Université du Québec en Abitibi-Témiscamingue

DISENTANGLING CLIMATE AND HUMAN INFLUENCES ON FIRE REGIMES AND FOREST COMPOSITION DYNAMICS IN THE TEMPERATE AND BOREAL ZONES OF THE NORTHERN HEMISPHERE

Thèse
présentée
comme exigence partielle
du doctorat sur mesure en Sciences Naturelles et Dendroclimatologie

Par
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DÉDICACE

To my mom Maggy

ÉPIGRAPHE

[Arriving at the next sampling site for the day]

Nina: "I will wait you in the car"

AVANT-PROPOS

This thesis is presented in the form of three scientific articles corresponding to Chapters 1, 2, and 3, as well as a general introduction (Chapter 0) and a general conclusion (Chapter 4). Chapter 1 has been published by the *Agricultural and Forest Meteorology* journal. Chapter 2 is being finalized for submission. Chapter 3 has been published by the *Landscape Ecology* journal.

Chapter 0 – General Introduction

Chapter 1 – Robles, D., Bergeron, Y., Meunier, J., Stambaugh, M., Raymond, P., Kryshen, A., Goebel, C., Eden, J., & Drobyshev, I. (2024). Climatic controls of fire activity in the red pine forests of eastern North America. *Agricultural and Forest Meteorology*, 358, 110219. https://doi.org/10.1016/j.agrformet.2024.110219

Chapter 2 – Robles, D., Bergeron, Y., Kryshen, A., Simpson, G.L., Palm, L.A., Ryzhkova, N., & Drobyshev, I. 500-year wildfire history in Sweden reveal consistent and non-monotonic relationships to population density and precipitation. [Manuscript in preparation].

Chapter 3 – Robles, D., Boulanger, Y., Pascual, J., Danneyrolles, V., Bergeron, Y., & Drobyshev, I. (2025). 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. *Landscape Ecology*, *40*(2), 26. https://doi.org/10.1007/s10980-025-02043-x

Chapter 4 – General Conclusion

The conceptualization for Chapter 1 was carried out by Igor Drobyshev, Yves Bergeron, and me. All analyses for Chapter 1 were carried out by me with Igor's direct supervision. It is important to mention that data collection for this projected had started before I began my PhD, and data was collected by the student Mari Robles under the supervision of Igor Drobyshev and Yves Bergeron. Jed Meunier and Michael Stambaugh contributed with essential datasets for Chapter 1. Jonathan Eden offered his climatology expertise to review the final manuscript for Chapter 1. Alexander Kryshen offered his botany expertise to review the final manuscript for Chapter 1. Patricia Raymond offered her expertise on mixed pine forests in the region to review the final manuscript for Chapter 1. I wrote the manuscript, and all coauthors revised the article, edited, and gave final approval for publication.

The conceptualization for Chapter 2 was carried out by Igor Drobyshev, Yves Bergeron, and me. I conducted all analyses with the supervision of Igor Drobyshev and Gavin Simpson. Lennart Palm contributed with essential datasets used in Chapter 2. Nina Ryzhova was involved in the data collection and processing of some of the datasets used. Alexander Kryshen offered his expertise on Eurasian boreal forests to review the manuscript. I wrote the manuscript, and all coauthors revised the article, edited, and gave final approval for publication.

The conceptualization for Chapter 3 was carried out by Igor Drobyshev, Yves Bergeron, and me. Igor Drobyshev, Yan Boulanger and I planned all analyses for Chapter 3. I conducted the analyses for Chapter 3 with the help of Yan Boulanger and Jesus Pascual. Victor Danneyrolles contributed to Chapter 3 by providing us with essential datasets and the study area map figure. I wrote the manuscript, and all coauthors revised the article, edited, and gave final approval for publication.

TABLE DES MATIÈRES

LISTE DES SIGLES ET DES ABRÉVIATIONS

AGB: Aboveground biomass

AL: Aleutian Low

BL: Baseline scenario

CNFDB: Canadian National Fire Database

CP ENSO: Central Pacific ENSO

ENSO: El Niño-Southern Oscillation

EP ENSO: Eastern Pacific ENSO

GAM: Generalized Additive Model

GLM: Generalized Linear Model

HFAY: High fire activity year

LFY: Large Fire Year

LIA: Little Ice Age

LSP: Low summer precipitation

MaxAGB: Maximum AGB

MM: Maunder Minimum

MWP: Medieval Warm Period

NADA: North American Drought Atlas

NAO: North Atlantic Oscillation

NFI: National Forest Inventory

NH: Northern Hemisphere

noCC: Without Climate Change scenario

noFE: Without Fire Exclusion Fire Regime scenario

noFRS: Without Fire Regime Shifts scenario

noSF: Without Settlement Fire scenario

noTH: Without Timber Harvesting scenario

OWDA: Old World Atlas

PDO: Pacific Decadal Oscillation

PDSI: Palmer Drought Severity Index

PERMANOVA: Permutational Multivariate Analysis of Variance

PFJ: Polar Front Jet Stream

PNA: Pacific North American pattern

RPDA: Red pine distribution area

SAT: Surface atmospheric temperature

SD: Standard deviation

SEP: Species establishment probabilities

SLP: Sea level pressure

SNWR: Seney National Wildlife Refuge

SST: Sea surface temperatures

TNH: Tropical Northern Hemisphere pattern

20CRv3: Twentieth Century Reanalysis version 3

LISTE DES SYMBOLES ET DES UNITÉS

% : percent

< : less than

> : greater than

≤ : less or equal than

≥ : greater or equal than

°C : Celsius degree

°N : North (latitude) degree

°E: East (longitude) degree

ha : hectare

hPa : hectopascal

km : kilometer

km^2 : square kilometer

mm : millimeter

tons/ha : tons per hectare

Z500 : mid-troposphere pressure at 500 hPa geopotential height

RÉSUMÉ

Les perturbations sont des agents importants dans les écosystèmes forestiers. Elles façonnent la composition et maintiennent la biodiversité. Les incendies de forêt sont l'une des perturbations naturelles les plus importantes dans les forêts boréales et hémiboréales, le climat ayant été leur principal moteur tout au long de l'Holocène. L'influence croissante de l'homme a modifié les régimes de perturbation et la composition de la végétation dans ces forêts au cours des derniers siècles. Cette thèse a permis de distinguer les contributions relatives de la variabilité climatique et des activités humaines aux changements historiques des régimes d'incendie et de la végétation dans deux sections de la zone boréale.

Dans l'est de l'Amérique du Nord, j'ai réalisé une synthèse de données sur l'historique des incendies dans les forêts de pins rouges (Pinus resinosa Ait.) et j'ai modélisé la dynamique de la végétation sous l'influence du climat, des incendies et de la récolte forestière. Dans cette région, où les changements historiques du régime des incendies ont été principalement attribués aux activités humaines, j'ai pu isoler le signal climatique expliquant l'historique des incendies pour la période 1700-1900. J'ai étudié la relation entre les années de forte activité du feu (HFAY) et la variabilité des indices climatiques à grande échelle. Les résultats ont montré que les années de forte activité du feu étaient associées aux états positifs de la configuration de l'Atlantique Pacifique Nord et de l'oscillation australe El Niño, qui à leur tour étaient liés à des conditions climatiques propices aux incendies (anomalies positives de la pression et de la température de la troposphère moyenne) dans la région. J'ai également examiné les effets individuels du changement climatique, des modifications du régime des incendies et de l'exploitation du bois en tant que facteurs d'évolution de la végétation forestière régionale entre 1830 et 2020. J'ai simulé la composition de la forêt et les perturbations dans le cadre de différents scénarios et j'ai déterminé que l'exploitation du bois avait le plus grand impact sur les changements dans la composition de la végétation, et que lorsque l'on contrôle l'exploitation du bois, l'écosystème était capable de maintenir sa résilience et sa composition forestière d'avant la colonisation.

En Suède, j'ai élaboré la première synthèse nationale de l'histoire des incendies afin de distinguer les effets de la variabilité climatique et de l'utilisation humaine des forêts sur la fréquence des incendies depuis la fin des années 1550. J'ai analysé les patrons spatio-temporels de la suppression des incendies et les effets individuels de la densité de la population humaine et des précipitations estivales sur l'activité des incendies. J'ai constaté que le sud de la Suède avait connu une extinction des incendies plus précoce que le nord, et que la densité de population et les précipitations estivales avaient toutes deux une influence significative sur l'activité des incendies. Dans l'ensemble, mon étude a démontré que même si les activités humaines sont devenues les principaux moteurs de l'activité des incendies au cours des derniers siècles dans les forêts de l'est de l'Amérique du Nord et de la Suède, le signal climatique est resté un moteur important de l'activité des incendies. Toutefois, ce sont les pratiques humaines, en particulier l'exploitation du bois, qui ont le plus contribué à modifier la composition de la végétation dans les forêts de l'est de l'Amérique du Nord.

Mots-clés : historique des feux de forêt, dendrochronologie, climat propice aux incendies, perturbations forestières

ABSTRACT

Disturbances are important agents in forest ecosystems, shaping their structure and sustaining biodiversity. Wildfire is one of the most important natural disturbances in boreal and hemiboreal forests, with climate acting as its primary driver throughout the Holocene. Growing human influence has altered disturbance regimes and vegetation composition in these forests over recent centuries. This thesis disentangled the relative contributions of climate variability and human activities to historical changes in fire regimes and vegetation in two sections of the boreal zone.

In eastern North America, I carried out the largest synthesis of fire history data for red pine (*Pinus resinosa* Ait.) forests and modelled vegetation dynamics as driven by climate, fire and timber harvesting. In this region, where historical fire regime shifts have primarily been attributed to human activities, I isolated the climate signal from the fire history data for the period 1700-1900. I studied the relationship between fire activity and large-scale modes of climate variability, captured by climate indices. The results indicated that high fire activity years were associated with the positive states of the Pacific North Atlantic pattern and El Niño-Southern Oscillation, which in turn were linked to fire-conducive climatic conditions (positive anomalies in mid-tropospheric pressure and temperature) in the region. I also examined the individual effects of climate change, shifts in fire regime, and timber harvesting as factors driving changes in regional forest vegetation from 1830 to 2020. I simulated the forest composition and disturbances under different scenarios and determined that timber harvesting had the greatest impact on changes in vegetation composition, and that when controlling for timber harvesting, the ecosystem was able to maintain resilience and its pre-settlement forest composition.

In Sweden, I developed the first national-level synthesis of fire history to disentangle effects of climate variability and human use of forests on fire occurrence since late 1550s. I analyzed the spatiotemporal patterns of fire suppression and the individual effects of human population density and summer precipitation on fire activity. I found that southern Sweden experienced earlier fire suppression compared to the north, and that both population density and summer precipitation significantly influenced fire activity. Overall, my study demonstrated that while human activities have become major drivers of fire activity in recent centuries in eastern North American and Swedish forests, the climate signal remained an important driver of fire activity. However, human practices, particularly timber harvesting, had the strongest effects on driving vegetation composition changes in forests of eastern North America.

Keywords: wildfire history, dendrochronology, fire-prone climate, forest disturbances, forest composition

CHAPTER 0: INTRODUCTION (IN ENGLISH)

Disturbances Although disturbances such as such as wildfire, windstorm, drought, and insect outbreaks are short-lived compared to the lifespan, reproduction rate, growth rate, or succession rate of species or ecosystems, they have significant, broad-scale impacts (Jentsch et al., 2022; White & Jentsch, 2001). Disturbances have been defined as discrete events that disrupt ecosystem structure and function, affecting resources and environmental conditions (Pickett & White, 1985). Disturbances play a crucial role in forest dynamics by shaping nutrient and energy cycling, biomass accumulation, primary production and biodiversity patterns (Sousa, 1984). Disturbances drive forest succession, by setting the stage for post-disturbance recovery. While disturbances may initially destroy or transform living biomass, they also release pulses of resources (e.g., growing space, light, nutrients, and water) that facilitate ecosystem renewal and regrowth (White & Jentsch, 2001).

