Timber harvesting was the most important factor driving changes in vegetation composition, as compared to climate and fire regime shifts, in the mixedwood temperate forests of Temiscamingue since AD 1830

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Abstract

Context The vegetation composition of northeastern North American forests has significantly changed since pre-settlement times, with a marked reduction in conifer-dominated stands, taxonomic and functional diversity. These changes have been attributed to fire regime shifts, logging, and climate change.

Methods In this study, we disentangled the individual effects of these drivers on the forest composition in southwestern Quebec from 1830 to 2000 by conducting retrospective modelling using the LANDIS-II forest landscape model. The model was run based on pre-settlement forest composition and fire history reconstructions, historical timber harvest records, and climate reanalysis data. We compared counterfactual scenarios excluding individual factors to a baseline historical scenario.

Results and Conclusions Our results indicated that timber harvesting had the greatest impact on forest dynamics over the past centuries. In the absence of timber harvesting, pre-settlement species abundances were largely maintained, preserving key functional

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traits like fire and shade tolerance that contribute to ecosystem resilience. Increased fire activity during the settlement period contributed to the increase of early-successional aspen (Populus tremuloides), but timber harvesting played the dominant role. Fire exclusion had no influence on vegetation composition, suggesting mesophication unfolds over longer timescales than those captured in this study. Climate change, characterized by modest increases in temperature and precipitation, had a minor effect on vegetation shifts, as increased precipitation might have mitigated the adverse effects of rising temperatures. However, future climate change is projected to become a more significant driver of forest composition. These findings underscore the importance of forest restoration and continued research on past forest dynamics to better understand current and future changes.

Keywords LANDIS-II · Retrospective modeling · Forest disturbances · Vegetation composition shifts · Logging · Fire regime shifts · Climate change · Northeastern North America · Mixedwood temperate forests

Abbreviations

LIA	Little ice age
MWP	Medieval warm period
AGB	Aboveground biomass
BL	Baseline scenario
noFRS	Without fire regime shifts scenario
noCC	Without climate change scenario
noTH	Without timber harvesting scenario
noFE	Without fire exclusion fire regime scenario
noSF	Without settlement fire scenario

Introduction

Forest vegetation composition is shaped by complex interactions among climate, disturbances, and other environmental factors, operating across multiple temporal and spatial scales (Oliver et al. 1996). While long-term vegetation dynamics at subcontinental scales have been driven by climate over millennia (Williams et al. 2004), abrupt climate change events can disrupt these trends (Shuman et al. 2009), causing rapid shifts in vegetation composition (Williams et al. 2002; Shuman et al. 2004; Yu 2007). Though

some taxa may respond more slowly, with time lags extending over centuries (Williams et al. 2002). Disturbances such as wildfires, windstorms, and insect outbreaks also shape forest ecosystems. Disturbances alter ecosystem structure and simultaneously release resources (e.g., growing space, light, and nutrients) that promote recovery and ecological succession (Pickett and White 1985; White and Jentsch 2001). Forests often exhibit resilience to natural disturbance regimes (Johnstone et al. 2016) due to adaptive traits shaped by long-term exposure (Sousa 1984; Keeley et al. 2011). However, disturbances that exceed the historical range of variability can severely impact ecosystems, as the prevailing communities may lack the traits needed to recover under novel conditions (Turner and Seidl 2023). Human land use and climate change have drastically altered disturbance regimes and forest composition, with potentially detrimental effects on ecosystem functioning, including carbon uptake (Ojima et al. 1994; Seidl et al. 2017; Thom et al. 2018; Danneyrolles et al. 2019).

Forests in northeastern North America (northeastern United States and southeastern Canada) have undergone major shifts in vegetation composition from pre-settlement times to the present. Forests dominated by white pine (Pinus strobus L.) and red pine (Pinus resinosa Ait.) were once widespread across the region. However, in some areas of their range, such as the Great Lakes region, as little as 0.6% of the pre-settlement primary red-white pine forests remains (Frelich 1995; Ziegler 2010). This drastic reduction in pine-dominated forests is part of broader regional vegetation changes. Slow-growing conifers such as pines (Pinus spp.), spruces (Picea spp.), balsam fir (Abies balsamea (L.) Mill.), and white cedar (Thuja occidentalis L.) have been largely replaced by fast-growing deciduous species, including poplars (Populus spp.), paper birch (Betula papyrifera Marsh.), and maples (Acer spp.) (Jackson et al. 2000a; Friedman and Reich 2005; Schulte et al. 2007; Dupuis et al. 2011a; Danneyrolles et al. 2016a; Terrail et al. 2019). These shifts contributed to the homogenization of taxonomic and functional diversity (Jackson et al. 2000b; Schulte et al. 2007; Pinto et al. 2008; Dupuis et al. 2011b; Hanberry et al. 2012; Danneyrolles et al. 2016b, 2021).

Frequent low- to moderate-severity surface fire with infrequent stand-replacing fires played a critical role in maintaining pine-dominated forests in

the region (Drobyshev et al. 2008). Low- to moderate-severity fires created conditions essential for pine regeneration by reducing the soil organic layer (Nyamai et al. 2014; Stambaugh et al. 2018), increasing light penetration to the forest floor by reducing canopy cover (McRae et al. 1994), and eliminating shade-intolerant competitors (Nyamai et al. 2014; Stambaugh et al. 2018). Occasional stand-replacing fires or other large-scale disturbances such as hurricanes, also favored pines' regeneration, especially that of white pine, by creating large canopy gaps and reducing competition for light and soil nutrients (Abrams 2001).

Changes in land use have influenced fire regime shifts in eastern North America. During the Euro-American settlement, fire activity increased due to land clearing, agricultural fires, and unintentional ignitions, such as those from railway sparks (Weir and Johnson 1998; Stambaugh et al. 2018; Terrail et al. 2020). Subsequently, fire activity declined due to fuel fragmentation caused by forest conversion to croplands and infrastructure development (Guyette et al. 2002; Stambaugh et al. 2018), and active fire suppression measurements introduced in the 1900s that became increasingly effective by the 1970s (Lauzon et al. 2007; Gauthier et al. 2008; Cardil et al. 2019).

Climate change likely directly influenced the vegetation composition of northeastern North America throughout the late Holocene. The Little Ice Age (LIA; ~ 1450–1850 CE) witnessed an abrupt decline in hardwoods (*Fagus, Acer,* and *Betula*) and the mesophytic *Tsuga*, coupled with an increase in boreal taxa (*Picea glauca* (Moench) Voss and *Abies balsamea* (L.) Mill.) (Houle et al. 2012; Paquette and Gajewski 2013). Climate change may have indirectly affected forest composition through its effects on fire regimes. Drought conditions during the 1910s and 1920s could have exacerbated the settlement-related fire activity (Girardin et al. 2004). Changes in atmospheric circulation patterns since the end of the LIA have led to lower drought severity, increased cyclonic activity, and the influx of moist air masses (Girardin et al. 2006), contributing to the lengthening of fire cycles in eastern North America (Drobyshev et al. 2017; Chavardès et al. 2022). Vegetation changes observed since the settlement period might, therefore, be a continuation of climate-mediated dynamics driven by large-scale changes in atmospheric circulation regimes (Gajewski et al. 1985; Houle et al. 2012; Paquette and Gajewski 2013).

Forest harvesting has been an important factor affecting vegetation composition in the region. Commercial logging in northeastern North American forests progressed from the extraction of square timber to sawn timber and ultimately pulpwood. Historical logging practices, including diameter-limit cutting and clear-cutting, considerably degraded these forests (Kenefic et al. 2005; Archambault et al. 2009). Selective cutting of large-diameter pines was particularly damaging as it left behind large volumes of surface and ladder fuels that favored the spread of surface fires into crowns, killing canopy pines (Lower 1933; Whitney 1987). Clear-cutting supported the invasion of fast-growing species, such as trembling aspen (*Populus tremuloides* Michx., hereafter aspen) (Graham et al. 2011), and decreased the proportion of coniferous to deciduous species (Archambault et al. 1998).

Despite the recognized impacts of climate change, changing fire regimes, and timber harvesting on the vegetation composition, their specific impacts on forest dynamics over recent centuries remain unclear (Abrams and Nowacki 2015; Nowacki and Abrams 2015; Liang et al. 2018, 2023; Brice et al. 2019, 2020; Danneyrolles et al. 2019). The variation in the spatial and temporal resolution of available historical data makes it challenging to isolate the individual effects of each driver. However, assessing their individual contributions to the dynamics of single species is critical for development of informed conservation and management strategies. To address this knowledge gap, we conducted a retrospective modeling analysis using LANDIS-II, a spatially explicit forest landscape model. This approach enabled hypothesis-testing of paleoenvironmental change (Berland et al. 2011; Klimaszewski-Patterson et al. 2018) and the possibility to distinguish the relative importance of the driving factors in vegetation shifts. We examined the Temiscamingue region of southwestern Quebec as a case study due to its well-documented historical ecology and the availability of historical data. We used (a) pre-settlement vegetation reconstructions to define the initial vegetation composition for the simulations, (b) fire regime reconstructions, (c) historical timber harvest data, and (d) climate reanalysis data from the pre-settlement times to the

present. We simulated vegetation dynamics and forest disturbances from 1830 to 2000 (170 years). We tested three hypotheses: (H1) timber harvesting had a greater impact on vegetation composition than fire regime shifts and climate variability. This is because logging represented a more substantial and immediate disturbance compared to fire regime shifts and particularly to the modest climate change observed during the study period; (H2) without timber harvesting, a strong driver, the ecosystem would have maintained its resilience by preserving pre-settlement species composition, and thus a diverse range of key functional traits; and (H3) the decline in fire activity since 1940, due to climate change and fire suppression, had a greater effect upon forest composition than the increased fire activity associated with the settlement period (1890–1940). By elucidating the distinct roles of climate change, fire activity, and forest harvesting on the vegetation dynamics of mixedwood temperate forests, our study provides critical insights to understand past and future dynamics to develop adapted conservation and management strategies.

Methods

Study area

The study area extended over 1300 km^2 in the Temiscamingue region in southwestern Quebec (Fig. 1). The area included the Opemican National Park (established in 2018), bordering the Temiskaming Lake on the west and the western parts of the Kipawa Lake on the east. The study area is within the Grenville geological province of the Canadian Shield, and its surficial deposits are primarily clays deposited by the pro-glacial Barlow Lake and rocky glacial till (Vincent and Hardy 1977; Brown 1981). The mean annual temperature in the area is 3.1 °C; with January and July having average temperatures of −15 °C and 18.3 °C, respectively. Average annual precipitation is 836.5 mm, according to the closest weather station in Ville Marie.

