{14}C dates. '+' indicates the median age for each calibrated ^{14}C date. (c) Composite kernel density estimates of the changing radiocarbon frequency of each species.

coexistence of red maple and sugar maple during the late-Holocene (since *c.* 2000 cal year BP). These results support pollen-based reconstructions from lake Labelle, located at the core of the RC forest (Paillard et al., 2023) and other SMCA-based historical reconstructions of leading-edge red maple stands elsewhere within the BTE (Mondou Laperrière et al., 2024). Additionally, we found support for the hypothesis that sugar maple establishment at its northern limit was likely contingent on the earlier presence of a generalist companion species, red maple (Dumont et al., 2024). Indeed, our data show that there was a *c.* 2000-year lag between the establishment of red maple and the arrival of sugar maple.

4.1 | Mid-Holocene climate optimum (*c.* 7000–4000 cal year BP)

Our data show that white pine is present in the RC forest at least since *c.* 7000 cal year BP, which is several millennia earlier than both maple species. Although it was impractical to date all white pine charcoal fragments, their pervasive distribution across the sampling grid suggests a historical prevalence of the species in the landscape. Additionally, we recovered white pine charcoal from all six plots representative of the three different stand types currently found within the RC, which suggests that the species was not limited by site-scale environmental properties (e.g. topographical, edaphic), as reported in other temperate tree species (Collin, Messier, Côté, et al., 2016; Solarik et al., 2020). As such, our data support previous historical reconstructions reporting northern expansion of leading-edge white pine populations during the mid-Holocene (Terasmae & Anderson, 1970). This greater historic abundance at the species northern limit likely reflects more favourable climatic conditions during the warmer mid-Holocene. For instance, increased temperatures allowed for earlier spring thawing and, consequently, a longer growing season (Tardif et al., 2001). Additionally, differences in air mass distribution led to a more stable climate, less conducive to severe, stand-replacing crown fires while maintaining a frequent low-severity surface fire regime (Carcaillet & Richard, 2000) to which white pine is well adapted (Wendel & Smith, 1990). Based on a fossil pollen record, fossil wood, cones and leaves *c.* 100 km north of the RC forest, Terasmae and Anderson (1970) suggested white pine expanded north of its present distribution limit during the mid-Holocene Hypsithermal interval and retreated southward during the cooler late-Holocene. Because the RC forest is located at the modern-day northern limit of the species, it was possible to detect the decline of white pine abundance by comparing the greater relative abundance of fossil evidence with that of living trees. With the decrease of summer temperature and, by corollary, of the growing season length, temperate species like white pine were probably disadvantaged, whereas boreal tree species such as spruces or balsam fir increased in abundance (Blarquez et al., 2015), a phenomenon referred to as coniferization (Remy et al., 2019). Boreal conifer species are also more fire-prone and their architecture is rather conducive to high-severity stand-replacing crown fires (Hély et al., 2000), to which white pine is ill-adapted (Wendel & Smith, 1990). Though some authors have suggested that interspecific competition with balsam fir might explain the reduction of white pine (Uprety et al., 2013), we posit that an altered wildfire regime likely contributed to white pine decline and restricted the species to small topographically fire-protected refugia at its northern limit within the BTE. Warm and dry conditions during the mid-Holocene favoured frequent, low-severity fires, fostering white pine establishment by removing soil organic matter and reducing competitive vegetation. A shift towards less frequent but more severe fires 4000 years ago—attributed to drier spring conditions despite the overall cooler and wetter climate of the Neoglacial—led to high-intensity crown fires, triggering cascading effects on vegetation composition (Ali et al., 2025). Based on pollen evidence from the BTE in Ontario, Genries et al. (2012) suggested that a decrease in fire return interval was the proximal cause for a white pine range retraction starting at *c.* 6500 cal year BP. Based on SMCA, Payette et al. (2021) reported similar results to ours, also suggesting that a change in the fire regime was responsible for a shift from white pine-dominated habitat to sugar maple at 4300 cal year BP, although their study was located *c.* 200 km south of the RC forest. It has already been reported that white pine forms disjunct fire-protected stands on islands or bare hilltops at its northern limit (Engelmark et al., 2000). Such white pine refugia are likely created by the presence of fire breaks, such as bodies of water and steep slopes. Indeed, our 390 observation points across the grid revealed that white pines were generally isolated individuals of large size that appeared to be the remnants of larger relict populations due to the presence of large woody debris in the vicinity of the living individuals. Notwithstanding the proximal causes, our data add to the existing literature suggesting white pine expansion during the mid-Holocene Climate Optimum and subsequent Neoglacial collapse at its northern limit (e.g. Bussières et al., 2023; Mondou Laperrière et al., 2024; Richard, 1993; Terasmae & Anderson, 1970). Similar timings of population expansion and decline tracking periods of warmer and cooler Holocene climate have been reported in other temperate tree species within the BTE, such as yellow birch (Larochelle et al., 2018), beech (Cogbill, 2005) and perhaps eastern white cedar (Jules et al., 2018). Studies have also shown that climate indirectly drives the modern-day distribution of these species (Drobyshev et al., 2014; Paul et al., 2014), further supporting this pattern. However, our data clearly suggest not all temperate species have responded likewise.