Disturbances leave legacies that serve as the ecological memory of ecosystems, shaping recovery and influencing responses to future disturbances. These legacies can be categorized into two types: information and material legacies (Johnstone et al., 2016). Information legacies refer to the evolutionary adaptations that species have developed from long-term exposure to reoccurring disturbances (Johnstone et al., 2016). Material legacies include surviving organisms, propagules, and structural elements such as standing dead trees, logs, and other woody debris. They serve critical roles by providing habitat for organisms, moderating microclimatic conditions, and supporting the reestablishment of vegetation (Franklin et al., 2000; Johnstone et al., 2016). The disturbance legacies persist for decades to centuries, enhancing the structural complexity of post disturbance ecosystems and sustaining their functions (Franklin et al., 2000; Turner, 2010).

Disturbance regimes describe the long-term spatial, temporal, and magnitude patterns of disturbances, as well as their interactions with other disturbances (Burton et al., 2020; Jentsch et al., 2022; Turner, 2010). Disturbance regimes are defined by spatial attributes (e.g., patch size, patch shape, and heterogeneity in the patch size at the landscape scale), temporal attributes (e.g., return interval, frequency, and seasonality), and magnitude attributes (e.g., severity, intensity) (Turner, 2010). Disturbance regimes also encompass interactions between disturbance events, weather from the same agent or different agents (Burton et al., 2020; Jentsch et al., 2022). These interactions occur when disturbance legacies influence the impact of and/or the response to subsequent disturbances, linking disturbances across spatial, temporal, and magnitude scales (Buma, 2015).

Ecological resilience describes the capacity of forests to recover their structure and functioning after disturbances (Holling, 1973). Ecological resilience is shaped by three interrelated processes: persistence, recovery, and reorganization that operate at increasing levels of biological organization - individual, population, and community (Falk et al., 2019). Persistence operates at the individual organism level and reflects its ability to withstand stress given its life history evolution and adaptations that affect survival and spread (Falk et al., 2019; Johnstone et al., 2016). For example, in fire-prone environments, some taxa have developed resprouting, serotiny, and germination by heat and smoke that allows them to persist (T. He et al., 2016; Keeley et al., 2011). If persistence is overcome as a result of widespread mortality, resilience depends on population-level recovery, which requires the establishment of new individuals from seed or other propagules (Falk et al., 2019). If recovery fails to reestablish the pre-disturbance communities, the ecosystem will reorganize into an alternative state. This alternate state may be transient, eventually returning to the pre-disturbance state (Falk et al., 2019, 2022; Seidl & Turner, 2022). However, if critical thresholds of ecological resilience are crossed, the system can reorganize into a new state that will not allow it to return to the pre-disturbance state (Falk et al., 2022; Johnstone et al., 2016; Seidl & Turner, 2022).

Anthropogenic influence has led to unprecedented global changes with impacts on forest disturbances and forest resilience. Anthropogenic-induced changes such as climate change, alterations of disturbance regimes, the introduction of novel disturbances, the invasion of non-native species, along with complex interactions are altering forest ecosystems with potential broad-scale future declines in forest health (Trumbore et al., 2015). Addressing these challenges requires a long-term perspective on disturbances and ecosystem responses. Palaeoecological research employing centennial to millennial scaled records can provide critical insights revealing how ecosystems have historically responded to disturbances, how disturbances have changed with climate change, and their historical range of variability (Whitlock et al. 2010; Nolan et al. 2018; Buma et al. 2019; Iglesias and Whitlock 2020). These insights are critical for forest management in the context of drastic and rapid global climate change (naturally and anthropogenically caused) and the effects of modern anthropogenic stressors that render future ecological dynamics uncertain (Millar et al., 2007).

Boreal and Hemiboreal forests The boreal biome is one of the largest biomes on Earth, forming a broad transcontinental belt that encompasses large areas of Canada, Alaska, Northern Europe, and Russia (Brandt, 2009; Burton et al., 2003). In European classifications, the boreal forest is often extended to include the hemiboreal subzone, a transitional area south of the boreal zone, while North American classifications typically exclude it (Brandt, 2009). The boreal/hemiboreal biome has vast expanses of forests, wetlands, and lakes that offer many services at regional and global scales. The boreal biome is an important global reservoir of stored carbon (Bradshaw et al., 2009; Bradshaw & Warkentin, 2015; Pan et al., 2011), and therefore has a critical role in the global carbon cycle and global climate (Chapin III et al., 2000; Lemprière et al., 2013). The boreal biome directly influence the global energy balance via biogeophysical properties, like albedo, which also affects climate (Bonan et al., 1992; Lemprière et al., 2013). Other ecosystem services of this biome include water and air purification, habitat for many organisms, reservoir for maintenance of biodiversity, erosion control, and provisioning of timber, food, and fresh water (Brandt, 2009).

Despite centuries of exploitation, the boreal biome retains significant areas of intact forest. The boreal biome is vital to the economies of Canada, Sweden, Finland, Norway, and Russia as a source of timber, minerals, and energy resources (Brandt, 2009). Nearly two-thirds of boreal forests are managed (Gauthier et al., 2015). The hemiboreal forests in Scandinavia and Russia have a long history of human use and a great portion has been converted to agricultural land (Nilsson, 1992; Pastor, 1992). Nonetheless, the boreal zone contains around 44% of the world's large undeveloped forests areas (Potapov et al., 2008). Most of the remaining natural and old-growth forests are located in northern, low-productivity sites (Kuuluvainen & Aakala, 2011).

Boreal forests are floristically simple, while hemiboreal forests can exhibit greater diversity. Boreal forests support cold-tolerant species adapted to a short growing season and severe winters. Coniferous species of fir (*Abies)*, larch (*Larix)*, pine (*Pinus)*, and spruce (*Picea)* typically dominate, although broadleaf species of poplar (*Populus)*, birch (*Betula)*, and alder (*Alnus)* are also present (Gauthier et al., 2015). Hemiboreal forests, located in the temperate-boreal ecotone, contain species from both boreal and temperate biomes with local segregation along moisture and temperature gradients (Pastor, 1992). Characteristic species found in the hemiboreal forests in eastern North America include eastern hemlock (*Tsuga canadensis* (L.) Carr.), eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.), red and sugar maples (Acer) and yellow birch (*Betula alleghaniensis* Britton). In contrast, Scandinavian hemiboreal forests are dominated by Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) as a result of a strong anthropogenic pressure that has operated in this region for many centuries (Nilsson, 1992).

Fire disturbance in boreal and hemiboreal forests Wildfire is one of the most important disturbance in both boreal and hemiboreal forests (Bergeron et al., 2001; Bergeron, Gauthier, et al., 2004; Drever et al., 2006; Granström, 2001; Sutheimer et al., 2021). Wildfire plays a key role in shaping successional pathways (Bergeron et al. 2004), contributes to global biogeochemical cycles (Bowman et al. 2009), and promotes landscape heterogeneity that supports biodiversity (Kuuluvainen 2002). Wildfire in hemiboreal forests of eastern North America played a critical role in maintaining red pine forests (Drobyshev et al., 2008b) by reducing the soil organic layer (Nyamai et al. 2014; Stambaugh et al. 2019), 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. 2019).

Climate has historically been the main driver of wildfires in both boreal and hemiboreal forests (Aakala et al., 2018; Carcaillet et al., 2001, 2007; Drobyshev et al., 2016). A key climatic condition conducive to wildfire is a persistent positive geopotential height anomaly (ridge) in the mid-troposphere (500 hPa) (Drobyshev et al., 2015, 2021; Fauria & Johnson, 2008). These anomalies disrupt zonal air flow, leading to warmer and drier conditions that facilitate fuel drying and increase fire risk (Fauria & Johnson, 2008). These atmospheric circulation anomalies are influenced by large-scale climate variability, captured by climate indices, such as the North Atlantic Oscillation (NAO), El Niño–Southern Oscillation (ENSO), Pacific North American pattern (PNA), or Pacific Decadal Oscillation (PDO). For instance, the summer NAO has been linked to fire activity in Sweden and across the European boreal zone (Drobyshev et al., 2021). Similarly, ENSO and PDO have been linked to fire activity in western North American boreal forests (Fauria & Johnson, 2006; Hess et al., 2001), while the PDO and NAO have been linked to fire activity in eastern North American boreal forests (LeGoff et al. 2007).

The fire regime in the boreal and hemiboreal forests varies regionally. The fire regime in boreal North American forests is typically characterized by high-intensity crown fires (Fauria & Johnson, 2008; E. Johnson et al., 2001), while in Eurasian boreal forests, lower-intensity surface fires are more common (Conard and Ivanova 1997; Stocks et al. 2001; Wooster and Zhang 2004). The fire regime in eastern North American hemiboreal forests consists of low-intensity surface fires similarly to that of Eurasian boreal forests (Drever et al. 2006; Nyamai et al. 2014; Meunier et al. 2019; Frelich et al. 2021). The differences in fire regimes are attributed to species-specific fire traits (Rogers et al., 2015; Stocks et al., 2001; Wooster & Zhang, 2004). In Eurasian boreal forests, fire resister species, which have evolved traits like self-pruning, high foliar moisture, and thick bark, help suppress crown fires and survive surface fires (Rogers et al., 2015). In contrast, North American boreal forests are dominated by fire embracer species, such as those with serotinous cones, which rely on crown fires to release their seeds (Rogers et al., 2015). Hemiboreal forests of eastern North America support lower-intensity surface fires due to presence of fire resister species like red pine, a higher abundance of less flammable deciduous species, greater landscape heterogeneity, and more humid conditions (Nowacki & Abrams, 2008).

Anthropogenic pressure upon boreal and hemiboreal forests Anthropogenic impacts on boreal and hemiboreal forests have varied across time and space. The onset of substantial human-induced alterations began earlier in Scandinavian hemiboreal and boreal forests than in eastern North American northern forests. Typically, southern areas were affected first, followed by a gradual expansion of human activities (e.g., settlement, timber harvesting, and mineral extraction) into northern regions.

Two major shifts in fire regimes followed socio-economic changes. The first shift coincided with the expansion of permanent settlements and was characterized by reduced fire size, increased fire frequency, and increased early season fires frequency (Niklasson & Drakenberg, 2001; Niklasson & Granström, 2000; Rolstad et al., 2017; Stambaugh et al., 2018). The second shift occurred with the abandonment of agricultural and pastoral burning practices, the expansion of settlements and roads that reduced fuel availability and increased forest fragmentation, and the introduction of fire suppression policies (Pinto, Niklasson, et al., 2020; Rolstad et al., 2017; Ryzhkova et al., 2022; Stambaugh et al., 2018; Wallenius, 2011).

Land use has directly altered the vegetation composition. Due to land use, deciduous forests in southern Sweden, once dominant 3 000 to 2 000 years ago, have been replaced by Norway spruce and Scots pine (Björse & Bradshaw, 1998; Lindbladh et al., 2000). Norway spruce likely spread due to its lower palatability to grazing animals compared to pines and broadleaf species (Lindbladh & Bradshaw, 1998). Scots pine's expansion from southeastern Sweden into western regions was likely facilitated by anthropogenic fires (Lindbladh et al., 2000). Norway spruce was also favored by the cessation of slash-and-burn agriculture during the agrarian revolution (1700-1879), the implementation fire suppression that led to darker forest environments, and artificial regeneration (Lindbladh et al., 2014; Niklasson & Drakenberg, 2001).

Industrial timber harvesting altered vegetation composition in boreal and hemiboreal forests. Selective-cutting of old, large-diameter pines in eastern North America during the 1800s square timber era was highly wasteful, leaving behind substantial volumes of surface and ladder fuels that increased the risk of crown fires, which further contributed to pine mortality (Lower, 1933; Whitney, 1987). Similarly, selective-cutting in Sweden decreased the presence of old-growth trees, and transformed many multi-storied stands into even-aged and single storied forests (Ostlund et al., 1997). Clear-cutting supported the invasion of fast-growing species, such as trembling aspen (*Populus tremuloides* Michx.) (Graham et al., 2011), and decreased the proportion of coniferous to deciduous species in mixedwood forests in eastern North America (Archambault et al., 1998).