The study area at the northern edge of the sugar maple–yellow birch bioclimatic domain of southwestern Quebec (Saucier et al. 1998), which is part of the broader Great Lakes-St. Lawrence forest region of eastern Canada (Rowe 1972). Common
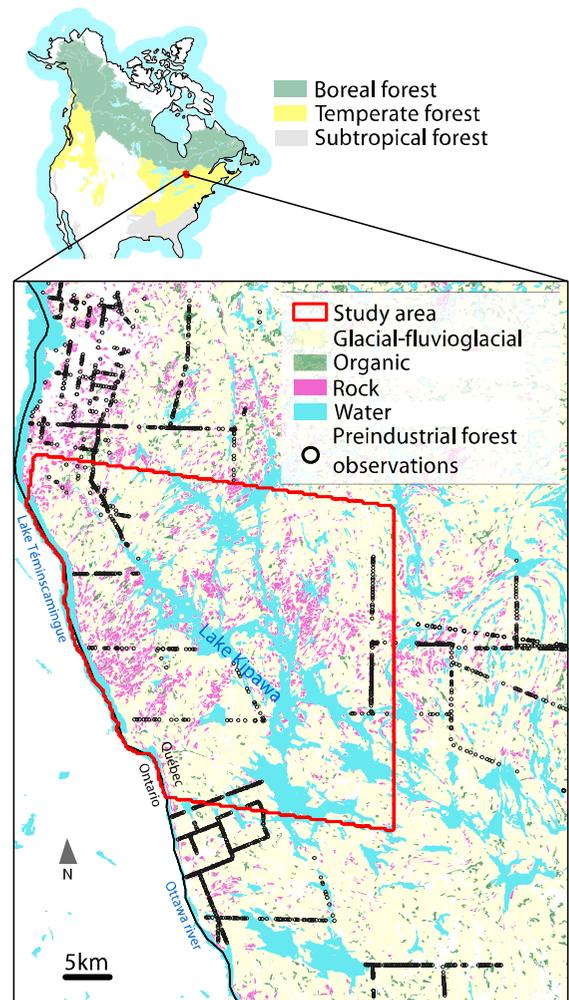
Fig. 1 Pre-industrial species lists point observations (black circles and lines, $N=1474$) located within our study area (perimeter shown as red-outlined polygon) and within a 20 km buffer area surrounding the study area that we used to populate our initial vegetation landscape raster based on the surface deposit class

tree species found in the study area include sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), white birch (*Betula papyrifera* Marsh.), aspen, large tooth aspen (*Populus grandidentata* Michx.), and fire-associated species such as red pine and white pine occurring in the more xeric sites.

Before the settlers' arrival, Temiscamingue was inhabited by various nomadic indigenous groups who were primarily part of the Algonquian language

family (Riopel 2002). The impact of these Native American groups on the forests of Temiscamingue is not well understood. Nonetheless, research conducted in southern Ontario suggested that Native American use of fire had significant effects on the pre-settlement forests (Clark and Royall 1995; Munoz and Gajewski 2010). However, this perspective has been a subject of debate among other scholars (Campbell and McAndrews 1995; Munoz et al. 2014; Danneyrolles et al. 2016a).

The Euro-American colonization began in 1885, facilitated by the construction of the railway in 1890 (Ville Temiscaming 1996; Riopel 2002). Forestry played a vital role for settlers and progressed through three phases with the focus on square timber, sawn timber, and pulpwood. The emergence of a new timber product did not necessarily replace the previous one but rather coexisted alongside it. Square timber harvesting, which started around 1860 (Riopel 2002) and ended in 1908 (Aird 2016), targeted white and red pine larger than 50 cm in diameter (Lorimer 2008). Sawn timber production began in 1887 (Ville Temiscaming 1996), with companies primarily using white pine, red pine, spruce, and birch (Gourd 1983). The pulpwood industry began in 1918 (Ville Temiscaming 1996). Logging operations gradually expanded northward into Abitibi by the 1920s, and by the mid-twentieth century, nearly half of the harvested wood came from this region (Gourd 1983). Pulpwood primarily used black spruce (*Picea mariana* (Mill.) B.S.P.), balsam fir (*Abies balsamea* (L.) Mill.), hemlock, and aspen (Howe 1923).

Data

Climate data

The climate data we used were spatially downscaled monthly time series from the Twentieth Century Reanalysis version 3 (20CRv3), an ensemble that provides sub-daily global atmospheric conditions from 1836 to 2015 with a spatial resolution of 1° (Slivinski et al. 2019). These reanalyses indicate that since 1836, the mean annual temperature in the study area has increased by 0.47 °C, while precipitation has modestly risen by 15.29 mm (1.66%). To increase the spatial resolution of the 20CRv3 and reflect local variation in climate within the simulations, we used BioSIM, a software that allowed us to interpolate

the georeferenced climate data to our landscape grid cells, adjusting for differences in latitude, longitude, and elevation using spatial regressions (Régnière 1996). We used the spatially downscaled average climate data for the period 1981–2010 as a reference and adjusted these data to reflect different average climate conditions for each 30 year period starting from 1836 (the first period 1836–1860 is 24 instead of 30 years). We used 30 year periods as this is the typical duration used in climate studies to provide robust estimates of average climate conditions (WMO 2017). This adjustment involved calculating the difference, or the "delta", between the average conditions for the reference period (1981–2010) and the average conditions of each 30 year periods: 1836–1860, 1861–1890, 1891–1920, 1921–1950, and 1951–1980. We then adjusted the spatially downscaled average climate data of the reference period (1981–2010) by subtracting the deltas of each period to estimate historical climate conditions for each 30 year period.

Historical forest composition data

We obtained the vegetation data from pre-settlement reconstructions of forest composition, developed from land surveys of forest concessions conducted in Temiscamingue starting from the 1850s (Danneyrolles et al. 2016b). The data consisted of species lists derived from surveyors' logbooks associated with georeferenced points along surveyed transects. We obtained 1474 of these georeferenced pre-settlement vegetation plots located both within our study area and within a 20 km buffer surrounding it (Fig. 1).

Fire regime data

We obtained the fire data from fire cycle reconstructions developed for the area from dendrochronological techniques and archival data from provincial and national government sources (Grenier et al. 2005). Our study period encompassed three distinct fire regimes: pre-settlement (1830–1890), settlement (1890–1940), and modern (1940–2000). The reconstructions indicate that the average fire cycle for the pre-settlement period was approximately 262 years, while for the settlement period it was about 96 years

(Grenier et al. 2005). In contrast, the modern fire cycle is longer than 3000 years (Boulanger et al. 2014).

Timber harvest data

We obtained the harvest data from the annual reports of the commissioners of the Crown lands for Quebec, which later became the Ministry of Lands and Forests of Quebec, retrieved from the Library of the National Assembly of Quebec (https://www.bibliotheque.assnat.qc.ca//fr/). We used data for the Upper Ottawa Valley region because Temiscamingue is located within the broader Upper Ottawa region, and data specifically for Temiscamingue were unavailable in these reports. We assumed that the extracted volume per surface area unit for each species in the Upper Ottawa valley was uniform across the region. Despite some inconsistencies and necessary assumptions, these reports present the most comprehensive and official source of information available for historical logging.

We distinguished four distinct timber harvesting phases: (a) selective cutting of large white and red pines for square timber during 1860–1910; (b) diameter-limit cutting of white and red pines, and cuttings of at least three species among white spruce, balsam fir, eastern hemlock, yellow birch, and aspen for sawn timber during 1890–1930; (c) clear-cutting of all species during 1930–1990 and (d) partial-cutting of all species during 1990–2000. Species-specific extracted volumes and minimum age information for each phase are summarized in Table 1. Detailed descriptions of timber harvest data processing, including diameter limits, volume conversions, and assumptions made are provided in Supplementary Information (SI) 1.

Modelling approach

Since we worked with a historical landscape, our retrospective simulations relied heavily on proxies we developed given that historical datasets are not as detailed as the modern ones. This was particularly the case for the initial vegetation conditions and harvesting data. For our simulations, we used LANDIS-II, a spatially explicit raster-based forest model that simulates stand- and landscape-level processes. At the stand-scale, LANDIS-II simulated establishment, competition, growth, and mortality based on species-specific life history traits. At the landscape-scale, LANDIS-II simulated seed dispersal and disturbances (Scheller et al. 2007). In the model, the landscape was represented as a grid of interacting cells each containing species-age cohort information. Cells were aggregated into spatial units, termed *landtypes*, with homogenous climatic and edaphic conditions.

Table 1 Timber extracted in tons over the whole landscape

The values for the square timber and sawn timber were obtained from the annual reports of the commissioners of the crown lands for Quebec. These reports documented the volumes extracted for species for different types of timber for the whole upper Saint Laurence region. We assumed that our landscape was within this region and the extraction occurred uniformly across the region. We converted volumes to mass in tons using the green wood density of each species

Period	Logging type	Sampling rule	Species	Min. age	Extracted mass (tons)
1830–1859					
1860–1889	Selective		Pinus strobus	200	96,354
1860–1889	Selective		Pinus resinosa	150	14,021
1890–1929	Diameter-limit		Pinus strobus	200	27,324
1890–1929	Diameter-limit		Pinus resinosa	150	97
1890–1929	Diameter-limit		Pinus strobus	70	127,889
1890–1929	Diameter-limit		Pinus resinosa	130	177,188
1890–1929	Diameter-limit	presence of > 3 mature species	Picea glauca	50	131,384
			Abies balsamea	50	
			Tsuga canadensis	60	
			Betula alleghaniensis	50	
			Populus tremuloides	80	
1930–1989	Clear-cut		all species	60	
1990–2000	Partial-cut		all species	60	

LANDIS-II has been used extensively to study the effect of disturbances and their interactions on the vegetation composition under climate change (e.g., Lucash et al. 2018; Molina et al. 2021, 2022). However, only a few studies have used it for retrospective analyses (Berland et al. 2011; Klimaszewski-Patterson et al. 2018; Wu et al. 2022). Building upon their methodologies, we utilized landscape modeling to create scenarios to investigate past landscape dynamics, enabling hypothesis testing on the drivers of past forest composition change.

Model parameterization

Our study area was represented as a grid of 20,800 cells, each with an area of 6.25 ha (250×250 m^2). To classify each cell in our landscape to a landtype, we used the national soil property maps for Canada (Mansuy et al. 2014). We classified our study area into three landtypes (Table 2): fluvioglacial and glacial (11,257 cells), organic (769), and rock (2961). The remaining 5723 cells were water. We ran the simulations in 10 year time steps.