4.2 | Onset of Neoglacial cooling (*c.* 4000–2000 cal year BP)

The earliest maple detected in the RC forest dated back *c.* 4800 cal year BP (*Acer* sp., likely red maple), meaning that the warm mid-Holocene climatic period could have fostered maple migration northward. Red maple appears to have been quite sporadic in the landscape as suggested by the low relative abundance of charcoal fragments compared to the ubiquitous distribution of living trees in the modern-day RC forest. Red maple is among the most generalist temperate trees: it tolerates the acidic soil of coniferous stands, it readily regenerates after a severe stand-replacing wildfire and it reproduces vegetatively (Tremblay et al., 2002; Walters & Yawney, 1990). Indeed, red maple appears to benefit from canopy instability, be that from wildfires, insect outbreaks or logging human activity. As such, the increase of red maple abundance suggested by radiocarbon density from charcoal particles dating back to the onset of the Neoglacial cooling (*c.* 4000–2000 cal year BP) should not be surprising. In essence, the same factors (climate, fires) pushing the distribution of white pine southward might have contributed to increasing red maple's foothold in the RC forest and across the northern BTE (Mondou Laperrière et al., 2024). The capacity of red maple to take advantage of historical stand-replacing fire disturbances characterizing the Neoglacial cooling reflects its recent increase in abundance in range-core stands (Fei & Steiner, 2007). While Neoglacial macroclimatic variables such as colder temperatures have seemingly degraded conditions for temperate tree species at the RC forest, red maple has thrived at its leading edge to the point that it currently covers most of our sampling grid. This area, however, is located close to the northern limit of the species, and its establishment further north is likely currently impeded by the colder climate of the boreal forest. Indeed, at its range edge near the northern border of the BTE, red maple stands are limited to hilltops where they can still successfully reproduce sexually (Mondou Laperrière et al., 2024). This, however, was not observed by all authors as Tremblay et al. (2002) found that, at its northern limit, red maple could not produce enough seeds to maintain a viable population. Instead, the species is reliant on periodic stand-clearing fires triggering regeneration from stump sprouting. As such, although the species appears at least in part climatically limited in northern environments, other factors might foster its persistence and expansion at its leading edge (Zhang et al., 2015).