Human-driven climate change is projected to affect disturbance regimes and vegetation composition in boreal and hemiboreal forests. Over the 21st century, the boreal biome is expected to experience the largest increase in temperatures of all forest biomes (Gauthier et al., 2015; Price et al., 2013). Climate change is expected to intensify disturbances regimes (Seidl et al., 2017), with projections suggesting increased fire activity in many regions within the circumboreal biome (Flannigan et al. 2009).

Objectives The primary objective of this thesis is to disentangle the individual effects of climatic and anthropogenic factors on wildfire dynamics over the past centuries and examine the individual effects of historical fire regime shifts, human land use, and climate change on forest composition from the pre-settlement times to the present. Understanding historical ecosystem behavior is essential for interpreting current ecosystem dynamics and predicting future conditions (Morgan et al., 1994). By investigating the long-term dynamics of disturbances and the forest responses, I aim to provide insights into ongoing ecological changes and help anticipate future transformations, which is an urgent priority in contemporary ecology (Seidl & Turner, 2022). My study spans centuries and covers both landscape and regional scales, recognizing that disturbance and resilience processes occur over long temporal periods and across broad spatial extents (Johnstone et al., 2016). To this end, I utilized various pre-existing datasets, enabling analysis at large spatial and temporal scales.

Chapter 1 and Chapter 2 focused on fire, one of the most important disturbances of boreal and hemiboreal forests. These two chapters utilized large syntheses of previously developed multi-centurial, annual fire history records resolved with dendrochronology. Chapter 1 examined fire history across a broad region in eastern North America, corresponding to the distribution range of red pine. The objective was to uncover the influence of climate on the fire chronology of the region for the period 1700-1900. The analysis focused exclusively on climate, as prior studies in the region have already examined the role of human activities in shaping fire dynamics in the area. By working at the regional scale, I was able to investigate the impact of large-scale models of climate variability, i.e., climate indices. In Chapter 2, I developed the first national-level synthesis of fire history reconstructions for Sweden. This chapter aimed to quantify the independent contributions of climatic and anthropogenic factors to historical fire activity for the period 1559-2000 and to resolve the spatiotemporal patterns of these drivers on fire dynamics. To this end, I capitalized on the availability of an extensive network of fire reconstructions, an exceptionally long record of human population at the municipality level, and gridded climate reconstructions to build a model of historical fire activity.

Chapter 3 examined the individual effects of fire regime shifts, logging, and climate change on forest compositions from pre-settlement to the present time. I focused on a landscape within the sugar maple–yellow birch bioclimatic domain of southwestern Quebec and relied on pre-settlement vegetation and fire history reconstructions, historical records of timber harvest, and climate reanalysis data. This chapter represents the first retrospective simulation of forest succession and disturbance in an eastern North American landscape with the LANDIS-II forest landscape simulation model, allowing us to test hypothesis about past forest dynamics.

CHAPITRE 0: INTRODUCTION (EN FRANÇAIS)

Perturbations Bien que les perturbations telles que les incendies de forêt, les tempêtes de vent, les sécheresses et les épidémies d'insectes soient de courte durée par rapport à la durée de vie, au taux de reproduction, au taux de croissance ou au taux de succession des espèces ou des écosystèmes, elles ont des impacts significatifs à grande échelle (Jentsch et al., 2022; White & Jentsch, 2001).Les perturbations ont été définies comme des événements discrets qui perturbent la structure et le fonctionnement des écosystèmes, affectant les ressources et les conditions environnementales (Pickett & White, 1985). Elles jouent un rôle crucial dans la dynamique forestière en façonnant les cycles des nutriments et de l'énergie, l'accumulation de biomasse, la production primaire et les schémas de biodiversité (Sousa, 1984). Les perturbations entraînent la succession forestière en préparant le terrain pour la récupération post-perturbation. Bien qu'elles puissent initialement détruire ou transformer la biomasse vivante, elles libèrent également des pulses de ressources (p. ex., espace de croissance, lumière, nutriments et eau) qui facilitent le renouvellement et la régénération des écosystèmes (White & Jentsch, 2001).

Les perturbations laissent des héritages écologiques qui servent de mémoire écologique aux écosystèmes, influençant leur récupération et leurs réponses aux perturbations futures. Ces héritages peuvent être classés en deux types : les héritages informationnels et matériels (Johnstone et al., 2016). Les héritages informationnels font référence aux adaptations évolutives que les espèces ont développées en réponse à une exposition à long terme à des perturbations récurrentes (Johnstone et al., 2016). Les héritages matériels comprennent les organismes survivants, les propagules et les éléments structurels tels que les arbres morts sur pied, les troncs et autres débris ligneux. Ces éléments jouent des rôles essentiels en fournissant un habitat pour les organismes, en modérant les conditions microclimatiques et en soutenant la réinstallation de la végétation (Franklin et al., 2000; Johnstone et al., 2016). Les héritages des perturbations persistent sur des décennies à des siècles, renforçant la complexité structurelle des écosystèmes post-perturbation et soutenant leurs fonctions (Franklin et al., 2000; Turner, 2010).

Les régimes de perturbations décrivent les schémas spatiaux, temporels et d'intensité des perturbations à long terme, ainsi que leurs interactions avec d'autres perturbations (Burton et al., 2020; Jentsch et al., 2022; Turner, 2010). Ces régimes sont définis par des attributs spatiaux (p. ex., taille et forme des parcelles, hétérogénéité à l'échelle du paysage), des attributs temporels (p. ex., intervalle de retour, fréquence, saisonnalité) et des attributs d'intensité (p. ex., sévérité, intensité) (Turner, 2010). Les régimes de perturbations englobent également les interactions entre événements perturbateurs, qu'ils proviennent du même agent ou d'agents différents (Burton et al., 2020; Jentsch et al., 2022). Ces interactions surviennent lorsque les héritages des perturbations influencent l'impact et/ou la réponse aux perturbations suivantes, établissant des liens entre les perturbations à différentes échelles spatiales, temporelles et d'intensité (Buma, 2015).

La résilience écologique décrit la capacité des forêts à retrouver leur structure et leur fonctionnement après des perturbations (Holling, 1973). Elle est façonnée par trois processus interconnectés : la persistance, la récupération et la réorganisation, qui opèrent à des niveaux croissants d'organisation biologique – individu, population et communauté (Falk et al., 2019). La persistance agit au niveau individuel et reflète la capacité d'un organisme à résister aux stress grâce à son évolution et à ses adaptations influençant sa survie et sa propagation spread (Falk et al., 2019; Johnstone et al., 2016). Par exemple, dans les environnements soumis aux incendies, certaines espèces ont développé des stratégies de rejets de souche, de sérotinie et de germination induite par la chaleur et la fumée, leur permettant de persister (T. He et al., 2016; Keeley et al., 2011). Si la persistance est dépassée en raison d'une mortalité généralisée, la résilience dépend alors de la récupération au niveau des populations, nécessitant l'établissement de nouveaux individus à partir de graines ou d'autres propagules (Falk et al., 2019). Si la récupération échoue à rétablir les communautés pré-perturbation, l'écosystème se réorganise dans un état alternatif. Cet état alternatif peut être transitoire et éventuellement revenir à l'état pré-perturbation (Falk et al., 2019, 2022; Seidl & Turner, 2022). Cependant, si des seuils critiques de résilience écologique sont franchis, le système peut se réorganiser dans un nouvel état qui l'empêche de retourner à son état initial (Falk et al., 2022; Johnstone et al., 2016; Seidl & Turner, 2022).

L'influence anthropique a entraîné des changements globaux sans précédent, ayant un impact sur les perturbations et la résilience des forêts. Les changements d'origine anthropique, tels que le changement climatique, l'altération des régimes de perturbations, l'introduction de nouvelles perturbations, l'invasion d'espèces exotiques et les interactions complexes qui en résultent, modifient les écosystèmes forestiers et pourraient entraîner un déclin généralisé de la santé des forêts (Trumbore et al., 2015). Relever ces défis nécessite une perspective à long terme sur les perturbations et les réponses des écosystèmes. La recherche paléoécologique, utilisant des archives à l'échelle du siècle au millénaire, peut fournir des connaissances essentielles sur la manière dont les écosystèmes ont historiquement répondu aux perturbations, comment les perturbations ont évolué avec le changement climatique et quelle était leur variabilité historique (Whitlock et al. 2010; Nolan et al. 2018; Buma et al. 2019; Iglesias and Whitlock 2020). Ces connaissances sont cruciales pour la gestion forestière dans un contexte de changements climatiques globaux drastiques et rapides (d'origine naturelle et anthropique) et d'effets des stress anthropiques modernes, qui rendent les dynamiques écologiques futures incertaines (Millar et al., 2007).

Forêts boréales et hémiboréales Le biome boréal est l'un des plus grands biomes de la planète, formant une large ceinture transcontinentale qui englobe de vastes régions du Canada, de l'Alaska, de l'Europe du Nord et de la Russie (Brandt, 2009; Burton et al., 2003). Dans les classifications européennes, la forêt boréale est souvent étendue pour inclure la sous-zone hémiboréale, une zone de transition située au sud de la zone boréale, alors que les classifications nord-américaines l'excluent généralement (Brandt, 2009). Le biome boréal/hémiboréal comprend de vastes étendues de forêts, de zones humides et de lacs qui offrent de nombreux services à l'échelle régionale et mondiale. Le biome boréal est un important réservoir mondial de carbone stocké (Bradshaw et al., 2009; Bradshaw & Warkentin, 2015; Pan et al., 2011), et joue donc un rôle essentiel dans le cycle mondial du carbone et le climat mondial (Chapin III et al., 2000; Lemprière et al., 2013). Le biome boréal influence directement le bilan énergétique mondial par le biais de propriétés biogéophysiques, telles que l'albédo, qui affecte également le climat (Bonan et al., 1992; Lemprière et al., 2013). Parmi les autres services écosystémiques de ce biome figurent la purification de l'eau et de l'air, l'habitat pour de nombreux organismes, le réservoir pour le maintien de la biodiversité, le contrôle de l'érosion et la fourniture de bois, de nourriture et d'eau douce (Brandt, 2009).

Malgré des siècles d'exploitation, le biome boréal conserve d'importantes zones de forêts intactes. Le biome boréal est vital pour les économies du Canada, de la Suède, de la Finlande, de la Norvège et de la Russie en tant que source de bois, de minéraux et de ressources énergétiques (Brandt, 2009). Près de deux tiers, des forêts boréales sont gérées (Gauthier et al., 2015). Les forêts hémiboréales de Scandinavie et de Russie ont une longue histoire d'utilisation humaine et une grande partie a été convertie en terres agricoles (Nilsson, 1992; Pastor, 1992). Néanmoins, la zone boréale contient environ 44% des grandes zones forestières non développées du monde (Potapov et al., 2008). La plupart des forêts naturelles et anciennes restantes sont situées dans des sites septentrionaux à faible productivité (Kuuluvainen & Aakala, 2011).