Initial vegetation conditions

Since it was impossible to retrieve an exact map of the pre-settlement forest composition, we employed a random assignment approach to generate the initial vegetation map representing the pre-settlement vegetation cover. This approach relied on randomly assigning a georeferenced pre-settlement vegetation plot ($N = 1474$) (Fig. 1, Historical forest composition data section above) to each cell in our landscape raster based on the matching characteristics of their surface deposit classes. In cases where the species lists provided only the

genus-level identification (*Picea*, *Pinus*, *Acer*, *Populus*, and *Fraxinus*), we randomly assigned one or the other or both (33.33–33.33–33.33% probability) of the two most common species within the taxonomic group that are found in our study area. If the reconstructed vegetation plot indicated the presence of *Picea* spp., we assigned to the plot either *Picea glauca*, *P. mariana*, or both. For *Pinus* spp., we assigned *Pinus resinosa*, *Pinus strobus*, or both. For *Acer* spp., we assigned *Acer rubrum*, *Acer saccharum*, or both. For *Populus* spp. and *Fraxinus* spp., we kept them aggregated as the individual species of these genera do not vary considerably in their life-trait properties in this area.

To assign an age structure to the landscape and establish age cohorts for all forested cells, we conducted spin-off simulations for 1000 years using the Base Fire extension of LANDIS-II (He and Mladenoff 1999). The Base Fire extension can simulate stochastic fire events based on a few parameters such as fire size, fire spread and ignition. Simulations were conducted using variations around the pre-settlement fire cycle by varying the *k* parameter, which determines the return interval based on the rate of accumulation of combustible materials, and the probability of ignition. In particular, we tested various reconstructed pre-settlement fire cycles within the estimated range of 141–519 years (95% confidence interval) for this region (Grenier et al. 2005). Fire size distribution was based on the one described under the current climate by Boulanger et al. (2014). We selected the combination of fire cycle and fire parameters that (a) preserved the presence of all initial species without causing extinctions, and (b) maintained the vegetation proportions consistent with the simulation's initial state. Based on these criteria, the 300 year fire cycle was determined to

Table 2 Summary statistics of the classification of the landscape's raster cells based on three surface deposit classes: fluvioglacial or glacial, organic, and rock types

Group	Number of cells	Surface deposit	Altitude (in meters)			Slope (in degrees)		
			Range	Mean	SD	Range	Mean	SD
1	11,257	Fluvioglacial or glacial	153–373	295.45	27.21	0–26.28	2.35	2.38
2	769	Organic	165–364	283.11	30.18	0–11.11	1.86	1.80
3	2961	Rock	147–389	288.10	32.40	0–24.86	2.66	2.74
0	5723	Water						

be the most suitable. For the climate, we used the spatially downscaled average climate conditions for the period of 1836–1860 for our study area (see Climate data section above) and kept these conditions constant for the whole duration of the spin-off simulation.

Climate change impacts on stand-level forest dynamics

To account for climate change impacts on stand-level forest dynamics from the pre-settlement to the present time, we used the Biomass Succession extension for LANDIS-II (Scheller and Mladenoff 2004). This extension models changes in cohort aboveground biomass (AGB) over time by accounting for tree species' cohort age, life-history traits, and species-specific responses to different landtypes. We gathered life-history trait data for species from various sources, including numerous past LANDIS-II studies on North American forest landscapes. We parameterized and calibrated three sets of dynamic inputs that respond to soil and climate conditions: (i) species establishment probabilities (SEP), (ii) maximum potential aboveground net primary productivity (maxANPP), and (iii) maximum aboveground biomass (maxAGB). This parameterization was performed using the individual tree-based forest patch model PICUS version 1.5 (Lexer and Hönninger 2001; Taylor et al. 2017). PICUS models the dynamics of individual trees within 10×10 m patches across forest stands and incorporates spatial interactions among patches using a 3D light module. It also simulates the effects of climate and soil characteristics on tree population dynamics (Lexer and Hönninger 2001). We utilized PICUS simulations with species-specific parameters for different tree species present in the study areas. To determine the three dynamic input parameters for the Biomass Succession extension, we conducted PICUS simulations of mono-specific 1-hectare stands for each of the tree species. A factorial design approach was used, simulating mono-specific stands by species and landtype under varying climate conditions across each landtype every 30 years. The simulations were run over 300 years, beginning from bare-ground, utilizing landtype-specific soil data and climate data corresponding to each period. Values for SEP, max-ANPP, and maxAGB were extracted from these simulations following (Boulanger et al. 2017).

Fire regime shifts

We simulated changes in fire regime using the Base Fire extension (He and Mladenoff 1999). Based on the historical fire regime parameters, we calibrated the extension by modifying the k and then the p parameters obtained from the spin-off exercise so that their combination would result in the historical fire cycles considered (see Fire regime data section above) at $\pm 10\%$. Fire size distribution was kept constant throughout the simulations. Fire regime parameters were set to change in 1830, 1890 and 1940 according to the different fire regime periods considered.

Simulations of timber harvest

Harvesting was performed using the Biomass Harvest extension in LANDIS-II (Gustafson et al. 2000). It is impossible to perform harvesting simulations in LANDIS-II based on dbh; rather, harvesting is performed based on biomass harvested over a specific area per timestep. As such, we calculated proxies to determine the percentage of cells affected for each species during selective cutting for square timber and diameter-limit cutting for sawn timber. We first calculated the historical volume harvested over an area equivalent to our study area for each species for a given time period. We converted these volumes to mass in tons using the green wood density of each species. Using accumulation curves, which plot cumulative biomass against the number of cells sampled, we determined the number of harvestable cells equivalent to the harvested biomass and the percentage of affected cells for each species. These were used to know the extent to which prescriptions in the Biomass Harvest extension had to be performed at each timestep. We identified four different harvesting periods: 1860–1890, 1890–1930, 1930–1990 and 1990–2000. These periods correspond to selective cutting, diameter-limit, clear-cut and modern harvesting eras, respectively. During the selective cutting era, harvesting was parameterized to be limited to white and red pine stands that were at least 200 years and 150 years old, respectively. Selective logging of white and red pines was performed at a rate of 18.7% and 0.124% of the landscape per timestep, respectively, during that era. During the diameter-limit era, two types of prescription mimicking

diameter-limit harvest were performed. The first type targeted stands that included either white or red pines, with a minimum age of 70 years and 130 years, respectively. These prescriptions were performed on 20.29% and 12.63% of the landscape per timestep, respectively. The second type of diameter-limit harvest was performed in stands including balsam fir, yellow birch, white spruce, aspen and eastern hemlock, with minimum ages of 50, 50, 80 and 60 years, respectively, and was performed on 2.2% of the landscape per timestep. We also accounted for the fact that there was still selective logging of white and red pines during this era at reduced rates of 13.15% and 0.0004%, respectively. For the clear-cutting era (1930–1989), stands had to be at least 60 years old to be eligible for harvest and all cohorts were harvested when selected. According to historical rates, clear-cutting was performed on 22.2% of the territory at each timestep. For the 1990–2000 period, we applied partial-cutting at a 30% rate per timestep for which 25% of the biomass is removed for all species. For all prescriptions, the minimum time between harvest in a given stand was set to 40 years while patch size was restrained to one cell (6.25 ha).

In simulating historical timber harvesting, we did not include plantations, fertilization, thinning, or other forms of intensive forest management.

Other disturbances included in the simulations

We accounted for two additional natural disturbances, budworm outbreaks and catastrophic wind events. Both disturbances were included in all simulations as background factors. Spruce budworm (*Choristoneura fumiferana*), known to affect our study area (Bouchard et al. 2005, 2006a, 2006b) was simulated using the base biological disturbance agent (BDA) extension (Sturtevant et al. 2004). To reflect historical outbreak patterns, we set the interval between budworm outbreaks to 40 years. This corresponds to the mean interval observed over the last 450 years in the Bas-Saint-Laurent region of southeastern Quebec (Boulanger and Arseneault 2004), which includes areas with the same bioclimatic domain as in this study. For the windthrow disturbance, we used the Base Wind extension (Mladenoff and He 1999) to simulate wind events with a recurrence interval of 2500 years.

Modelling scenarios

We modelled six scenarios, all spanning from 1830 to 2000 (Fig. 2) with five simulation replicates each. We ended the simulations in year 2000 to align with the 2001 Canadian National Forest Inventory (NFI), which provided the most comprehensive and relevant data for validating our retrospective model (see Analysis section below). We used a 10 year timestep. The baseline scenario included all historical disturbances and served as the reference scenario. To test H1, we isolated the individual effects of fire regime shifts, climate change, and timber harvesting on vegetation changes by creating three counterfactual scenarios, each excluding one of these disturbances. The scenario that excludes timber harvesting also addresses H2. To test H3, we included two additional counterfactual scenarios to isolate the effects of the fire regimes associated to fire exclusion and Euro-American settlement. The six scenarios were:

1. Baseline scenario (BL): this scenario included all disturbances that historically affected the landscape: fire regime shifts (pre-settlement, settlement, and modern), timber harvesting, climate change, background epidemics and catastrophic wind disturbances.
2. Succession without Fire Regime Shifts scenario (noFRS): this counterfactual scenario isolated the effect of shifting fire regimes by maintaining the pre-settlement fire regime throughout the entire simulation period.
3. Succession without Climate Change scenario (noCC): this counterfactual scenario isolated the effect of climate change by keeping climate conditions constant throughout the entire simulation.
4. Succession without Timber Harvesting scenario (noTH): this counterfactual scenario isolated the effect timber harvesting by excluding all logging activities during the entire simulation. Thus, we evaluated the historical evolution of timber harvesting practices as a single factor in our study.
5. Succession without Fire Exclusion scenario (noFE): This counterfactual scenario isolated the effect of the fire exclusion era by replacing the modern fire regime with slightly lower fire activity than the pre-settlement fire regime to account for wetter conditions in the most recent period.
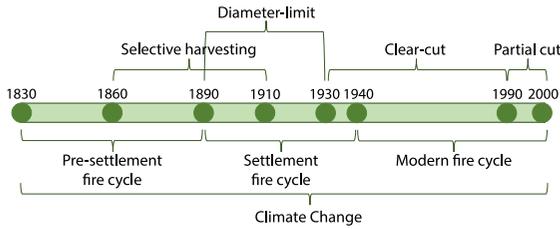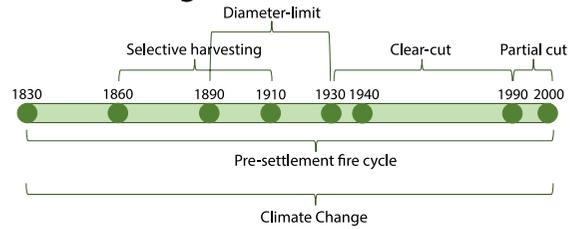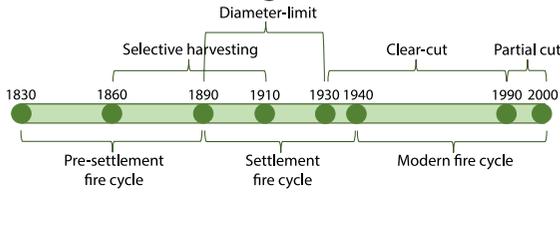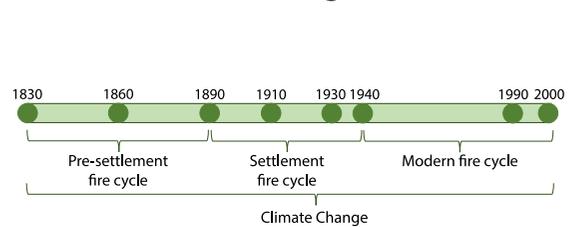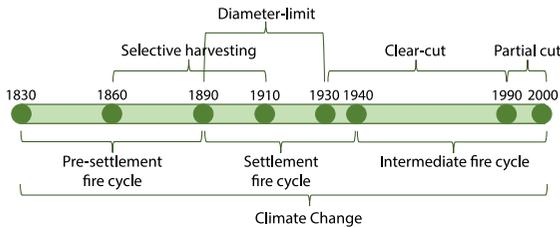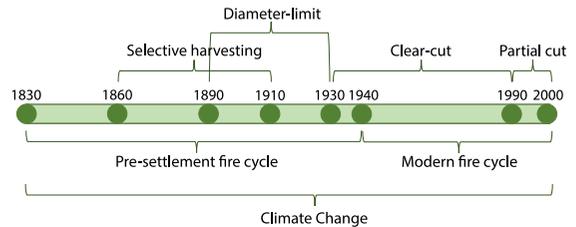
Fig. 2 Timeline of all scenarios simulated: **A** Baseline scenario (BL) that included all disturbances that historically affected the landscape, **B** Succession without Fire Regime Shifts scenario (noFRS), **C** Succession without Climate Change scenario (noCC), **D** Succession without Timber Harvesting scenario (noTH), **E** Succession without Fire Exclusion scenario (noFE), **F** Succession without Settlement Fire scenario (noSF)