Sugar maple was first detected in the RC forest *c.* 2000 cal year BP, that is, far into the cool late-Holocene. This establishment period coincides with the paleopollen record obtained from lake Labelle, located at the centre of the RC forest (Paillard et al., 2023), but is in sharp contrast with patterns reported for other temperate species, such as white pine (Uprety et al., 2013) or yellow birch (Larochelle et al., 2018). The latter species expanded their northern limits during the warmer mid-Holocene but were forced to retract southward likely due to the late-Holocene cooling and associated change in the fire regime. This was not the case for sugar maple, which might suggest that its range dynamics are somewhat decoupled from strict macroclimatic limitations. Indeed, northernmost sugar maple stands can readily self-regenerate from seeds (Graignic et al., 2014), whereas cool temperatures inhibit seed recruitment of northernmost red maple stands, which rather depend on vegetative regeneration (Fei & Steiner, 2009; Tremblay et al., 2002). Hence, if leading-edge sugar maple populations are not exposed to the environmental conditions at the cold limit of the species' climatic tolerance envelope, then other driving factors must dictate their northern distribution within the BTE. For instance, Collin et al. (2018) suggested that the lack of arbuscular mycorrhizae in coniferous forest soil limits sugar maple's access to nutrients. Additionally, Collin, Messier, and Bélanger (2016); Collin, Messier, Côté, et al. (2016) and Carteron et al. (2020) have all shown a reduced capacity of sugar maple to extract nutrients from coniferous forest soils, thus limiting its survival in environments dominated by conifer trees such as the boreal landscape. This incapacity is largely attributable to the lingering effects of decomposing coniferous foliage on the soil, which affect edaphic physicochemical properties through podzolization (including soil acidification, reduced cation exchange capacity, decreased base saturation and leaching of essential nutrients; Sanborn et al., 2011) over millennia and can thus persist even after the coniferous canopy is removed. Solarik et al. (2020) referred to these soil alterations as priority effects and suggested that the presence of a deciduous forest cover is generally indicative of better growing conditions for sugar maple. Our data paint a similar picture, as illustrated by the fact that living sugar maple and white pine individuals seldom coexist in the

RC forest. If the presence of a coniferous cover has hindered the establishment of sugar maple, how was it possible for the species to infiltrate and eventually form stands within the otherwise conifer-dominated RC forest over the last 2000 years?

4.3 | Late-Holocene (since 2000 cal year BP)

In the RC forest, as elsewhere in the BTE, the transition between the warm mid-Holocene and cool late-Holocene translated into major changes in the forest cover (Carcaillet & Richard, 2000). A shift from a frequent, low-severity, surface fire regime to an infrequent, high-severity, crown fire regime likely contributed to the collapse of white pine in the BTE and its replacement by fire-adapted boreal conifer species (Ali et al., 2012, 2025). Based on a pollen record at lake Labelle, Paillard et al. (2023) suggested that pioneer broadleaf species, such as white birch and trembling aspen (*Populus tremuloides*), have also benefited from such severe stand-replacing wildfires. Their conclusion was that the increase of aspen and birch served as an intermediate to the spreading of sugar maple around lake Labelle, by facilitating maple via a change in edaphic properties that broke conifer-established soil priority effects. However, there are some shortcomings with using lacustrine paleopollen analysis to study the history of marginal stands, and more specifically in the case of maple marginal stands. First, pollen can be transported over long distances; hence, it is difficult to decipher between the local presence of a small, isolated population and the long-distance pollen transport from large extra-local sources. Additionally, because it is difficult, if not impossible, to robustly detect red maple marginal stands in pollen analysis due to their underrepresentation (Paillard et al., 2023), its presence was not considered. As such, the combination of different retrospective approaches, such as lacustrine sediment pollen used in Paillard et al. (2023) with SMCA (this study) should improve the overall resolution of past reconstructions because the different spatio-temporal scales allow for a better detection of processes that can easily be missed by relying on a single method (Minchev & de Lafontaine, 2024).