Les forêts boréales sont floristiquement simples, tandis que les forêts hémiboréales peuvent présenter une plus grande diversité. Les forêts boréales abritent des espèces tolérantes au froid, adaptées à une saison de croissance courte et à des hivers rigoureux. Les espèces de conifères telles que le sapin (Abies), le mélèze (Larix), le pin (Pinus) et l'épicéa (Picea) dominent généralement, bien que des espèces de feuillus telles que le peuplier (Populus), le bouleau (Betula) et l'aulne (Alnus) soient également présentes (Gauthier et al., 2015). Les forêts hémiboréales, situées dans l'écotone tempéré-boréal, contiennent des espèces des biomes boréal et tempéré avec une ségrégation locale le long des gradients d'humidité et de température (Pastor, 1992). Les espèces caractéristiques des forêts hémiboréales de l'est de l'Amérique du Nord comprennent la pruche du Canada (*Tsuga canadensis* (L.) Carr.), le pin blanc (*Pinus strobus* L.), le pin rouge (*Pinus resinosa* Ait.), les érables rouge et à sucre (Acer spp) et le bouleau jaune *Betula alleghaniensis* Britton). En revanche, les forêts hémiboréales scandinaves sont dominées par l'épicéa commun (*Picea abies* (L.) Karst.) et le pin sylvestre (Pinus sylvestris L.) en raison de la forte pression anthropique qui s'exerce dans cette région depuis de nombreux siècles (Nilsson, 1992).

Perturbation par le feu dans les forêts boréales et hémiboréales Les incendies sont l'une des perturbations les plus importantes dans les forêts boréales et hémiboréales (Bergeron et al., 2001; Bergeron, Gauthier, et al., 2004; Drever et al., 2006; Granström, 2001; Sutheimer et al., 2021). Les incendies de forêt jouent un rôle clé dans l'évolution des successions (Bergeron, Gauthier, et al., 2004), contribuent aux cycles biogéochimiques mondiaux (Bowman et al., 2009) et favorisent l'hétérogénéité du paysage qui soutient la biodiversité (Kuuluvainen, 2002). Les incendies de forêt dans les forêts hémiboréales de l'est de l'Amérique du Nord ont joué un rôle essentiel dans le maintien des forêts de pins rouges (Drobyshev et al., 2008b) en réduisant la couche organique du sol (Nyamai et al., 2014; Stambaugh et al., 2019), en augmentant la pénétration de la lumière dans le sol forestier en réduisant la couverture de la canopée (McRae et al., 1994) et en éliminant les concurrents intolérants à l'ombre (Nyamai et al., 2014; Stambaugh et al., 2019).

Le climat a toujours été le principal moteur des incendies de forêt dans les forêts boréales et hémiboréales (Aakala et al., 2018; Carcaillet et al., 2001, 2007; Drobyshev et al., 2016). L'une des principales conditions climatiques propices aux incendies de forêt est une anomalie positive persistante de la hauteur du géopotentiel (crête) dans la troposphère moyenne (500 hPa) (Drobyshev et al., 2015, 2021; Fauria & Johnson, 2008). Ces anomalies perturbent le flux d'air zonal, entraînant des conditions plus chaudes et plus sèches qui facilitent l'assèchement des combustibles et augmentent le risque d'incendie (Fauria & Johnson, 2008). Ces anomalies de la circulation atmosphérique sont influencées par la variabilité du climat à grande échelle, qui est représentée par des indices climatiques tels que l'oscillation nord-atlantique (ONA), l'oscillation El Niño-Sud (ENSO), la configuration pacifique nord-américaine (PNA), ou l'oscillation décennale du Pacifique (ODP). Par exemple, l'ONA estivale a été associée à l'activité des incendies en Suède et dans la zone boréale européenne (Drobyshev et al., 2021). De même, l'ENSO et l'ODP ont été associées à l'activité des incendies dans les forêts boréales de l'ouest de l'Amérique du Nord (Fauria & Johnson, 2006; Hess et al., 2001), tandis que l'ODP et l'ONA ont été associées à l'activité des incendies dans les forêts boréales de l'est de l'Amérique du Nord (LeGoff et al. 2007).

Le régime des incendies dans les forêts boréales et hémiboréales varie selon les régions. Le régime des incendies dans les forêts boréales d'Amérique du Nord est généralement caractérisé par des feux de cime de forte (Fauria & Johnson, 2008; E. Johnson et al., 2001), tandis que dans les forêts boréales d'Eurasie, les feux de surface de faible intensité sont plus fréquents (Conard & A. Ivanova, 1997; Stocks et al., 2001; Wooster & Zhang, 2004). Le régime des incendies dans les forêts hémiboréales de l'est de l'Amérique du Nord consiste en des incendies de surface de faible intensité similaires à ceux des forêts boréales eurasiennes (Drever et al. 2006; Nyamai et al. 2014; Meunier et al. 2019; Frelich et al. 2021). Les différences entre les régimes d'incendie sont attribuées aux caractéristiques des incendies propres à chaque espèce (Rogers et al., 2015; Stocks et al., 2001; Wooster & Zhang, 2004). Dans les forêts boréales d'Eurasie, les espèces résistantes au feu, qui ont développé des caractéristiques telles que l'auto-élagage, une humidité foliaire élevée et une écorce épaisse, aident à supprimer les incendies de cime et à survivre aux incendies de surface (Rogers et al., 2015). En revanche, les forêts boréales d'Amérique du Nord sont dominées par des espèces qui embrassent le feu, telles que les espèces à cônes sérotineux, qui dépendent des feux de cime pour libérer leurs graines (Rogers et al., 2015). Les forêts hémiboréales de l'est de l'Amérique du Nord supportent des incendies de surface de moindre intensité en raison de la présence d'espèces résistantes au feu comme le pin rouge, d'une plus grande abondance d'espèces de feuillus moins inflammables, d'une plus grande hétérogénéité du paysage et de conditions plus humides (Nowacki & Abrams, 2008).

Pression anthropique sur les forêts boréales et hémiboréales Les impacts anthropiques sur les forêts boréales et hémiboréales ont varié dans le temps et dans l'espace. Les altérations substantielles dues à l'homme ont commencé plus tôt dans les forêts hémiboréales et boréales scandinaves que dans les forêts septentrionales de l'est de l'Amérique du Nord. En règle générale, les zones méridionales ont été touchées en premier, suivies par une expansion progressive des activités humaines (par exemple, la colonisation, l'exploitation du bois et l'extraction de minéraux) dans les régions septentrionales.

Deux changements majeurs dans les régimes d'incendie ont suivi les changements socio-économiques. Le premier changement a coïncidé avec l'expansion des établissements permanents et s'est caractérisé par une réduction de la taille des incendies, une augmentation de la fréquence des incendies particulièrement les incendies en début de saison (Niklasson & Drakenberg, 2001; Niklasson & Granström, 2000; Rolstad et al., 2017; Stambaugh et al., 2018). Le deuxième changement s'est produit avec l'abandon des pratiques de brûlage agricole et pastoral, l'expansion des établissements et des routes qui ont réduit la disponibilité des combustibles et accru la fragmentation des forêts, et l'introduction de politiques de suppression des incendies (Pinto, Niklasson, et al., 2020; Rolstad et al., 2017; Ryzhkova et al., 2022; Stambaugh et al., 2018; Wallenius, 2011).

L'utilisation des terres a directement modifié la composition de la végétation. En raison de l'utilisation des terres, les forêts de feuillus du sud de la Suède, autrefois dominantes il y a 3 000 à 2 000 ans, ont été remplacées par l'épicéa commun et le pin sylvestre (Björse & Bradshaw, 1998; Lindbladh et al., 2000). L'épicéa commun s'est probablement répandu en raison de sa moindre appétence pour les animaux de pâturage par rapport aux pins et aux espèces de feuillus (Lindbladh & Bradshaw, 1998). L'expansion du pin sylvestre du sud-est de la Suède vers les régions occidentales a probablement été facilitée par les incendies anthropogéniques (Lindbladh et al. 2000). L'épicéa commun a également été favorisé par l'arrêt de l'agriculture sur brûlis pendant la révolution agraire (1700-1879), la mise en œuvre de la suppression des incendies qui a conduit à des environnements forestiers plus sombres, et la régénération artificielle (Lindbladh et al., 2014; Niklasson & Drakenberg, 2001).

L'exploitation industrielle du bois a modifié la composition de la végétation dans les forêts boréales et hémiboréales. La coupe sélective des vieux pins de grand diamètre dans l'est de l'Amérique du Nord au cours de l'ère du bois carré dans les années 1800 était un gaspillage considérable, laissant derrière elle d'importants volumes de combustibles en surface et en échelle qui augmentaient le risque de feux de cime, ce qui contribuait encore à la mortalité des pins (Lower, 1933; Whitney, 1987). De même, les coupes sélectives en Suède ont réduit la présence d'arbres anciens et transformé de nombreux peuplements à plusieurs étages en forêts équiennes et à un seul étage (Ostlund et al., 1997). Les coupes à blanc ont favorisé l'invasion d'espèces à croissance rapide, telles que le peuplier faux-tremble (*Populus tremuloides* Michx.) (Graham et al., 2011), et ont diminué la proportion d'espèces de conifères par rapport aux espèces de feuillus dans les forêts mixtes de l'est de l'Amérique du Nord (Archambault et al., 1998).

Le changement climatique induit par l'homme devrait affecter les régimes de perturbation et la composition de la végétation dans les forêts boréales et hémiboréales. Au cours du 21e siècle, le biome boréal devrait connaître la plus forte augmentation de température de tous les biomes forestiers (Gauthier et al., 2015; Price et al., 2013). Le changement climatique devrait intensifier les régimes de perturbation (Seidl et al., 2017), les projections suggérant une augmentation de l'activité des incendies dans de nombreuses régions du biome circumboréal (Flannigan et al. 2009).

Objectifs L'objectif principal de cette thèse est de distinguer les effets individuels des facteurs climatiques et anthropogéniques sur la dynamique des incendies de forêt au cours des derniers siècles et d'examiner les effets individuels des changements historiques du régime des incendies, de l'utilisation des terres par l'homme et du changement climatique sur la composition des forêts depuis la période précédant la colonisation jusqu'à aujourd'hui. Il est essentiel de comprendre le comportement historique des écosystèmes pour interpréter la dynamique actuelle des écosystèmes et prévoir les conditions futures (Morgan et al., 1994). En étudiant la dynamique à long terme des perturbations et les réponses des forêts, je vise à fournir des informations sur les changements écologiques en cours et à aider à anticiper les transformations futures, ce qui est une priorité urgente dans l'écologie contemporaine (Seidl & Turner, 2022). Mon étude s'étend sur plusieurs siècles et couvre à la fois les échelles du paysage et régionale, reconnaissant que les processus de perturbation et de résilience se produisent sur de longues périodes temporelles et sur de vastes étendues spatiales (Johnstone et al., 2016). À cette fin, j'ai utilisé divers ensembles de données préexistants, permettant une analyse à de grandes échelles spatiales et temporelles.

Les chapitres 1 et 2 sont consacrés aux incendies, l'une des perturbations les plus importantes des forêts boréales et hémiboréales. Ces deux chapitres ont utilisé de vastes synthèses de données séculaires et annuelles sur l'historique des incendies, résolues à l'aide de la dendrochronologie. Le chapitre 1 a examiné l'historique des incendies dans une vaste région de l'est de l'Amérique du Nord, correspondant à l'aire de répartition du pin rouge. L'objectif était de découvrir l'influence du climat sur la chronologie des incendies de la région pour la période 1700-1900. L'analyse s'est concentrée exclusivement sur le climat, étant donné que des études antérieures dans la région ont déjà examiné le rôle des activités humaines dans la dynamique des incendies dans la région. En travaillant à l'échelle régionale, j'ai pu étudier l'impact des modèles à grande échelle de la variabilité climatique, c'est-à-dire des indices climatiques. Dans le chapitre 2, j'ai élaboré la première synthèse nationale des reconstructions de l'histoire des incendies pour la Suède. Ce chapitre visait à quantifier les contributions indépendantes des facteurs climatiques et anthropogéniques à l'activité historique des incendies pour la période 1559-2000 et à résoudre les schémas spatio-temporels de ces facteurs sur la dynamique des incendies. À cette fin, j'ai tiré parti de la disponibilité d'un vaste réseau de reconstitutions d'incendies, d'un enregistrement exceptionnellement long de la population humaine au niveau municipal et de reconstitutions climatiques maillées pour construire un modèle de l'activité historique des incendies.