6. Succession without Settlement Fire scenario (noSF): This counterfactual scenario isolated the effect of increased fire activity during to settlement activities by maintaining the pre-settlement fire regime during the period of colonization.

Analysis

To validate our retrospective landscape model, we assessed whether the simulated forest vegetation for the year corresponding to 2000 AD in the BL approximated the modern forest vegetation. We constructed forest composition matrices based on the total aboveground biomass of each species within our landscape. The forest composition matrix for the LANDIS output was derived by averaging the five replicates of the BL. The matrix representing true modern conditions was derived from the Canadian National Forest Inventory (NFI) for year 2001. We employed the Bray–Curtis index to quantify the compositional differences between the simulated and the observed forest vegetation. We obtained the Beta diversity indices using the function *beta.pair. abund* from the R package *betapart* (Baselga et al. 2018).

To assess the impact of the different disturbances on vegetation change, we performed a PERMANOVA (Permutational Multivariate Analysis of Variance) on the forest composition matrices based on the total aboveground biomass per species. The analysis compared the BL with each of the counterfactual scenarios. We used Bray–Curtis

dissimilarities to calculate pairwise distances in the PERMANOVA between the BL and each counterfactual scenario for each time step of the simulation and reported the resulting R^2 values. We performed these analyses using the *adonis* function of the *vegan* package in R (Oksanen et al. 2013).

Results

Validation of LANDIS-II model

The output of the BL for the year 2000 AD closely approximated contemporary vegetation conditions, as indicated by a turnover component of the Bray–Curtis dissimilarity of 0.32, a nestedness component of 0.10, and an overall Bray–Curtis dissimilarity of 0.41 (Table 3). The model overestimated aspen biomass while underestimating yellow birch.

Evolution of the landscape composition under the baseline scenario

Total biomass under the BL varied throughout the simulated time period, mostly reflecting different harvesting eras. Total biomass remained relatively stable until 1890, after which it sharply dropped, reaching its lowest point around 1950, followed by a gradual recovery (Fig. 3). Species composition varied throughout the studied period. For instance, early successional, deciduous species such as aspen, red maple, and paper birch exhibited substantial increases in their abundance after 1900 that intensified around 1950. Specifically, aspen's relative abundance increased from ~13 to 44%, and its cumulative biomass from 9 to 30 tons/ha (Fig. 3). Red maple's relative abundance increased from ~3 to 13%, and its cumulative abundance from 2 to 8 tons/ha (Fig. 3).

Table 3 Abundance-based Bray–Curtis dissimilarity and its components for the comparison of the simulated landscape forest composition under the Baseline scenario for year 2000 and the observed forest composition from the national inventory for the year 2001

Metric	Value
Bray–Curtis Dissimilarity	0.41
Turnover	0.32
Nestedness	0.10

Paper birch's relative abundance increased from ~3 to 8%, and its cumulative abundance from 3 to 5 tons/ha (Fig. 3).

Conversely, mid- and late successional species such as pines, spruce, balsam fir, and sugar maple experienced declines over time under the BL scenario. The pines' relative abundance decreased from 13% in 1850 to 3% in 2000, with their cumulative abundance decreasing from 10 to 2 tons/ha (Fig. 3). Black spruce's relative abundance decreased from 32% in 1850 to 18% by 2000, and its cumulative abundance decreased from 20 tons/ha in 1900 to 11 tons/ha by 2000 (Fig. 3). Balsam fir's relative abundance decreased from 12.5% in 1850 to 4% by 2000, and its cumulative abundance decreased from 8 tons/ha in 1850 to 2 tons/ha in 1950, then recovering slightly to 4 tons/ha by 2000 (Fig. 3). Sugar maple's relative abundance decreased from ~17% in 1850 to 8% by 2000, and its cumulative abundance decreased from 25 tons/ha in 1850 to around 5 tons/ha by 2000 (Fig. 3).

Relative impacts of timber harvesting on forest composition

The noTH, controlling for timber harvesting, showed the greatest deviation from the BL in vegetation composition among all the counterfactual scenarios. It had the highest R^2 values in the PERMANOVA analysis, reaching 0.70 around 1950 and 0.80 by 2000 (Fig. 4). Unlike the BL and the other counterfactual scenarios, the noTH showed relatively stable species abundance over time (Fig. 3). However, the noTH showed an increase in black spruce and a decrease in red maple. Specifically, the relative abundance of black spruce increased from 26% in 1900 to 38% by 2000, and its cumulative abundance increased from 20 to 30 tons/ha (Fig. 3). In contrast, red maple's relative abundance decreased from 19% in 1850 to 13% in 2000, and its cumulative abundance decreased from 12 to 10 tons/ha (Fig. 3). Aspen exhibited a temporary increase from 16% in 1900 to 18% in 1950, but declined to 16% by 2000, resulting in no net change by the end of the simulation (Fig. 3A). Similarly, aspen's cumulative abundance increased from 10 tons/ha in 1900 to 14 tons/ha in 1950 but decreased to 11 tons/ha by 2000 (Fig. 3B).
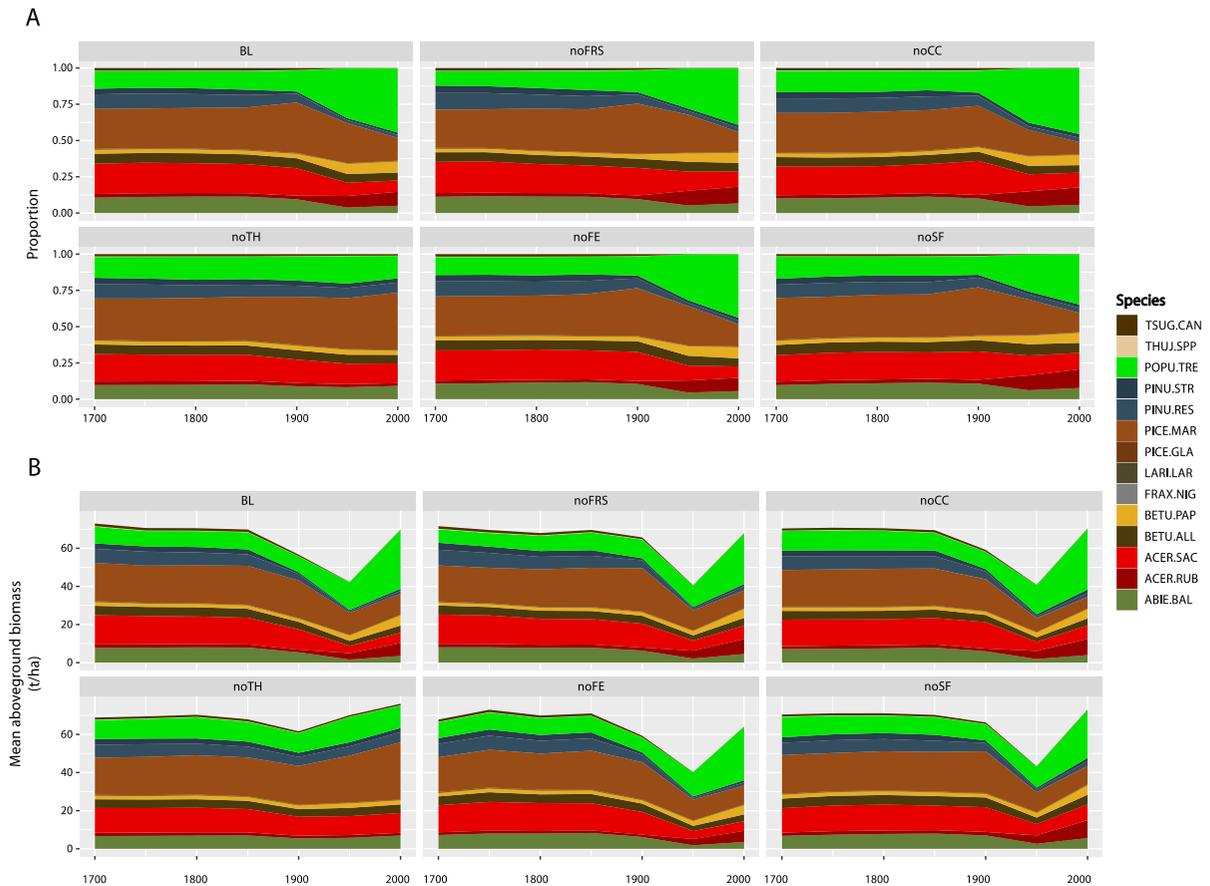
Fig. 3 A Relative abundance of each species over time and **B** Cumulative biomass over time under the baseline scenario (BL) and each of the counterfactual scenarios: without fire regime shifts scenario (noFRS), without climate change scenario (noCC), without timber harvesting scenario (noTH), without fire exclusion scenario (noFE), without settlement fire scenario (noSF)

Relative impact of fire regimes on forest composition

The noFE, controlling for fire exclusion, showed minimal divergence in vegetation composition from the BL, with R^2 values from the PERMANOVA consistently remaining below 0.10 throughout the study period (Fig. 4). In contrast, the noSF, controlling for settlement increased fire activity, exhibited the highest divergence after the noTH, with R^2 values increasing from 0.25 in 1930 to 0.40 by 2000 (Fig. 4). Similarly, the noFRS, controlling for fire regime shifts, showed an increase in R^2 beginning in 1900 reaching 0.30 by 2000 (Fig. 4). The changes in species biomass under the noFRS, noFS, and noFE closely resembled those observed under the BL. Under the noSF, the relative and

cumulative abundances of aspen increased after the 1900s similarly to what was simulated under the BL; however, the increase was smaller than under the BL yet greater than under the noTH (Fig. 3).