The increase in deciduous cover detected in both studies might have contributed to breaking the priority effects imposed by the conifer-dominated forest on soil conditions. However, red maple was already present sporadically during the mid-Holocene and gradually became more abundant thanks to canopy openings from severe wildfires (Mondou Laperrière et al., 2024). Unlike stands of pioneer broadleaf species that are ultimately replaced by boreal conifers as succession proceeds, red maple stands can self-regenerate without disturbance in mature stands and also readily reestablish after a stand-replacing disturbance (Nolet et al., 2008). Red maple rarely achieves stand dominance in the BTE, but it was likely codominant in the balsam fir-white birch forest that established across the BTE at the onset of the Neoglacial (Mondou Laperrière et al., 2024). A gradual increase in red maple abundance in the RC forest might have fostered the spreading of beneficial arbuscular mycorrhizae and the foundation of suitable microsites instrumental to a later establishment of sugar maple (Carteron et al., 2020). According to this tentative scenario, earlier establishment of red maple, a generalist congeneric, was instrumental in facilitating the later establishment of the more specialist sugar maple through removal of edaphic constraints brought about by a conifer forest cover. Indeed, a *c.* 2000-year lag between the first detection of red maple and the first detection of sugar maple likely reflects the time necessary for the former to reach the critical abundance necessary to actually modify growing conditions and facilitate the establishment of the latter. A similar pattern was also reported by Dumont et al. (2024) further east at the leading edge of maple distribution, showing a 3000-year gap between red maple and sugar maple establishment, which they attributed to modification of soil conditions or dispersal limitation.

A facilitation process is likely to be synergistic, rather than additive, to the abundance of both interacting species (Brandt et al., 2023). It can therefore be hypothesized that such facilitative interaction will be key to the response of tree species to ongoing climate change, as the relationship between red and sugar maple is unlikely to be unique. That being said, the multi-millennial lag and facilitation hypothesis imply that models predicting sugar maple expansion in the boreal forest as a response to anthropogenic global warming (e.g. Boulanger et al., 2022) could greatly overestimate the species' actual migration capacity. Indeed, models suggesting that the abundance of sugar maple should substantially increase by the year 2100 in the BTE and even in the boreal forest (Boulanger et al., 2022) might reach a different outcome when accounting for a putative multi-millennial lag necessary to complete the facilitation process. This underlines the importance of integrating historical data from small marginal populations into broader predictive models to more accurately predict the effects of anthropogenic climate change on forests, rather than viewing biomes as discrete units whose boundaries closely follow macroclimate.

It is, however, unlikely that a single factor explains the dynamics of the BTE. For instance, the offset in maple establishment reported here and by Dumont et al. (2024) might also reflect interspecific differences in samara dispersal capacity. However, despite the higher wing loading (heavier seed per wing surface area) for sugar maple samaras compared to red maple, propagules of both species exhibit similar terminal velocity (Shaeffer et al., 2024), indicating that their dispersal capacity is effectively equivalent. These results do not account for intraspecific trait variability; yet, dispersal traits can vary within species, as exemplified by enhanced propagule dispersal ability at the expansion front, which is attributable to spatial sorting eco-evolutionary dynamics (Pothier Guerra & de Lafontaine, 2024). Intraspecific variability in terminal velocity expressed at the colonization front of each maple species might be more important than mean interspecific differences between red maple and sugar maple for migration (Des Roches et al., 2018), though this remains to be tested. Furthermore, although sugar maple is usually associated with richer substrates (Godman et al., 1990), the species can tolerate poorer boreal soils (Kellman, 2004). However, sugar maple is disadvantaged in the absence of symbiotic mycorrhizae (Carteron et al., 2020; Collin et al., 2018). By contrast, red maple has broader tolerance to sites of different moisture and disturbance regimes (Abrams, 1998). The delayed establishment of the specialist sugar maple, compared to the more generalist red maple within the boreal matrix of the northern BTE, could be attributed to a combination of rare long-distance dispersal events, the need for appropriate mycorrhizal symbionts and narrower ecological requirements, particularly regarding soil nutrition and disturbances.