Le chapitre 3 a examiné les effets individuels des changements de régime des feux, de l'exploitation forestière et des changements climatiques sur la composition des forêts depuis la période précédant la colonisation jusqu'à aujourd'hui. Je me suis concentré sur un paysage situé dans le domaine bioclimatique de l'érable à sucre et du bouleau jaune dans le sud-ouest du Québec et je me suis appuyé sur des reconstitutions de la végétation et de l'historique des incendies avant la colonisation, sur des registres historiques de la récolte du bois et sur des données de réanalyse du climat. Ce chapitre représente la première simulation rétrospective de la succession forestière et des perturbations dans un paysage de l'est de l'Amérique du Nord avec le modèle de simulation de paysage forestier LANDIS-II, ce qui nous permet de tester des hypothèses sur la dynamique forestière passée.

1 - CHAPTER 1: CLIMATIC CONTROLS OF FIRE ACTIVITY IN THE RED PINE FORESTS OF EASTERN NORTH AMERICA

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1.1. Résumé

Les modes de variabilité climatique à grande échelle influencent l'activité des feux de forêt et pourraient moduler les schémas futurs des perturbations naturelles. Nous avons étudié les effets des changements climatiques à long terme sur le régime des feux dans les forêts de pin rouge de l'est de l'Amérique du Nord en utilisant (a) un réseau de sites avec des reconstructions dendrochronologiques des historiques de feux entre 1700 et 1900 après, (b) des chronologies reconstruites d'indices climatiques (1700-1900), et (c) des enregistrements d'observations du 20ème siècle sur les indices climatiques, le climat local de surface et les feux (des années 1950 à 2021). Nous avons émis l'hypothèse que (H1) il existe des états de la circulation atmosphérique systématiquement associés à une augmentation de l'activité des feux, (H2) ces états marquent des périodes de danger climatique accru pour les feux, et (H3) le déclin observé de l'activité des feux au vingtième siècle est associé à une diminution à long terme de la fréquence des états favorables aux feux.

À l'échelle annuelle, les années présentant une activité des feux significativement plus élevée, tant dans les enregistrements de feux reconstruits que modernes, étaient systématiquement associées aux phases positives de la configuration pacifique nord-américaine (PNA), soit indépendamment, soit en combinaison avec la phase positive de l'oscillation El Niño-Southern (ENSO). Pendant les années où l'ENSO et le PNA étaient tous deux dans leur phase positive, la région a connu des hauteurs troposphériques moyennes et des anomalies de température positives entraînant des conditions de sécheresse. Les états climatiques propices aux feux identifiés dans les enregistrements reconstruits sont devenus moins fréquents à partir de 1850, mais ont réapparu au vingtième siècle. Bien que notre étude ne démontre pas de manière concluante une influence directe du climat sur la baisse observée de l'activité des feux au vingtième siècle, elle révèle un signal climatique clair inscrit dans la reconstitution de l'historique des feux de la région au cours des derniers siècles. Cette étude souligne l'importance de prendre en compte les schémas climatiques à grande échelle pour comprendre les régimes de feux historiques et met en lumière leur rôle pour les dynamiques des feux futurs dans la région ainsi que leurs effets écologiques.

Mots-clés : lien climat-feu, indices d'oscillations climatiques, ENSO, historique des feux dans l'est de l'Amérique du Nord, forêts mixtes de pins, PNA, PDO.

1.2. Abstract

Large-scale modes of climate variability influence forest fire activity and may modulate the future patterns of natural disturbances. We studied the effects of long-term changes in climate upon the fire regime in the red pine forests of eastern North America using (a) a network of sites with dendrochronological reconstructions of fire histories over 1700-1900 A.D., (b) reconstructed chronologies of climate indices (1700-1900), and (c) 20th century observational records of climate indices, local surface climate and fire (1950s-2021). We hypothesized that (H1) there are states of atmospheric circulation that are consistently associated with increased fire activity, (H2) these states mark periods of increased climatological fire hazard, and (H3) the observed decline in fire activity in the 20th century is associated with a long-term decline in the frequency of fire-prone states.

At the annual scale, years with significantly higher fire activity in the reconstructed and modern fire records were consistently associated with the positive phases of the Pacific North American pattern (PNA), either independently or in combination with the positive phase of the El Niño-Southern Oscillation (ENSO). During years with both ENSO and PNA in their positive state, the region experienced positive mid-tropospheric heights and temperature anomalies resulting in drought conditions. The fire-prone climate states identified in the reconstructed records became less frequent in 1850 but re-emerged in the 20th century. While our study does not conclusively demonstrate a direct influence of climate on the observed decrease in fire activity in the 20th century, it does reveal a clear climate signal embedded within the fire history reconstruction of the region over the past centuries. This study underscores the importance of considering large-scale climatic patterns in understanding historical fire regimes and highlights their role for future fire dynamics in the region and shaping ecological effects of future fires.

Key words: Climate-fire link, Climate oscillation indices, ENSO, eastern North America Fire history, Mixed-pine forests, PNA, PDO

1.3. Introduction

Fire is a fundamental Earth system process influencing most terrestrial ecosystems (T. He & Lamont, 2018; McLauchlan et al., 2020), as well as global processes (e.g., surface albedo and the global carbon balance) (Liu et al., 2019). Changes in fire disturbance severity and/or frequency have a strong impact on the Earth's surface radiative budget and climate, especially at high latitudes (Liu et al., 2019). A positive trend in wildfire activity in high latitudes has been particularly pronounced in the last decades, with increases in greenhouse gases and atmosphere aerosols providing positive feedback that further accelerates climate change (Zhao et al. 2021). The 2023 fire season in Canada exemplified this impact, burning a record-breaking 18 401 197 hectares and causing thousands to be evacuated, major cities to suffer poor air quality, and necessitating extensive firefighting efforts with assistance from various countries (Natural Resources Canada, 2023).

Fire has been an essential natural disturbance in the mixed-pine forests of the boreal-temperate interface in eastern North America (Drever et al. 2006; Nyamai et al. 2014; Meunier et al. 2019; Frelich et al. 2021). Historically, frequent low- to moderate-severity surface fires maintained the dominance of fire-dependent conifers (i.e., red pine [*P. resinosa* Ait.] and white pine [*Pinus strobus* L.]) in these forests (Drobyshev et al., 2008b; R. Guyette & Dey, 1995b; Stambaugh et al., 2018). This fire regime created the necessary conditions for pines' regeneration by removing or reducing the organic layer of the soil (Nyamai et al., 2014; Stambaugh et al., 2019), augmenting light conditions at the forest floor by reducing canopy cover (McRae et al., 1994), and eliminating shade-tolerant competitors (Nyamai et al., 2014; Stambaugh et al., 2019). In this way, frequent low-severity fires with occasional mixed-severity fires, led to complex, multi-cohort stands (Drobyshev et al., 2008a; Fraver & Palik, 2012; Meunier et al., 2019).

Studies of the historical fire regimes of red pine forests have suggested a significant role of Native American land-use practices in shaping the frequent-surface fire regime. This assertion has gained support from multiple lines of evidence, including the documented widespread use of fire by Native Americans and comparisons with the modern rate of lightning-caused fires, which alone fail to explain the historical high fire frequency (L. B. Johnson & Kipfmueller, 2016; Loope & Anderton, 1998). Nonetheless, even with dense pre-European population in some regions in eastern North America, there were regions with forests that experienced a limited anthropogenic impact (Oswald et al., 2020). Indigenous fire management practices were often localized (Roos, 2020), indicating that at the regional scale, climate remained a significant determinant of the historical fire regime (Bergeron 1991; Drobyshev et al. 2012; Oswald et al. 2020).

The 1930s witnessed a sharp decline in area burned in the eastern North American forests, including the region corresponding to the natural distribution range of red pine (Drobyshev et al., 2008b) (Fig. 1.1). These changes in fire activity had a profound negative impact on the regeneration of fire-adapted species, such as red pine and mixed pine forests, at the regional scale. Fire exclusion (Nowacki & Abrams, 2008) and logging (Friedman & Reich, 2005) gave competitive advantage to fire-intolerant and mesophytic hardwoods (e.g., maples [*Acer* spp.] and birch [*Betula* spp.]). The higher foliar moisture content of these deciduous trees and, therefore, the lower flammability of these fuels as compared to coniferous fuels, promoted moist and generally less fire-prone conditions (Nowacki & Abrams, 2008). The decreased flammability in forests historically dominated by pines (often in combination with oaks) contributed to the conversion of mixed pine forests to northern hardwoods stands with abundant aspen (*Populus* spp.), birch, maples, and oaks (*Quercus* spp.). This pattern has been reported throughout eastern North America over most of the 20th century (Friedman & Reich, 2005; Schulte et al., 2007). In contrast, in the northern fringes of the red pine distribution, where conifers (*Abies* and *Picea*) are present in the subcanopy, the lack of fire increases the amounts of easily burnable ladder fuels. Such fuels favor crown and lethal fires, decreasing the relative proportion of surface fires in the total pool of fires. Dominance of crown fires in the boreal forest has been reported as the factor explaining the northern limit of red pine (M. d. Flannigan & Bergeron, 1998). These changes have led to the disappearance of these forests, with red and white pine forests now covering only 0.6% of their pre-settlement range (L. Frelich, 1995). The well-documented effect of European colonization on fire regimes and the subsequent changes in the composition of mixed pine forests led to broad acceptance of human land-use as the main driver of observed changes (e.g. Guyette et al. 2016; Kipfmueller et al. 2017). However, at the northern limit of the distribution range of red and white pines, where human population density is low and colonization began later, climate variability has been suggested as the main driver of the decline in fire activity in the mid-1800s (Bergeron & Archambault, 1993).

Atmospheric circulation anomalies can create fire-conducive conditions and synchronize fire activity at the regional and sub-continental scales (Fauria & Johnson, 2006, 2008). This observation warrants a study of broad-scale climate forcing upon regional fire regimes, including the red pine distribution range. Anomalies in atmospheric circulation and local winter climate of the red pine distribution area (RPDA) have been linked to various climate oscillation indices, including El Niño–Southern Oscillation (ENSO), Pacific North American pattern (PNA), and Pacific Decadal Oscillation (PDO) (Bai & Wang, 2012; S. Rodionov & Assel, 2000, 2003; J. Wang et al., 2018).

The PNA pattern plays a crucial role in shaping the region's local climate by directly affecting the strength and position of tropospheric anomalies over North America, the Polar Front Jet Stream (PFJ), and ultimately the regional climate. The PNA manifests as a distinct Rossby wave train with four action centers extending from the North Pacific across the North American continent (Wallace & Gutzler, 1981). The most prominent action center of the PNA is a low-pressure system (cyclone) in the North Pacific around the Aleutian Islands known as the Aleutian Low (AL). South of the AL is a high-pressure system (anticyclone) around Hawaii. Downstream, the PNA features a mid-tropospheric ridge-trough system over North America, characterized by an above-normal geopotential height anomaly over western Canada and a below-normal height over the southeastern United States (Wallace & Gutzler, 1981). This configuration strongly correlates with positive temperature anomalies over western Canada and negative ones over southeastern U.S. (Wallace & Gutzler, 1981), ultimately linking these dynamics to forest fuel conditions at the regional scale (Fauria & Johnson, 2008). The ridge-trough pattern significantly influences the position of the jet stream and associated storm tracks over North America. The PNA results in a meridional flow of the jet stream, which brings fewer Pacific-derived winter storm tracks and dry anomalies, particularly in the West coast of North America (Rodysill et al., 2018). However, variability in the intensity and position of the AL can alter the ridge-trough pattern, giving rise to different local climate patterns (Lin et al., 2023; S. Rodionov & Assel, 2003; P. Wang et al., 2012). During a negative PNA phase, a more zonal and northerly jet stream over eastern North America allows for increased moisture from the Gulf of Mexico to penetrate in this region (Rodysill et al., 2018).