Relative impact of climate change on forest composition

The noCC, controlling for climate change, exhibited modest divergence from the BL in forest composition, as indicated by R^2 values in the PERMANOVA analysis that increased from 0.20 in 1860 to 0.30 by 1930 and reached 0.35 by 2000 (Fig. 4). The overall evolution of species composition under the noCC closely resembled that of the BL. However, the
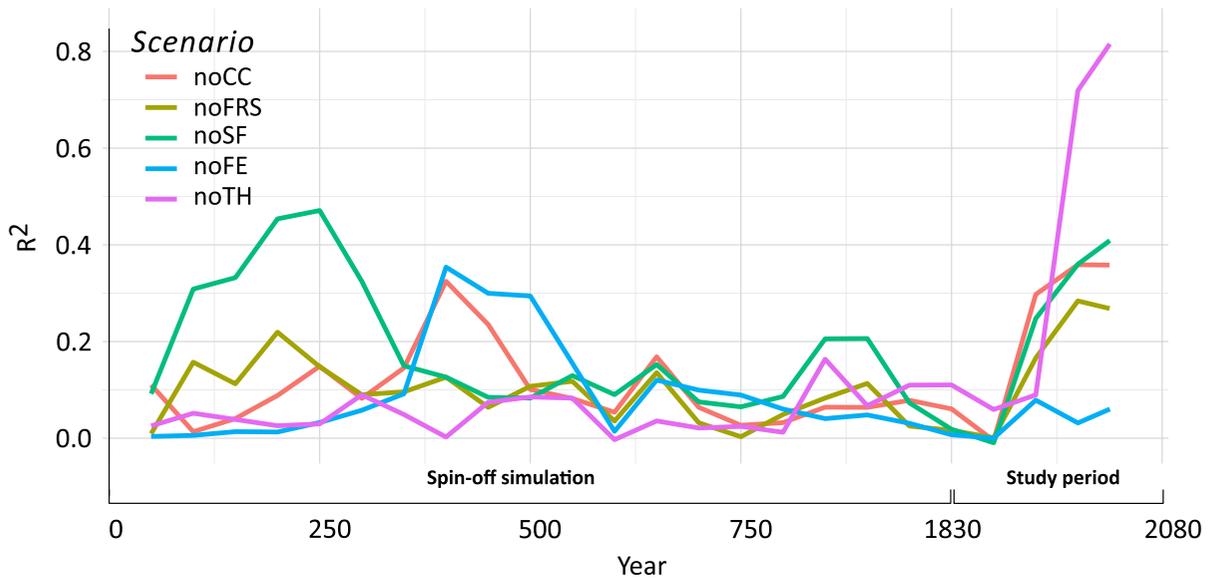
Fig. 4 PERMANOVA of the forest composition matrices between the historical baseline scenario (BL) and each of the counterfactual scenarios: without fire regime shifts scenario (noFRS), without climate change scenario (noCC), without timber harvesting scenario (noTH), without fire exclusion scenario (noFE), without settlement fire scenario (noSF). Shown is the spin-off simulation of 1000 years followed by our study period (1830–2000)

decline in black spruce observed under the BL was slightly more pronounced under the noCC.

Discussion

This study represents the first retrospective modelling of forest dynamics and disturbances in the mixedwood temperate forests of southwestern Quebec. It demonstrated the enduring influence of past forest use, as these legacies have shaped distinct successional trajectories and still influence the regional forest composition. Although previous studies based on historical land survey records have reported the transformation in the forest composition from pre-settlement to settlement times in the region (Jackson et al. 2000b; Danneyrolles et al. 2016a), they have not examined the individual effects of various disturbances on driving these shifts.

Our results suggested that timber harvesting had the greatest impact on dynamics of vegetation composition, supporting H1. This is consistent with the extensive and intense historical timber harvesting in the region. In the absence of timber harvesting (noTH), biomass abundance for most species remained relatively stable throughout the simulation,

indicating ecosystem resilience and supporting H2. The settlement-related increased fire activity had a modest effect on the vegetation composition, while fire exclusion had a minimal effect, rejecting H3 and indicating that the effects of fire exclusion on mesophication is a slow, gradual process that may take longer time to observe. While the direct effects of climate change were not as pronounced as the impacts of timber harvesting, due to the modest climate change observed during the study period, it still contributed to the dynamics observed in black spruce.

Our conclusions relied on a well-verified baseline scenario (BL) that aligned closely with observed data from the national inventory for the present day. The evolution of aboveground biomass simulated by the BL was consistent with the findings from previous studies in the region (Jackson et al. 2000a; Friedman and Reich 2005; Schulte et al. 2007; Dupuis et al. 2011a; Danneyrolles et al. 2016a; Terrail et al. 2019). The successful performance of the BL scenario underscored the reliability of pre-settlement vegetation and historical fire regime reconstructions in the area.

Table 4 Comparison of composition changes per species in the baseline scenario of this study and those reported by Danneyrolles et al.'s (2016a)

Species	This study's baseline scenario	Danneyrolles et al. (2016a)	
	Relative abundance % change (%)	Dominance % change (%)	Prevalence % change (%)
Spruces (*Picea*)	− 43.75	− 59.35	− 8.19
Basam fir (*Abies balsamea*)	− 68.00	− 37.50	+ 0.43
Pines (*Pinus*)	− 76.92	+ 53.85	− 23.17
Poplars (*Populus*)	+ 238.46	+ 228.74	+ 155.65
Paper birch (*Betula papyfera*)	+ 166.67	+ 110.96	+ 19.93
Red maple (*Acer rubrum*)	+ 333.33	+ 3000	+ 4272.73
Sugar maple (*Acer saccharum*)	− 52.94		

Dominance % is the percentage of each taxon occurring in the first rank of enumeration in the taxon lists. Prevalence % is the percentage occurrence of each taxon in all taxon lists, regardless of its rank in those lists (See Danneyrolles et al. 2016a for further details on these values)

Evolution of vegetation composition in the baseline scenario

The BL scenario revealed a significant increase in fast-growing broadleaf species, including aspen, paper birch, and red maple, alongside a decline in late-successional, long-lived conifers such as pines, spruce, and balsam fir, but also a decrease in sugar maple, a broadleaf, late-successional species over the last 170 years (Fig. 3, Table 4). In general, these results were consistent with previous studies of forest dynamics from pre-settlement to modern times (Jackson et al. 2000a; Friedman and Reich 2005; Schulte et al. 2007; Dupuis et al. 2011a; Danneyrolles et al. 2016a; Terrail et al. 2019), validating our simulation and supporting the evaluation of the counterfactual scenarios.

The increase in the broadleaved species was largely due to their ability to thrive in disturbance-prone environments. Aspen's relative abundance tripled during the twentieth century, rising from 13% in 1900 to around 44% in 2000 (Fig. 3A). Aspen is able to regenerate vegetatively through root suckering when the aboveground portion of the tree is removed or damaged (Frey et al. 2003). Normally, aspen roots do not develop suckers when intact aboveground parts are present, as auxins hormones that inhibit sucker initiation are transported to the root system (Wan et al. 2006). When the aboveground portion of the tree is removed, the lack of auxins allows cytokines, signaling proteins produced in the roots, to promote the development of stem buds and shoots (Wan et al. 2006). This vegetative strategy enables aspen to quickly colonize open spaces following disturbances, particularly when a large portion of the basal area is removed (Prévost and Pothier 2003). Furthermore, increased soil temperatures on disturbed sites have been shown to facilitate re-sprouting (Frey et al. 2003).Paper birch more than doubled in relative abundance, increasing from 3% in 1900 to 8% by 2000 (Fig. 3A). Paper birch, like aspen, thrives under disturbances due to its ability to reproduce vegetatively, resprouting from the base or roots when cut or damaged. Both sprouting or seeding of paper birch are abundant, enabling it to dominate in the absence of aspen (Bergeron 2000). Red maple, while not strictly a shade-intolerant pioneer or fire-adapted species (Nowacki and Abrams 2008) like aspen and paper birch, showed a remarkable fourfold increase in relative abundance, from 3 to 13% (Fig. 3A). This increase is due to its status as a "super generalist" favored by disturbances and having shade tolerance (Abrams 1998). Red maple is one of the fastest growing trees in the region (Zhang et al. 2015), growing rapidly after germination, maturing early and producing abundant seeds (Abrams 1998). Red maple seedlings can persist under shaded conditions, but quickly increase growth in response to gap openings (Abrams 1998). This adaptability allows red maple to thrive both in understory and open environments (Archambault et al. 2009).

The decline in conifers is explained by early timber harvesting specifically targeting them. The relative abundance of pines had a fourfold decrease, going from 13% in 1850 to 3% by 2000 (Fig. 3A). This decline started earlier than the decrease of the other conifers, 1850 compared to 1900. The earlier decrease coincides with the square timber harvesting period (1860–1910), during which the largest pines were targeted, resulting in the extraction of a total of *ca* 138 kilotons of white and red pine combined across our landscape (Table 1).

The decline in conifers can also be attributed to competition with the fast-growing broadleaved species that expanded following intensive cutting. As slow growers, conifers take longer to reach sexual maturity, making species like black spruce particularly vulnerable when disturbance occur at short intervals (Brown and Johnstone 2012). This vulnerability likely contributed to a decrease in black spruce's relative abundance from 32 to 18% (Fig. 3A). As a fire-adapted species, black spruce relies on its aerial seed bank, storing its seeds in semi-serotinous cones. These cones typically remains closed until a fire melts the sealing resin, triggering seed release and enabling a regeneration pulse (Brown and Johnstone 2012; Viglas et al. 2013). Black spruce trees may produce cones by age 30 but are more likely to do so by age 100 (Viglas et al. 2013). If fires or other disturbances occur too frequently before the trees have matured and produced sufficient cones, it can severely compromise recruitment.

The decline in sugar maple, with a relative abundance of 17% in 1850 that dropped to 8% by 2000, can be attributed to its status as a late-successional species (Barrette et al. 2024). However, this decrease does not agree with previous research that have reported an increase in both red maple and sugar maple from pre-settlement to modern times in the region (Dupuis et al. 2011a; Danneyrolles et al. 2016a). Notably, Danneyrolles et al. (2016a) conducted their study in Temiscamingue and used the same dataset as in this study. The discrepancy might be due to model idiosyncrasies, particularly the life trait parameters we used in our simulations, which more closely follow sugar maple's late-successional status in this region. While the increase in sugar maple has been explained by its high phenotypic plasticity and sprouting ability after disturbances

(Nolet et al. 2008), these traits are known to vary with latitude (Nolet et al. 2008).