Species exclusions such as those caused by priority effects, suggested here between boreal conifers and sugar maple, are already well documented (Solarik et al., 2020). However, further research is needed to better understand how ecological processes can overcome priority effects, such as the facilitation hypothesis put forward here between red maple and sugar maple. A similar facilitation process has been uncovered in invading herbaceous species (see examples in Brandt et al., 2023), but studies on trees remain scant. The abundance of red maple is currently increasing at the northern limit of its distribution as direct and indirect results of human activity (Boisvert-Marsh et al., 2014; Bussières et al., 2023; Mondou Laperrière et al., 2024). Sugar maple populations also seem to be migrating northward, though the lag associated with the facilitation process might mean they are still responding to a late-Holocene climate shift (Dumont et al., 2024). Unlike red maple, which remains sparse in the canopy, once established, sugar maple takes over stands and self-regenerates under its own canopy, thus excluding boreal species thanks to intense shading (Godman et al., 1990). As it keeps on filling the role of the dominant landscape-structuring species south of the BTE, its greater abundance within the northern BTE might lead to a drastic functional change for the ecotone. The greater abundance of fire-resisting deciduous stands within the BTE could thus alter the fire regime, with greater challenges for recruiting new generations of fire-prone boreal species. However, the presence of a multi-millennial lag in the increase of the abundance of sugar maple could make the potential shift in the forest composition of the BTE an unlikely event under the influence of rapid anthropogenic climate change. While some suggest that a wise course would be to assist the colonization of temperate species, such as sugar maple, into the boreal landscape (e.g. Xu & Prescott, 2024), it can also be argued that the multi-millennial lag is rather indicative of the resilience of the boreal forest in the face of major environmental fluctuations.

5 | CONCLUSIONS

Our study falls within a rich body of literature, representing yet another demonstration of the individual (idiosyncratic) species response to historical global change (Davis, 1981; Gleason, 1926). Contrary to a deterministic view whereby local communities of a given biome shall inexorably converge through ecological succession towards a steady-state climax assemblage primarily dictated by climate (Clements, 1916), modern-day northern temperate forest may have no historical analogue (Overpeck et al., 1992; Williams et al., 2004) and may not represent a reference for future states. In the BTE, we inferred a time-transgressive transition of temperate forest species that have shifted in abundance within the community according to climatic conditions, fire regime, edaphic conditions and migration lag without ever reaching a stable state with long-lasting coexistence of temperate taxa. In a similar way, modern-day temperate forests across the temperate biome might also represent unique and transient realizations of individual temperate species responses. Idiosyncratic species responses and the possibility of novel assemblages without past or modern analogues admittedly complicate the picture but should still be properly acknowledged when developing models forecasting biotic responses to predicted climate change.

AUTHOR CONTRIBUTIONS

Todor S. Minchev: Data curation; formal analysis; validation; visualization; writing—original draft and writing—review and editing. Julia Cigana: Data curation; formal analysis; investigation; methodology and writing—original draft. Pierre Grondin: Conceptualization; funding acquisition; methodology; supervision and writing—review and editing. Yves Bergeron: Conceptualization; funding acquisition; project administration; supervision and writing—review and editing. Guillaume de Lafontaine: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; visualization; writing—original draft and writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjtg2 (Minchev et al., 2025).

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SUPPORTING INFORMATION

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

Table S1. Details of 59 radiocarbon dates from macrofossil wood charcoal particles recovered from inorganic soil samples of the Ruisseau-Clinchamp forest.

Figure S1. Summed probability distributions of the calibrated ^{14}C dates of *Acer rubrum*, *Acer saccharum*, *Acer* sp. and *Pinus strobus* charcoal particles at sugar maple-red maple (SRM) stands, balsam fir-white birch (WBF) stands, and eastern white cedar-yellow birch (YBC) stands representative of the Ruisseau-Clinchamp forest. '+' indicates the median age for each calibrated ^{14}C date (blue: *Pinus strobus*; red: *Acer rubrum*; orange: *Acer saccharum*; pink: *Acer* sp.).

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