ENSO is another important factor driving regional climate in eastern North America as it plays a key role in triggering the PNA pattern and shaping drought conditions over the continent. Warm SST anomalies in the Tropical Pacific occur during El Niño phase of ENSO and cooling anomalies during La Niña events. El Niño events are generally associated with the deepening of the AL and the PNA pattern (Taschetto et al., 2020). However, the influence of ENSO on the AL and its broader extratropical effects varies significantly among individual events. This variability is attributed to several factors collectively termed "ENSO diversity": the asymmetry between El Niño and La Niña events, the magnitude of ENSO events, and the spatial distribution of the ENSO-related SST anomalies (Capotondi et al., 2015). Previous studies have highlighted the asymmetrical response of the winter climate in the Great Lakes region to ENSO, with strong El Niño events associated with milder winters, while the link between cold winters and La Niña events are notably weaker (Bai et al., 2012). The response of the winter climate in the region to ENSO is also nonlinear, where strong El Niño events result in milder winters, yet the effect of moderate El Niño events are less predictable (Rodionov and Assel 2003).

The PDO signal in the eastern North American winter climate is realized through its association with the AL and the PNA. The PDO is the dominant low-frequency climate variability in the North Pacific and is significantly influenced by anomalies in the AL (Mantua et al., 1997). The PDO`s positive phase is characterized by warm SST anomalies along the west coast of the U.S. and cold SST anomalies from the western North Pacific, and the negative phase exhibits the opposite pattern (Mantua et al., 1997). The positive phase of PDO is associated with a deeper AL, whereas the negative phase is associated with a shallow AL (S. M. Larson et al., 2022; Newman et al., 2016). Although ENSO plays an important influence on the PDO (Zhao et al. 2021; Larson et al. 2022), the PDO results from complex interactions beyond that of tropical variability (Newman et al., 2016). The "atmospheric bridge" connecting tropical Pacific to the North Pacific is bi-directional and the PDO can also influence the tropical Pacific (Alexander et al., 2002; Newman et al., 2016). Studies have reported constructive and destructive interference between the ENSO and PDO according to their relative phases, with stronger and more coherent ENSO effects when the ENSO and PDO are in phase (e.g., El Niño and positive PDO) (Gershunov & Barnett, 1998; Hu & Huang, 2009).

While circulation patterns represented by these indices typically exert their strongest effects on the local climate during winter, their impacts may extend beyond the cold season. For example, winter ENSO and PDO anomalies have been associated with variations in summer moisture availability in Canada (Shabbar, 2006). Mild winters can result in a thinner snowpack that melts earlier, accelerating fuel drying and widening the period for effective ignitions (Westerling et al. 2006). Consequently, the connection between winter climate indices and subsequent fire activity has been widely reported across North America (P. M. Brown, 2006; Duffy et al., 2005; Heyerdahl et al., 2002; Kitzberger et al., 2007). Previous research has demonstrated links between climate indices and fire activity in eastern North American boreal forests, located north of the red pine distribution range (Girardin et al. 2004; Girardin et al. 2006; Goff et al. 2007). Within the RPDA itself, historical associations between fire activity and local climate conditions have been documented (Drobyshev et al. 2012), despite abundant human fire ignitions likely masking the climate signal during the colonization waves (Stambaugh et al., 2018). However, despite these insights, the association between historical fire activity across RPDA and modes of climate variability, such as ENSO, PNA, and PDO remains poorly documented.

The current study addresses the gap in understanding the influence of large-scale climate variability, such as ENSO, PNA, and PDO on fire regimes in eastern North American mixed-pine forests with red pine. We compiled a network of sites with dendrochronologically reconstructed fire histories and focused specifically on the High Fire Activity Years (HFAYs), which are more likely to be climate-driven (Drobyshev et al., 2014; Falk et al., 2011; Farris et al., 2010). By broadening our analyses to a regional scale, we aimed to capture climate signals influencing the variability of fire occurrence, which might have been obscured by unique characteristics of single sites and the possible impact of human-related ignitions (Stambaugh et al., 2018).

Geographically, the network covered the present range of red pine and stretched over a 200-year period, 1700-1900 A.D. The period partially covered the Little Ice Age (LIA, ~1300-1800s) and the subsequent warming period, and ended before the onset of the industrial era and active fire suppression (1920s and 1930s). The selected period featured abundant fires and lack of fire suppression policies that could affect climate signal in fire chronologies. We focused on red pine forests, which we defined as forests with red pine in the overstory, since these stands are surface fire-dominated. High fire frequencies facilitated the detection of climate-driven changes in fire regimes, as compared to forests that burn infrequently and are often dominated by deciduous trees or coniferous shade-tolerant and fire-intolerant species (e.g., spruce and fir, *Picea* and *Abies*, respectively).

We explored the association between fire activity and the climate indices ENSO, PNA, and PDO. We tested three hypotheses: (H1) there are states of atmospheric circulation captured by climate indices that are consistently associated with increased fire activity over the distribution of red pine forests in eastern North America; (H2) these states mark periods of increased climatological fire hazard over the study area, as quantified by instrumental observations of the local surface climate; and (H3) the observed decline in fire activity in the 20th century is due to a long-term decline in the frequency of fire-prone states. We tested H1 on both dendrochronological and modern (1959-2021) fire datasets using a contingency analysis framework. We tested H2 by contrasting the fire-prone states we identified in the reconstructed records with observational high-resolution climate over the modern record (1950-2021). In doing so, we borrowed heavily from the climate analogue technique applied in a study of wildfire synchrony over western North America (Kitzberger et al., 2007). We tested H3 by conducting a regime shift analysis for each identified fire-prone climate state over the 1675-2021 period. Through testing these hypotheses, we re-approached the discussion on the contribution of the climate in addition to human factors, which have already been established at more localized scales, in shaping fire regimes in eastern North America. In addition to building a knowledge base on climate controls of disturbance regimes in mixed pine forests, our results contribute to quantifying the range of natural variability in the levels of fire activity and establishing reference points for conservation-oriented management of these ecosystems. The study helps quantify large-scale climate controls of historical, current, and future dynamics of fire activity in an ecoregion that faces a high risk of negative climate change impacts (Montour et al., 2020).

1.4. Methods

1.4.1. Study area

We studied mixed-pine forests across the temperate-boreal ecotone of eastern North America (from 38° 42' to 48° 30' N, and from 67° 58' to 95° 00' W, Fig. 1.1). The ecosystem represents a transition between boreal forest, central hardwoods, eastern forests and grassland (Commission for Environmental Cooperation (Montréal & Secretariat, 1997).

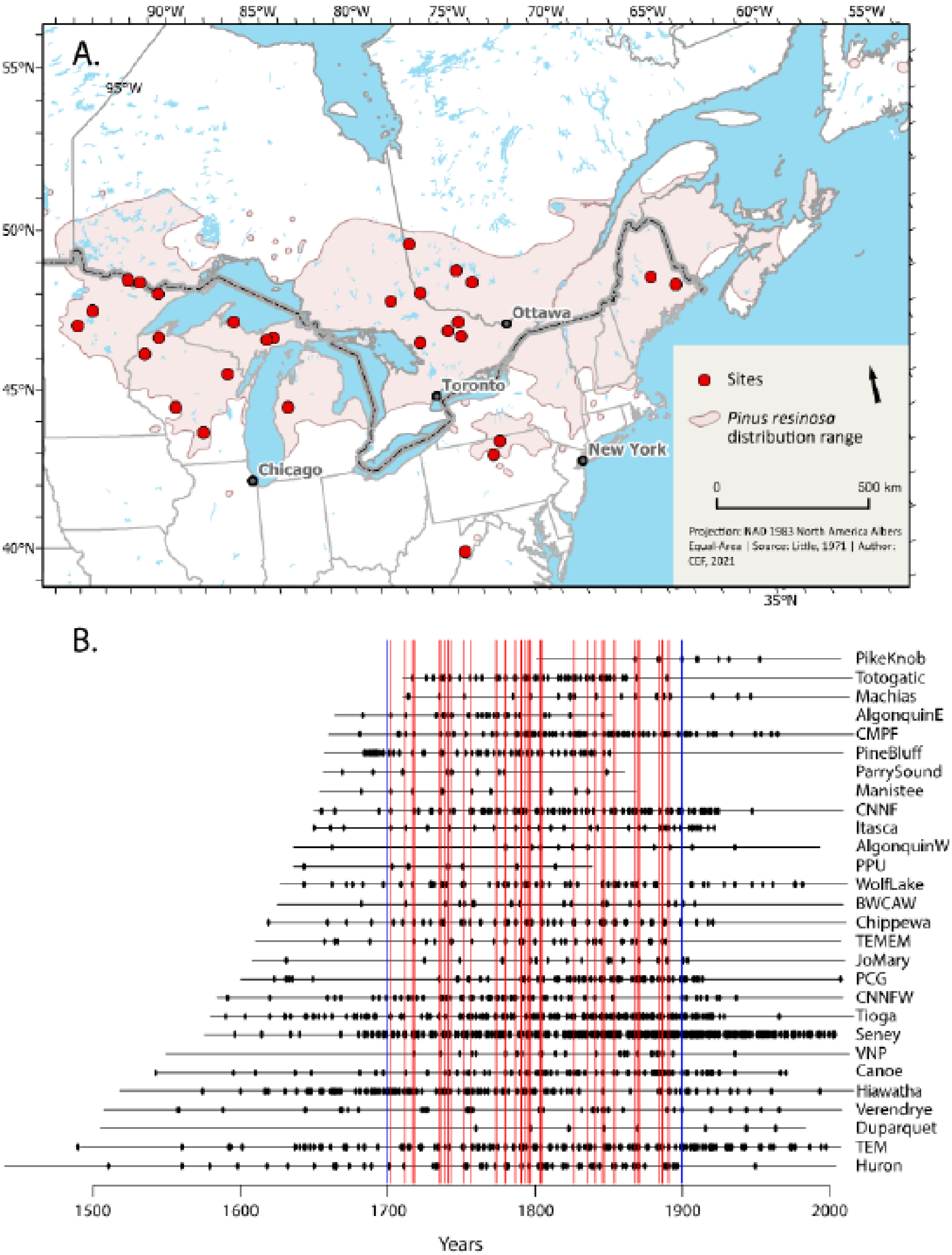

Figure 1.1.
(A) Map of the studied region with distribution range of red pine shown in pink, and sites with dendrochronological reconstructions of forest fire history, red dots. (B) Fire chronologies from sites included in the analyses. The black dots denote fire years. The vertical red lines represent the High Fire Activity Years (HFAYs). The blue lines delimit the study period.

A humid-continental climate with cold winters and warm to hot summers is prevalent over the region (Peel et al., 2007). The study area encompasses a considerable gradient in average annual precipitation, average minimum temperature for January, and average maximum temperature for July: 889.8 mm, -24.6° C, and 23.5° C at the northernmost site, Duparquet, QC, for 1971-2000 (Environment Canada 2011); 866.9 mm, -5.8° C, and 28.8° C at the southernmost site, Pike Knob Preserve, WV, for 1906-2008 (A. H. Young et al., 2018); 520 mm, -15.6° C, and 25.7° C at the easternmost site, Fourth Machias Lake, ME, for 1948-1998 (A. H. Young et al., 2018); and 644.4 mm, -20.9° C, and 27° C at the westernmost site, Itasca State Park, MN, for 1911-2021 (A. H. Young et al., 2018).

The study area roughly corresponds to the distribution of red pine, which extends eastward from Manitoba and Minnesota to Newfoundland, and southward from Central Quebec to West Virginia (Roberts & Mallik, 1994). Our network of sites had high replication in the area where red pine attains its maximum abundance, i.e., along a northwest-southeast line close to the southern limit of its range, the Great Lakes-St. Lawrence-Acadian forest (M. D. Flannigan & Woodward, 1994). The network contained 28 sites within the Great Lakes-St. Lawrence forest region (Rowe, 1972), and covered an area of approximately $2.73 \cdot 10^6$ km^2. Sites were located in seven U.S. states (Maine, Michigan, Minnesota, New York, Pennsylvania, Virginia, and Wisconsin) and two Canadian provinces (Quebec and Ontario).