Controlling for timber harvesting

Timber harvesting emerged as the primary driver of the vegetation shifts observed, supporting H1. The counterfactual scenario that excluded timber harvesting (noTH) deviated the most from the BL, with an R^2 of 0.85 by 2000 (Fig. 4). Under the noTH, the aboveground biomass of most species remained relatively stable in contrast to the more pronounced shifts observed under the BL and other counterfactual scenarios (Fig. 3). However, there were some exceptions. For instance, black spruce increased, while sugar maple decreased. Aspen exhibited a temporary increase but later declined, resulting in no net change by the end of the simulation.

Timber harvesting focusing on a particular set of canopy dominants likely overrode effects of other factors in shaping vegetation of the studied landscape. A similar pattern was reported in another study in the forests of central Ontario (Jackson et al. 2000b). The decrease of spruce and pine in eastern Quebec (Dupuis et al. 2020), and the widespread increase in red maple in the region (Fei and Steiner 2009) have been largely attributed to logging. Projections of forest dynamics under future climate change have equally identified timber harvesting as an important driver of changes in mixedwood boreal forests of eastern Canada (Molina et al. 2021). Our findings corroborate these conclusions. However, changes in the abundance of certain species have also been attributed to other factors. For example, the increase in aspen in eastern Quebec has been attributed to increased fire activity related to settlement activities (Dupuis et al. 2020).

By removing timber harvesting from our simulations (noTH), we allowed the forests to experience only natural disturbances particularly during the last 60 years of the simulation (1940–2000), when settlement-related fire activity ended. Under the noTH scenario, after 1940, disturbances were limited to budworm outbreaks and windthrow. These partial disturbances, along with small gap dynamics, could have promoted both constant and pulse recruitment (Després et al. 2014). Intermediate disturbances may have facilitated the persistence of early-successional species, like aspen and paper birch (Kneeshaw and

Bergeron 1998), a pattern observed in old temperate hardwood forests under natural disturbance regimes in the region (Frelich and Reich 1995). The modest increase in the relative biomass of the shade-tolerant black spruce (from 26% in 1900 to 38% by 2000), could be attributed to black spruce's lower susceptibility to budworm outbreaks, allowing it to expand following the decline of balsam fir.

The relatively stable biomass of all species throughout the simulation suggests that ecosystem resilience was maintained, supporting H2. In the absence of timber harvesting, functional traits present during the pre-settlement period such as fire tolerance and shade tolerance were preserved. The removal of species with key functional traits, such as fire tolerance, reduces the system's ability to recover and increases its vulnerability to novel disturbances (Johnstone et al. 2016; Seidl et al. 2016).

Controlling for fire regimes

The effect of the settlement-related increased fire activity on the forest composition, although modest, was greater than that of fire exclusion. Controlling for settlement fires (noSF), resulted in the second highest values of dissimilarity from the BL, with an R^2 that reached 0.40 by 2000 (Fig. 4). Although the biomass evolution under the noSF was not markedly different from the BL, the increase in aspen was less pronounced. This finding aligns with the increase in aspen being driven by higher fire activity during the settlement period (Dupuis et al. 2020). However, our study suggests that settlement-related increased fire activity was only part of the story, with logging playing the dominant role.

In contrast, modern fire exclusion (noFE) had the lowest impact on vegetation composition, with R^2 values consistently below 0.10 throughout the simulation (Fig. 4), and biomass changes closely mirroring those in the BL. This contradicts H3 and previous research that identified fire exclusion as the main driver of forest mesophication, where fire-sensitive mesophytic species like maple and birch increase while fire-dependent xerophytic species like pine decline (Nowacki and Abrams 2008; Frelich et al. 2021). This discrepancy may be due to the mesophication process likely unfolding over longer timescales than those captured by this study.

Unpublished data provided by Stathopoulos (Theodore Stathopoulos, pers. comm.) indicate that the present recruitment of red pine, a fire-adapted species, in our study area is poor to non-existent. Red pine's regeneration in these forests was largely confined to periods before fire exclusion, with most tree ring piths dating to the late 1800s and early 1900s. The more pronounced effect of settlement-related fires (noSF) compared to fire exclusion (noFE) can be attributed to the immediate impacts of increased fire activity, which promotes the rapid establishment of early-successional species. In contrast, the effects of fire exclusion are more gradual, with a slow replacement of fire-adapted species by fire-sensitive ones over time.

Controlling for climate change

Direct effects of climate change had a modest impact on the forest composition. When climate change was controlled for (noCC), the R^2 value reached 0.35 by the end of the simulation in 2000. The biomass evolution largely mirrored that of the BL. However, the decline in black spruce was slightly more pronounced under the noCC compared to the BL and the other counterfactual scenarios, suggesting that climate change in our study area favored the growth of black spruce. A positive growth response for black spruce has been particularly observed in the eastern, wetter regions of North America, including our study area (Wang et al. 2023). The parameters used to model black spruce growth in our simulations were informed by Wang et al.'s (2023). In contrast, Girardin et al. (2016) projected that black spruce at the southern edge of its distribution, where temperatures are higher, experiences reduced growth due to increased respiratory demand. Nevertheless, the concurrent increase in mean annual precipitation of 1.66% in our study area could mitigate evapotranspiration and positively influence black spruce growth. In forests located south of 49°N latitude, higher solar radiation leads to increased evapotranspiration, resulting in a more moisture-limited environment compared to northern forests (Lesven et al. 2024).

The scenarios controlling for fire exclusion (noFE) and for the increased fire activity during the settlement period (noSF) partly reflected the indirect effects of climate change. Fire exclusion was influenced

by increased moist conditions in the area (Girardin et al. 2006; Drobyshev et al. 2017; Chavardès et al. 2022). However, the noFE scenario had the lowest impact on the vegetation composition among all the counterfactual scenarios (Fig. 4), suggesting that the indirect effects of climate change through fire exclusion during our study period were minimal. Similarly, increased fire activity during the settlement period was affected by climate, as drought conditions during 1910–1920 contributed to higher fire hazard (Girardin et al. 2009). The noSF had the second strongest effect on the vegetation composition (Fig. 4) and contributed to some extent to the increase of aspen (see Controlling for fire regimes section above). However, the extent to which these effects were driven by indirect climate influences remains uncertain.

The relatively modest impact of climate change on vegetation compositions changes from the pre-settlement to the present aligns with research showing that increased precipitation in this area over the past century has offset rising temperatures (Girardin et al. 2009, 2013). This has helped prevent the modern record drought-induced declines in forest productivity and diebacks seen in boreal forests in western Canada and Alaska (Hogg and Bernier 2005; Soja et al. 2007), and the increased fire activity in northwestern North America (Hanes et al. 2018; Chavardès et al. 2022). However, the future effects of climate change on the forest composition, whether directly or through climate-sensitive disturbances, in the area remain uncertain. Projections under the AR4 A2 scenario suggest that eastern North America will continue receiving enough precipitation to offset increased evapotranspiration in 2090 (Gauthier et al. 2015). Meanwhile, under the RCP 8.5 scenario, climate change effects on tree growth, competition, and area burned are projected to cause drastic shifts in forest composition by 2100 (Boulanger et al. 2018).

Study limitations

We acknowledged several limitations of this research. The primary limitation is related to the challenges of precisely recreating the pre-settlement vegetation conditions and accurately replicating the timing of the disturbances. Even though our retrospective simulations showed overall meaningful trends, our inability to perfectly reconstruct historical conditions that led us to employ several simplifying assumptions in the simulations introduced some uncertainty that affects the interpretation of our findings.

We did not test interactions between disturbances. Our experimental design focused on isolating the effects of single disturbance types. However, disturbances can have interactive effects when occurring successively in a stand (Kulakowski et al. 2003; Buma 2015).

Implications for southwestern Quebec's temperate hardwood forests

Our study shows that legacies from past forest use, primarily timber harvesting but also settlement-related increased fire activity, have altered the vegetation composition of southwestern Quebec's forests, leading to a decline in long-lived fire-adapted conifers, like red pine, and the rise of early successional broadleaf trees, like aspen. With climate change projected to further alter forest composition, current management should prioritize restoring forests with a diversity of functional traits to enhance their resilience to future disturbances (Boulanger et al. 2018; Lucash et al. 2018). Increasing species and functional diversity can enhance ecosystems' response flexibility to changing conditions, helping maintain ecosystem functioning and services under changing environmental conditions (Mori et al. 2013; Seidl et al. 2016). Disentangling the effects of different global change-related drivers of forest ecosystem dynamics will remain a key research topic to ensure that forests can provide their essential ecosystem functions and services, including biodiversity, carbon storage, and wood production.

Author contributions DR, ID, and YB planned analyses. DR, YB, and JP conducted analyses. DR, YB, JP, and VD collected data. DR, YB, and VD designed figures. ID acquired funding. ID and YBerg supervised and contributed to study's

conception. DR wrote the manuscript's first draft. All authors revised the article and gave final approval for publication.

Data availability Data are available upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

References

Abrams MD (1998) The red maple paradox. Bioscience 48(5):355–364

Abrams MD (2001) Eastern white pine versatility in the presettlement forest: this eastern giant exhibited vast ecological breadth in the original forest but has been on the decline with subsequent land-use changes. Bioscience 51(11):967–979

Abrams MD, Nowacki GJ (2015) Large-scale catastrophic disturbance regimes can mask climate change impacts on vegetation–a reply to Pederson et al. (2014). Ecol Appl 7:753–769

Aird PL (2016) Logging and rafting square timber in Ontario and Québec for shipment to Great Britain circa 1870 to 1908. For Chron 92(04):394–400

Archambault L, Morissette J, Bernier-Cardou M (1998) Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Québec, Canada. For Ecol Manag 102(1):61–74

Archambault L, Delisle C, Larocque GR (2009) Forest regeneration 50 years following partial cutting in mixedwood ecosystems of southern Quebec, Canada. For Ecol Manag 257(2):703–711

Barrette M, Dumais D, Auger I, Boucher Y (2024) Clearcutting of temperate forests in late successional stages triggers successional setbacks extending compositional recovery by an additional century. For Ecol Manag 566:122084

Baselga A, Orme D, Villéger S, De Bortoli J, Leprieur F, Logez M (2018) Betapart: partitioning beta diversity into turnover and nestedness components. R Package Version. 1.1

Bergeron Y (2000) Species and stand dynamics in the mixed woods of Quebec's Southern Boreal Forest. Ecology 81(6):1500–1516

Berland A, Shuman B, Manson SM (2011) Simulated importance of dispersal, disturbance, and landscape history in long-term ecosystem change in the big woods of Minnesota. Ecosystems 14(3):398–414

Bouchard M, Kneeshaw D, Bergeron Y (2005) Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. For Ecol Manag 204(2):297–313

Bouchard M, Kneeshaw D, Bergeron Y (2006a) Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. Ecology 87(9):2319–2329

Bouchard M, Kneeshaw D, Bergeron Y (2006b) Tree recruitment pulses and long-term species coexistence in mixed forests of western Québec. Écoscience 13(1):82–88

Boulanger Y, Arseneault D (2004) Spruce budworm outbreaks in eastern Quebec over the last 450 years. Can J For Res 34(5):1035–1043

Boulanger Y, Gauthier S, Burton PJ (2014) A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. Can J For Res. https://doi.org/10.1139/cjfr-2013-0372

Boulanger Y, Taylor AR, Price DT, Cyr D, McGarrigle E, Rammer W, Sainte-Marie G, Beaudoin A, Guindon L, Mansuy N (2017) Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. Landsc Ecol 32(7):1415–1431

Boulanger Y, Taylor AR, Price DT, Cyr D, Sainte-Marie G (2018) Stand-level drivers most important in determining boreal forest response to climate change. J Ecol 106(3):977–990

Brice M, Cazelles K, Legendre P, Fortin M (2019) Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. Glob Ecol Biogeogr 28(11):1668–1681

Brice M, Vissault S, Vieira W, Gravel D, Legendre P, Fortin M (2020) Moderate disturbances accelerate forest transition dynamics under climate change in the temperate–boreal ecotone of eastern North America. Glob Change Biol 26(8):4418–4435

Brown JL (1981) Les forets du Temiscamingue, Quebec. Ecologie et photo-interpretation. Etudes Ecologiques Laboratorie d'Ecologie Forestiere Universite Laval

Brown CD, Johnstone JF (2012) Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. For Ecol Manag 266:34–41

Buma B (2015) Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere. 6(4):art70

Campbell ID, McAndrews JH (1995) Charcoal evidence for Indian-set fires: a comment on Clark and Royall. Holocene 5(3):369–370

Cardil A, Lorente M, Boucher D, Boucher J, Gauthier S (2019) Factors influencing fire suppression success in the province of Quebec (Canada). Can J For Res 49(5):531–542

Chavardès RD, Danneyrolles V, Portier J, Girardin MP, Gaboriau DM, Gauthier S, Drobyshev I, Cyr D, Wallenius T, Bergeron Y (2022) Converging and diverging burn rates in North American boreal forests from the Little Ice Age to the present. Int J Wildland Fire 31(12):1184–1193

Clark JS, Royall PD (1995) Transformation of a northern hardwood forest by aboriginal (Iroquois) fire: charcoal evidence from Crawford Lake, Ontario, Canada. Holocene 5(1):1–9

Danneyrolles V, Arseneault D, Bergeron Y (2016a) Pre-industrial landscape composition patterns and post-industrial changes at the temperate-boreal forest interface in western Quebec, Canada. J Veg Sci 27:470–481

Danneyrolles V, Arseneault D, Bergeron Y (2016b) Pre-industrial landscape composition patterns and post-industrial changes at the temperate–boreal forest interface in western Quebec, Canada. J Veg Sci 27(3):470–481

Danneyrolles V, Dupuis S, Fortin G, Leroyer M, de Römer A, Terrail R, Vellend M, Boucher Y, Laflamme J, Bergeron Y, Arseneault D (2019) Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nat Commun 10(1):1265

Danneyrolles V, Vellend M, Dupuis S, Boucher Y, Laflamme J, Bergeron Y, Fortin G, Leroyer M, de Römer A, Terrail R, Arseneault D (2021) Scale-dependent changes in tree diversity over more than a century in eastern Canada: Landscape diversification and regional homogenization. J Ecol 109(1):273–283

Després T, Asselin H, Doyon F, Bergeron Y (2014) Structural and spatial characteristics of old-growth temperate deciduous forests at their Northern distribution limit. For Sci 60(5):871–880

Drobyshev I, Goebel PC, Hix DM, Corace RG, Semko-Duncan ME (2008) Pre- and post-European settlement fire history of red pine dominated forest ecosystems of Seney National Wildlife Refuge, Upper Michigan. Can J For Res 38(9):2497–2514

Drobyshev I, Bergeron Y, Girardin MP, Gauthier S, Ols C, Ojal J (2017) Strong gradients in forest sensitivity to climate change revealed by dynamics of forest fire cycles in the post little ice age era. J Geophys Res Biogeosciences 122(10):2605–2616

Dupuis S, Arseneault D, Sirois L (2011a) Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada: change from pre-settlement to present-day forest composition. J Veg Sci 22(3):564–575

Dupuis S, Arseneault D, Sirois L (2011b) Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. J Veg Sci 22(3):564–575

Dupuis S, Danneyrolles V, Laflamme J, Boucher Y, Arseneault D (2020) Forest transformation following European settlement in the Saguenay-Lac-St-Jean valley in Eastern Québec, Canada. Front Ecol Evol 10:2

Fei S, Steiner KC (2009) Rapid capture of growing space by red maple. Can J for Res 39(8):1444–1452

Frelich L (1995) Old forest in the lake states today and before European settlement. https://www.semanticscholar.org/paper/Old-forest-in-the-lake-states-today-and-before-Frelich/cf9358ddb0f8041b4e599df84d3841f76f78c138. Accessed 13 Jul 2021

Frelich LE, Reich PB (1995) Spatial patterns and succession in a Minnesota Southern-Boreal Forest. Ecol Monogr 65(3):325–346

Frelich LE, Lorimer CG, Stambaugh MC (2021) History and future of fire in hardwood and conifer forests of the Great Lakes-Northeastern Forest Region, USA. In: Greenberg CH, Collins B (eds) Fire ecology and management: past, present, and future of US forested ecosystems. Springer International Publishing, Cham, pp 243–285

Frey BR, Lieffers VJ, Landhäusser SM, Comeau PG, Greenway KJ (2003) An analysis of sucker regeneration of trembling aspen. Can J For Res 33(7):1169–1179

Friedman SK, Reich PB (2005) Regional legacies of logging: departure from presettlement forest conditions in Northern Minnesota. Ecol Appl 15(2):726–744

Gajewski K, Winkler MG, Swain AM (1985) Vegetation and fire history from three lakes with varved sediments in northwestern Wisconsin (U.S.A.). Rev Palaeobot Palynol 44(3):277–292

Gauthier S, Nguyen T, Bergeron Y, Leduc A, Drapeau P, Grondin P (2008) Chapter 18. Developing forest management strategies based on fire regimes in Northwestern Quebec. In: Perera AH, Buse LJ, Weber MG (eds) Concepts and applications. Columbia University Press, New York Chichester, West Sussex, pp 219–229

Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015) Boreal forest health and global change. Science 349(6250):819–822

Girardin MP, Tardif J, Flannigan MD, Bergeron Y (2004) Multicentury reconstruction of the Canadian Drought Code from eastern Canada and its relationship with paleoclimatic indices of atmospheric circulation. Clim Dyn 23(2):99–115

Girardin MP, Tardif JC, Flannigan MD, Bergeron Y (2006) Forest fire-conducive drought variability in the Southern Canadian Boreal forest and associated climatology inferred from tree rings. Can Water Resour J Rev Can Ressour Hydr 31(4):275–296

Girardin MP, Ali AA, Carcaillet C, Mudelsee M, Drobyshev I, Hely C, Bergeron Y (2009) Heterogeneous response of circumboreal wildfire risk to climate change since the early 1900s. Glob Change Biol 15(11):2751–2769

Girardin MP, Ali AA, Carcaillet C, Gauthier S, Hély C, Le Goff H, Terrier A, Bergeron Y (2013) Fire in managed forests of eastern Canada: risks and options. For Ecol Manag 294:238–249

Girardin MP, Hogg EH, Bernier PY, Kurz WA, Guo XJ, Cyr G (2016) Negative impacts of high temperatures on growth of black spruce forests intensify with the anticipated climate warming. Glob Change Biol 22(2):627–643

Gourd BB (1983) Angliers et le remorqueur de bois TE Draper: L'exploitation forestière et le flottage du bois au Témiscamingue.

Graham NE, Ammann CM, Fleitmann D, Cobb KM, Luterbacher J (2011) Support for global climate reorganization during the "Medieval Climate Anomaly." Clim Dyn 37(5):1217–1245

Grenier DJ, Bergeron Y, Kneeshaw D, Gauthier S (2005) Fire frequency for the transitional mixedwood forest of Timiskaming, Quebec. Canada 35:11

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30(1):32–43

Guyette RP, Muzika RM, Dey DC (2002) Dynamics of an anthropogenic fire regime. Ecosystems 5(5):472–486

Hanberry BB, Palik BJ, He HS (2012) Comparison of historical and current forest surveys for detection of homogenization and mesophication of Minnesota forests. Landsc Ecol 27(10):1495–1512

Hanes CC, Wang X, Jain P, Parisien M-A, Little JM, Flannigan MD (2018) Fire-regime changes in Canada over the last half century. Can J For Res. https://doi.org/10.1139/cjfr-2018-0293

He HS, Mladenoff DJ (1999) Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. Ecology 80(1):81–99

Hogg EH, Bernier PY (2005) Climate change impacts on drought-prone forests in western Canada. For Chron 81(5):675–682

Houle D, Richard PJH, Ndzangou SO, Richer-Laflèche M (2012) Compositional vegetation changes and increased red spruce abundance during the Little Ice Age in a sugar maple forest of north-eastern North America. Plant Ecol 213(6):1027–1035

Howe CD (1923) The forests and forest industries of Canada. Ann Am Acad Pol Soc Sci 107(1):95–101

Jackson SM, Pinto F, Malcolm JR, Wilson ER (2000a) A comparison of pre-European settlement (1857) and current (1981–1995) forest composition in central Ontario. Can J For Res 30(4):605–612

Jackson SM, Pinto F, Malcolm JR, Wilson ER (2000b) A comparison of pre-European settlement (1857) and current (1981–1995) forest composition in central Ontario. Can J For Res 30:8

Johnstone JF, Allen CD, Franklin JF, Frelich LE, Harvey BJ, Higuera PE, Mack MC, Meentemeyer RK, Metz MR, Perry GL, Schoennagel T (2016) Changing disturbance regimes, ecological memory, and forest resilience. Front Ecol Environ 14(7):369–378

Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA (2011) Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci 16(8):406–411

Kenefic LS, Sendak PE, Brissette JC (2005) Comparison of fixed diameter-limit and selection cutting in Northern Conifers. North J Appl for 22(2):77–84

Klimaszewski-Patterson A, Weisberg PJ, Mensing SA, Scheller RM (2018) Using Paleolandscape modeling to investigate the impact of native American-set fires on pre-columbian forests in the Southern Sierra Nevada, California, USA. Ann Am Assoc Geogr 108(6):1635–1654

Kneeshaw DD, Bergeron Y (1998) Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79(3):783–794