To select the sites for this study, we focused on fire histories developed in forests with a red pine component. Our site selection criterium was solely based on the availability of fire history data in the forests where red pine was present. A review of the metadata from our sites and the other published sites indicated that red pine was an important but not always the dominant component in the forest canopies. Red pine is an effective recorder of fire history because (1) it is adapted to survive low- (surface fires) to moderate-severity fires (mixture of surface and stand replacing fires); and (2) it has a relatively slow decomposition rate, especially in xeric sites (L. B. Johnson & Kipfmueller, 2016). Sites were, at the time of sampling, comprised of (a) pure red pine stands; (b) conifer stands or mixed-wood stands where red pine was a co-dominant species in the canopy; or (c) hardwood-dominated stands (e.g., dominated by red oak, *Quercus rubra*) that previously consisted of red pine, as suggested by dendrochronological reconstructions.

Coniferous species in the canopy of the study sites included white pine, red pine, jack pine (*Pinus banksiana* Lamb.), pitch pine (*P. rigida* Mill.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*P. glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and northern white cedar (*Thuja occidentalis* L.). Deciduous species comprised northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* L.), sweet birch (*Betula lenta* L.), paper birch (*B. papyrifera* Marsh.), yellow birch (*B. alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), tamarack (*Larix laricina* (Du Roi) K. Koch), basswood (*Tilia americana* L.), quaking aspen (*Populus tremuloides* Michx.), American elm (*Ulmus americana* L.), and black ash (*Fraxinus nigra* Marsh.). We did not attempt to partition the study region into sub-regions, since we were primarily interested in broad-scale climate-fire relationships while retaining adequate sample depth.

1.4.2. Fire history database

We compiled a network of 28 sites (Table Supplementary Information SI 1.1) comprised primarily of existing datasets via the authors or published literature. We also analyzed limited unpublished datasets collected and dated by the authors covering southwestern Quebec and Ontario. Our database contained coordinates, fire years by site, and the period covered by sites.

For the fire years by site, we opted not to apply a minimum threshold for the number of scarred trees required to identify a fire year. This decision was based on several considerations. First, including years where fires were recorded by only one tree allowed us to capture the full extent of fire occurrence. Second, our analysis focused on fire frequencies rather than burned areas, making the size of individual fires at the site level irrelevant. Third, we ensured the robustness of our analyses by using only climate-driven HFAYs for later analyses, which inherently prioritized significant events influenced by climatic conditions, as supported by our contingency analysis which accounts for variability in site replication and fire frequencies (see next subsection below). Finally, applying a consistent threshold across all sites was not feasible as we did not have access to raw data from all sites.

We ensured that all site chronologies represented spatially independent observations by establishing a minimum distance of 40 km between neighboring sites. The rationale for this threshold was based on the spatial reconstruction of fires at Seney National Wildlife Refuge (SNWR), MI, covering the 1700-2007 period (Drobyshev et al., 2008b). The reconstruction revealed several years during the 1700s and 1800s, when fires covered most of the SNWR landscape (386 km^2). A circle covering this area would have a diameter of approximately 20 km. We doubled this value to arrive at the selected threshold of 40 km. We combined sites in proximity to each other, within 40 km radius, so that they became one site with a composite fire chronology. The implementation of this threshold resulted in 25% of all sites (n = 7) being combined in this manner.

The SNWR study stands as the sole example of a spatially explicit reconstruction of fire activity in a landscape characterized by (a) abundant red pine, particularly as the dominating mixed pine forest species; and (b) a lack of numerous water bodies making “perfect” firebreaks, similar to the conditions described in Kipfmuller et al.’s (2017) study. This approach reflects our primary focus on investigating the climate effects on fires, rather than delving into the fire histories of specific sites or areas. By adopting this focus, we addressed spatial autocorrelation, which could potentially inflate estimations of High Fire Activity Years (HFAYs) frequencies.

An exception to the 40 km threshold was made for the Seney site within the SNWR given that sampling at Seney was more exhaustive as it was designed to reconstruct annual area burned, and the number of fires recorded there was higher. Thus, this site was not pooled with nearby sites in the Hiawatha National forest despite their close proximity.

We acknowledge that any solution involves a trade-off between keeping the number of areas sufficiently high to allow for a more statistically stable identification of HFAYs and removing autocorrelation. Such autocorrelation may, in fact, originate from both regional climate forcing and annual synchrony in the implementation of land use policies within parts of the RPDA. We were also aware of the growing subjectivity in data treatment that arises when introducing site-specific clustering algorithms. We thoroughly explored various options of site clustering in the early stages of our analyses, seeking to establish a minimal number of straightforward rules that could accommodate the considerations presented above. We ultimately opted for the 40 km separation threshold.

Our statistical framework was based entirely on the analysis of fire occurrence data because the spatial estimates (i.e., fire sizes) were not available for most of the sites. We selected the historical (reconstructed) period based on two criteria: (1) the time period covered ≥ 95% of all sites, and (2) it did not include periods with declining fire activity, whether due to climatic reasons (Drobyshev et al., 2017) or due to fire suppression. The inclusion of the second criterium was due to our concern that a declining number of fire events would compromise our ability to quantify climate-fire links in the dataset and likely introduce non-climatic trends in the chronology. To objectively define the period of decreased fire activity, we conducted regime shift analyses for each site on smoothed decadal fire occurrence using Rodionov's sequential t-test algorithm (S. N. Rodionov, 2004). We explored different choices for the L parameter, or moving timeframe, including both 5 and 10 years. We chose an L of 5, which allowed us to make algorithm more sensitive to the changes in fire regime. The Hubert weight parameter was set to 1, and α was set at 0.05 to ensure statistical robustness setting the L parameter, or moving timeframe, to five years.

We analyzed the reconstructed fire activity during 1700-1900. The start year, 1700, marked the onset of the regime shift towards a higher fire activity at the oldest part of the reconstructions (Fig. SI 1.2). By selecting the start of the record in this way, we address the "fading record problem" that refers to the decline in replication at the oldest part of the reconstruction, thereby compromising its reliability (Swetnam et al., 1999). The end year, 1900, marked the onset of a lower fire activity period that broadly coincided with the introduction of fire suppression policies.

1.4.3. Identifying climate-driven fires and assessing their association with local climate

We used synchrony in annual fire occurrence across the network of sites as a proxy of climate forcing upon regional fire activity (Drobyshev et al., 2014; Falk et al., 2011; Farris et al., 2010). We identified HFAYs as those years when the synchrony of burned sites was higher than expected under the assumption of a random distribution of fire years across sites and years (Drobyshev et al. 2015). To test for non-randomness in the synchrony level of burned sites, we used contingency analysis along with non-parametric bootstrapping (1 000 runs with replacement). Specifically, we compared the observed synchrony levels of burned sites to a null distribution generated through non-parametric bootstrapping. Contingency analysis accounted for the “density of the process”, i.e., the frequency (“density”) of fires at a site over a time period. To define HFAYs, we assumed a binominal distribution of the fire occurrence across sites and calculated expected frequencies using the following formula:

$$p(X) = \frac{N!}{X!(N-X)} p^x q^{N-X},$$

where N is the total number of recording sites in the analysis of a specific period; X is the number of burned sites in a single year; p is the probability of a site burning in any year, and q is the inverse of this probability. Calculating p(X) in this way accounted for variability in both site replication and fire frequencies at each site, i.e., number of fires recorded in a site. To further account for the changing trends in the number of burned sites over the studied period, revealed by a fitted segmented linear regression on the number of burned sites versus time (Fig. SI 1.1), we partitioned our reconstructed fire data into four subperiods (1700-1749, 1750-1799, 1800-1849, 1850-1900) and calculated p(X) for each using the period-specific “process density”, which was the number of fire years at each site.

We then examined if the reconstructed HFAYs occurred concomitantly with fire-prone local climate. Specifically, we tested if summer drought, temperature, precipitation, and mid-troposphere pressure at 500 hPa geopotential height (Z500) differed significantly from their means during HFAYs for the reconstructed record. We conducted spatial composite analyses and produced maps for the region 35° to 50° N and -95° to -65° E. The temporal resolution and coverage differed for the different gridded climate fields because we used different sources. We examined drought during historical HFAYs at the annual scale for the whole reconstructed record (1700-1900). On the other hand, for temperature, precipitation, and 500 hPa geopotential height, we conducted the analyses at a higher temporal resolution, i.e., seasonal, looking at two seasonal periods: (1) winter-early spring (January-April) and (2) late spring-summer (May-August). These seasonal analyses, however, covered only part of the reconstructed record (1836-1900). For the drought field, we used the North American Drought Atlas (NADA), a millennial gridded (2.5° x 2.5°) annual tree-ring based reconstruction of the summer (June-August) Palmer Drought Severity Index (PDSI) (Cook et al., 2004). For the temperature, precipitation, and mid-tropospheric pressure fields, we used the Twentieth Century Reanalysis version 3 (20CRv3) datasets, which comprises grided (1.0° x 1.0°) three-hourly estimates of meteorological variations extending back to 1836 (Slivinski et al., 2019). We used the online tool ClimateExplorer (Trouet & Van Oldenborgh, 2013) to conduct these analyses.

1.4.4. Climate indices

We examined three climate indices: ENSO, PNA, and PDO as previous research has demonstrated their influence on local climate conditions within our study area (Bai & Wang, 2012; S. Rodionov & Assel, 2000, 2003). For analyses over the historical record (1700-1900), we relied on reconstructions of these indices, while for analyses spanning the modern record (1950s-2021), we used observational data.

In the case of ENSO, we focused on the canonical Eastern Pacific (EP) ENSO because the EP El Niño has a more significant impact on winter climate conditions over the RPDA compared to the Central Pacific (CP) El Niño (J. Yu et al., 2012). This effect arises from the EP El Niño's eastward displacement of the AL, which brings the PNA's ridge over the North American continent closer to the RPDA (Beniche et al., 2024). We used Freund et al.'s (2019) coral-based reconstruction of the winter (December-February) EP ENSO. This reconstruction used Empirical Orthogonal Function (EOF) analysis to separate the two ENSO flavors, which is the most common method to separate the two ENSO flavors. However, we acknowledge that EP and CP events can spill into each other's zones, and the identification of EP and CP ENSO may vary depending on the methodology used (Kao and Yu 2009).

For the PNA pattern, we used Liu et al.'s (2017) millennium-long winter (December-March) PNA reconstruction developed with the help of tree-ring records from different PNA-sensitive regions. We chose this reconstruction because it is the only PNA reconstruction that covers the entire historical period we studied and because it incorporated diverse geographic sources providing potentially a more accurate depiction of the PNA.

For the PDO, we used Macdonald and Case's (2005) annual (January-December) tree-ring-based reconstruction based on midlatitude western North American trees. While this reconstruction aligns with the prevailing methodological approach of using tree-ring data to reconstruct this index, we acknowledge the potential impact of reconstruction selection on our findings. As highlighted by Kipfmuller et al. (2012), different reconstructions of the PDO have led to varied conclusions in previous studies regarding its association with regional fire activity. Hence, interpretations of historical PDO effects may entail a degree of uncertainty. Nonetheless, this study provides a valuable starting point for understanding these complexities.

For analyses focusing on the modern record, we used monthly observational data of the climate indices EP ENSO, PNA, and PDO. To represent the canonical EP ENSO, we employed a qualitative approach, considering the region where the action center for the EP occurs. Despite potential overlap between EP and CP events, our selection of the Niño 3 region (5 S-5 N and 150-90 W), aligns closely with the eastern equatorial Pacific, making it an appropriate index to measure EP ENSO (Kug et al., 2009). To ensure consistency with reconstructed indices, we averaged monthly observational data over the corresponding months. Specifically, we averaged December-February for ENSO, December-March for PNA, and January-December for PDO. Monthly observational data for all climate indices was obtained from the National Oceanic and Atmospheric Administration (NOAA) – Climate Prediction Center (CPC) website (https://www.cpc.ncep.noaa.gov/data/indices/).