Kulakowski D, Veblen TT, Bebi P (2003) Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J Biogeogr 30(9):1445–1456

Lauzon È, Kneeshaw D, Bergeron Y (2007) Reconstruction of fire history (1680–2003) in Gaspesian mixedwood boreal forests of eastern Canada. For Ecol Manag 244(1):41–49

Lesven JA, Druguet Dayras M, Cazabonne J, Gillet F, Arsenault A, Rius D, Bergeron Y (2024) Future impacts of climate change on black spruce growth and mortality: review and challenges. Environ Rev 32(2):214–230

Lexer MJ, Hönninger K (2001) A modified 3D-patch model for spatially explicit simulation of vegetation composition in heterogeneous landscapes. For Ecol Manag 144(1–3):43–65

Liang Y, Duveneck MJ, Gustafson EJ, Serra-Diaz JM, Thompson JR (2018) How disturbance, competition, and dispersal interact to prevent tree range boundaries from keeping pace with climate change. Glob Change Biol 24(1):e335–e351

Liang Y, Gustafson EJ, He HS, Serra-Diaz JM, Duveneck MJ, Thompson JR (2023) What is the role of disturbance in catalyzing spatial shifts in forest composition and tree species biomass under climate change? Glob Change Biol 29(4):1160–1177

Lorimer CG (2008) Eastern White Pine Abundance in 19th Century Forests: a reexamination of evidence from land surveys and lumber statistics. J For 106(5):253–260

Lower ARM (1933) The trade in square timber. Contrib Can Econ 6:40–61

Lucash MS, Scheller RM, Sturtevant BR, Gustafson EJ, Kretchun AM, Foster JR (2018) More than the sum of its parts: how disturbance interactions shape forest dynamics under climate change. Ecosphere 9(6):e02293

Mansuy N, Thiffault E, Paré D, Bernier P, Guindon L, Villemaire P, Beaudoin A (2014) Digital mapping of soil properties in Canadian managed forests at 250 m of resolution using the k-nearest neighbor method. Geoderma 235:59–73

McRae DJ, Lynham TJ, Frech RJ (1994) Understory prescribed burning in red pine and white pine. For Chron 70(4):395–401

Mladenoff DJ, He HS (1999) Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. Spatial modeling of forest landscape change. Cambridge University Press, Cambridge, pp 125–162

Molina E, Valeria O, De Grandpre L, Ramirez JA, Cyr D, Boulanger Y (2021) Projecting future aboveground biomass and productivity of managed eastern Canadian mixedwood boreal forest in response to climate change. For Ecol Manag 487:119016

Molina E, Valeria O, Martin M, Montoro Girona M, Ramirez JA (2022) Long-term impacts of forest management practices under climate change on structure, composition,

and fragmentation of the Canadian boreal landscape. Forests 13(8):1292

Mori AS, Furukawa T, Sasaki T (2013) Response diversity determines the resilience of ecosystems to environmental change. Biol Rev 88(2):349–364

Munoz SE, Gajewski K (2010) Distinguishing prehistoric human influence on late-Holocene forests in southern Ontario, Canada. Holocene 20(6):967–981

Munoz SE, Mladenoff DJ, Schroeder S, Williams JW (2014) Defining the spatial patterns of historical land use associated with the indigenous societies of eastern North America. J Biogeogr 41(12):2195–2210

Nolet P, Delagrange S, Bouffard D, Doyon F, Forget E (2008) The successional status of sugar maple (*Acer saccharum*), revisited. Ann for Sci 65(2):1

Nowacki GJ, Abrams MD (2008) The demise of fire and "Mesophication" of forests in the Eastern United States. Bioscience 58(2):123–138

Nowacki GJ, Abrams MD (2015) Is climate an important driver of post-European vegetation change in the Eastern United States? Glob Change Biol 21(1):314–334

Nyamai PA, Goebel PC, Hix DM, Corace III RG, Drobyshev I (2014) Fire history, fuels, and overstory effects on the regeneration-layer dynamics of mixed-pine forest ecosystems of eastern Upper Michigan, USA. For Ecol Manag 322:37–47

Ojima DS, Galvin KA, Turner BL (1994) The global impact of land-use change. Bioscience 44(5):300–304

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, Ohara R, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) Package 'vegan.' Commu Ecol 2(9):1–295

Oliver CD, Larson BC, Oliver C (1996) Forest stand dynamics. Wiley, New York

Paquette N, Gajewski K (2013) Climatic change causes abrupt changes in forest composition, inferred from a high-resolution pollen record, southwestern Quebec, Canada. Quat Sci Rev 75:169–180

Pickett S, White P (1985) The ecology of natural disturbance and patch dynamics. Elsevier, Amsterdam

Pinto F, Romaniuk S, Ferguson M (2008) Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada. Can J For Res 38(7):1842–1854

Prévost M, Pothier D (2003) Partial cuts in a trembling aspen—conifer stand: effects on microenvironmental conditions and regeneration dynamics. Can J For Res 33(1):1–15

Régnière J (1996) Generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environ Entomol 25(5):869–881

Riopel M (2002) Le Témiscamingue: son histoire et ses habitants. Les Editions Fides.

Rowe JS (1972) Forest regions of Canada. For Reg Can. (No. 1300). https://www.cabdirect.org/cabdirect/abstract/19730606372. Accessed 8 May 2021

Saucier JP, Bergeron JF, Grondin P, Robitaille A (1998) Les régions écologiques du Québec méridional: un des éléments du système hiérarchique de classification écologique du territoire mis au point par le Ministère des Ressources Naturelles. Supplément pp. 1–12

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol Model 180(1):211–229

Schulte LA, Mladenoff DJ, Crow TR, Merrick LC, Cleland DT (2007) Homogenization of northern U.S. Great Lakes forests due to land use. Landsc Ecol 22(7):1089–1103

Seidl R, Spies TA, Peterson DL, Stephens SL, Hicke JA (2016) REVIEW: searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. J Appl Ecol 53(1):120–129

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ (2017) Forest disturbances under climate change. Nat Clim Change 7(6):395–402

Shuman B, Newby P, Huang Y, Webb T III (2004) Evidence for the close climatic control of new England vegetation history. Ecology 85(5):1297–1310

Shuman BN, Newby P, Donnelly JP (2009) Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. Quat Sci Rev 28(17):1693–1709

Slivinski LC, Compo GP, Whitaker JS, Sardeshmukh PD, Giese BS, McColl C, Allan R, Yin X, Vose R, Titchner H, Kennedy J (2019) Towards a more reliable historical reanalysis: improvements for version 3 of the Twentieth Century Reanalysis system. Q J R Meteorol Soc 145(724):2876–2908

Soja AJ, Tchebakova NM, French NHF, Flannigan MD, Shugart HH, Stocks BJ, Sukhinin AI, Parfenova EI, Chapin FS, Stackhouse PW (2007) Climate-induced boreal forest change: predictions versus current observations. Glob Planet Change 56(3):274–296

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Stambaugh MC, Marschall JM, Abadir ER, Jones BC, Brose PH, Dey DC, Guyette RP (2018) Wave of fire: an anthropogenic signal in historical fire regimes across central Pennsylvania, USA. Ecosphere 9(5):e02222–e02222

Sturtevant BR, Gustafson EJ, Li W, He HS (2004) Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. Ecol Model 180(1):153–174

Taylor AR, Boulanger Y, Price DT, Cyr D, McGarrigle E, Rammer W, Kershaw JA (2017) Rapid 21st century climate change projected to shift composition and growth of Canada's Acadian Forest Region. For Ecol Manag 405:284–294

Terrail R, Dupuis S, Danneyrolles V, Fortin M-J, Boucher Y, Arseneault D (2019) Reorganization of tree assemblages over the last century in the northern hardwoods of eastern Canada. Appl Veg Sci 22(4):474–483

Terrail R, Morin-Rivat J, de Lafontaine G, Fortin MJ, Arseneault D (2020) Effects of 20th-century settlement fires on landscape structure and forest composition in eastern Quebec, Canada. J Veg Sci 31(1):40–52

Thom D, Rammer W, Garstenauer R, Seidl R (2018) Legacies of past land use have a stronger effect on forest carbon exchange than future climate change in a temperate forest landscape. Biogeosciences 15(18):5699–5713

Turner MG, Seidl R (2023) Novel disturbance regimes and ecological responses. Ann Rev Ecol Evol Syst 54:63–83

Viglas JN, Brown CD, Johnstone JF (2013) Age and size effects on seed productivity of northern black spruce. Can J For Res 43(6):534–543

Ville Temiscaming (1996) Témiscaming 1921–1996: [nos racines, notre histoire]. Témiscaming? s.n

Vincent JS, Hardy L (1977) L'évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géographie Phys Quat 31(3–4):357–372

Wan X, Landhäusser SM, Lieffers VJ, Zwiazek JJ (2006) Signals controlling root suckering and adventitious shoot formation in aspen (*Populus tremuloides*). Tree Physiol 26(5):681–687

Wang J, Taylor AR, D'Orangeville L (2023) Warming-induced tree growth may help offset increasing disturbance across the Canadian boreal forest. Proc Natl Acad Sci 120(2):e2212780120

Weir JMH, Johnson EA (1998) Effects of escaped settlement fires and logging on forest composition in the mixedwood boreal forest. Can J For Res. https://doi.org/10.1139/x98-001

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. In: Esser K, Lüttge U, Kadereit JW, Beyschlag W (eds) Progress in botany: genetics physiology systematics ecology. Springer, Berlin, Heidelberg, pp 399–450

Whitney GG (1987) An ecological history of the great lakes forest of Michigan. J Ecol 75(3):667–684

Williams JW, Post DM, Cwynar LC, Lotter AF, Levesque AJ (2002) Rapid and widespread vegetation responses to past climate change in the North Atlantic region. Geology 30(11):971–974

Williams JW, Shuman BN, Webb T III, Bartlein PJ, Leduc PL (2004) Late-quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecol Monogr 74(2):309–334

WMO W (2017) WMO guidelines on the calculation of climate normals. WMO Rep. 2017:1203

Wu MM, Zou X, Liang Y, Stambaugh M, Fraser JS, Xu W, He HS (2022) The impact of typhoon on post-volcanic-eruption forest landscape recovery: a study in Changbai mountain through 300 years of historic landscape reconstruction. Landsc Ecol 37(5):1401–1416

Yu Z (2007) Rapid response of forested vegetation to multiple climatic oscillations during the last deglaciation in the northeastern United States. Quat Res 67(2):297–303

Zhang Y, Bergeron Y, Zhao X-H, Drobyshev I (2015) Stand history is more important than climate in controlling red maple (*Acer rubrum* L.) growth at its northern distribution limit in western Quebec, Canada. J Plant Ecol. 8(4):368–379

Ziegler SS (2010) The past and future of white pine forests in the Great Lakes region. Geogr Compass. https://doi.org/10.1111/j.1749-8198.2010.00369.x

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