1.4.5. Historical fire – climate associations

To test H1, we analyzed the associations between HFAYs within the RPDA and climate index states or combinations of states using contingency analysis with non-parametric bootstrapping. To this end, we categorized each climate index reconstruction chronology into positive or negative “states” (Bai et al., 2012) based on whether the annual climate index value exceeded or fell below its mean during the study period. While this binary classification of climate states did not differentiate between a strong index value and a moderate one, it facilitated standardized comparisons across all climate indices. It also enabled us to extend this analysis to the modern fire record (see next section), spanning only 60 years, as it ensured sufficient frequency of occurrences in all climate state combinations.

We examined the associations between HFAYs and states of single climate indices as well as pairwise combinations (ENSO-PNA, ENSO-PDO, and PDO-PNA). We limited the number of indices to two in a single analysis to maintain meaningful frequencies in the contingency table, $n \geq 5$, for robust bootstrap routines. We ran the analyses for the whole historical period 1700-1900 and for two subperiods, 1700-1800 and 1800-1900. We summarized the occurrence of HFAYs and non-HFAYs for each climate state and pairwise combination of climate states to identify historical fire-prone climate states where the occurrence of HFAYs exceeded chance expectations.

1.4.6. Fire-prone climate states in the modern record

To validate the fire-prone climate states identified in the reconstructed record, we extended the analysis to the instrumental record, employing the same methodology. For the fire data, we used a multi-sourced burned area record from the Canadian National Fire Database (CNFDB). This dataset covered only a portion of our study area that corresponds to Quebec and Ontario, but provided a relatively long temporal coverage (1959-2021) (Canadian Forest Service, 2019). We defined HFAYs as years within the upper 20% of the distribution of the annually burned area. We chose this threshold to capture the most extreme fire activity years while ensuring we had enough occurrences for meaningful statistical analysis. For the climate data, we focused on modern observations of the canonical EP ENSO, PNA, and PDO indices.

We examined associations between the fire-prone climate states and fire-conducive conditions across the study area (H2). The fire-prone climate states studied in this analysis were those identified in the reconstructed record and validated on the modern record. We ran spatial composite analyses for each fire-prone climate state and the 500 hPa geopotential height, drought, temperature, and precipitation fields for the winter-early spring and for the late spring-summer season over 1950-2021. We obtained the 500 hPa geopotential height from the gridded (0.25° resolution) fifth generation European Centre for Medium-Range Weather Forecast (ECMWF) Re-Analysis (ERA5, Hersbach et al. 2020), the temperature and monthly precipitation data from the Climatic Research Unit gridded (0.5°) Time Series (CRU TS) Version 4.04 (Harris et al., 2020), and the drought data from the global land map of monthly self-calibrated Palmer's Drought Severity Index (scPDSI) (Dunn et al., 2021; van der Schrier et al., 2013).

1.4.7. Long-term trends of fire activity

To test whether the observed decline in fire activity since the end of the LIA is associated with a long-term decline in the frequency of fire-prone states (H3), we conducted regime shift analyses on the occurrence of fire-prone climatic states. We identified these states in the reconstructed record and validated them with modern instrumental record of area burned and local climate conditions. We employed Rodionov's Regime Shift algorithm (2004) independently for each fire-prone climate state over the period jointly covered by reconstructions and modern data. We attempted to separate the spring (March to May) from the summer (June to August) HFAYs, but discovered that they are the same, so we used only one set of HFAYs. We used an L parameter of 10 and binned the data at 5-year intervals. The Hubert weight parameter was set to 1, and the $\alpha = 0.05$. This analysis produced binary annual chronologies for all fire-prone states according to whether or not (1/0) the states occurred for the analyzed time period.

1.5. Results

We identified 32 HFAYs for the reconstructed historical record (1700-1900; Fig. 1.1B). The threshold for detecting significant synchrony in the annual number of sites recording fire varied across the different subperiods: ≥ 6 for 1700-1749, and ≥ 8 for 1750-1799, 1800-1849, and 1850-1900 (Table 1.1).

Tableau 1.1.
Annual fire events synchrony thresholds for sub-periods and for the entire period with reconstructed data. We used thresholds at the 0.999 quantile to identify high fire activity years (HFAYs). Synchrony levels refer to number of sites recording fire.

synchrony level	Quantiles for subperiods				Quantiles for the entire period (1700-1900)
	1700-1749	1750-1799	1800-1849	1850-1900	
≥ 4	0.96	0.92	0.94	0.94	0.82
≥ 5	0.99	0.95	0.95	0.94	0.85
≥ 6	0.999	0.98	0.97	0.96	0.89
≥ 7	0.999	0.99	0.99	0.99	0.92
≥ 8	0.999	0.999	0.999	0.999	0.96
≥ 9	0.999	0.999	0.999	0.999	0.999

1.5.1. Historical fire association with the local climate

During historical HFAYs, the winter-early springs and the late spring-summer season were associated with mid-troposphere ridging in the northern part of the study area ($p < 0.1$) (Fig. 1.2A). The late spring-summer season was also associated with increased temperatures (Fig. 1.2A). Historical HFAYs showed lower PDSI levels for a modest region in the western parts of our study area (Fig. 1.2B). There were no associations between HFAYs and seasonal precipitation (not shown).

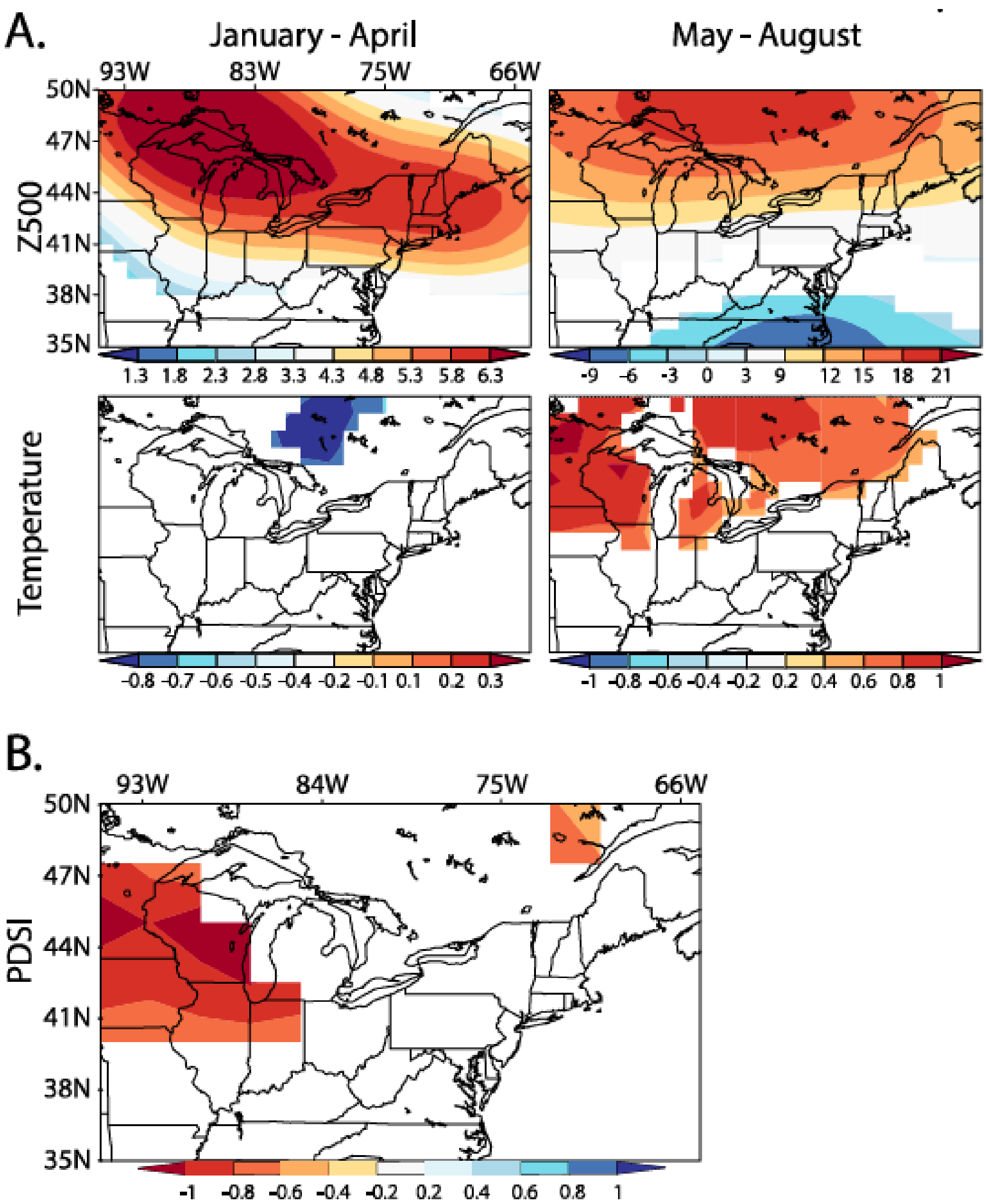

Figure 1.1.
(A) Seasonal spatial composite analyses of the reconstructed High Fire Activity Years (HFAYs) (1836-1900) and the 500 hPa geopotential height (Z500, m2/s2) and temperature (K) from the Twentieth Century Reanalysis version 3 (20CRv3) dataset. Colored contours represent the significant anomalies ($p < 0.10$) from the 1836-1900 averages. The results are presented for winter-early spring (January-April), and late spring-summer (May-August). (B) Annual spatial composite analysis of HFAYs (1700-1900) and the PDSI reconstruction from the North American Drought Atlas (NADA). Note that color bars are not centered on 0.

1.5.2. Historical fire – climate associations

Contingency analysis revealed distinct fire-prone climate states for different periods within the reconstructed record (Table 1.2 and Table SI 1.2, 1.3, and 1.4). Across the entire 1700-1900 period, four fire-prone climate states emerged: PNA+, ENSO+/PNA+, ENSO-/PDO+, and PDO-/PNA+. Within the subperiod 1700-1800, four states emerged: PNA+, PDO+, ENSO+/PNA+, and PDO+/PNA+. While within the subperiod 1800-1900, four states emerged: PNA+, ENSO+/PNA+, ENSO-/PDO+, and PDO+/PNA+. The states PNA+ and ENSO+/PNA+ were consistent across the entire reconstructed period and both reconstructed subperiods (1700-1800 and 1800-1900) (Table 1.2).

Tableau 1.2.
Results of contingency analyses of years with high fire activity (HFAY) and circulation indices' state combinations for the entire reconstructed period (1700-1900), two sub-periods of the reconstructed period (1700-1800 and 1800-1900), and the modern times (1959-2021). Only fire-prone climate states significant at 0.90 are shown.

	Time period	Fire-prone climate states
Reconstructed data	1700-1900	PNA+ ENSO+/PNA+ ENSO-/PDO+ PDO-/PNA+
	1700-1800	PNA+ PDO+ ENSO+/PNA+ PDO+/PNA+
	1800-1900	PNA+ ENSO+/PNA+ ENSO-/PDO+ PDO+/PNA+
Observational data	1959-2021	ENSO+ PNA+ PDO- ENSO+/PNA+ PDO-/PNA+

1.5.3. Fire-climate associations in the modern record

Contingency analysis revealed five fire-prone climate states for the modern period (1959-2021): ENSO+, PDO-, PNA+, ENSO+/PNA+, and PDO-/PNA+, (Table 1.2 and Table SI 1.5). Two of these states, ENSO+/PNA+ (Fig. 1.3) and PNA+ (Fig.

1.4), also appeared consistently in both subperiods and the entire reconstructed record. Consequently, we examined local climate conditions during years characterized by these two states from 1950 to 2021.

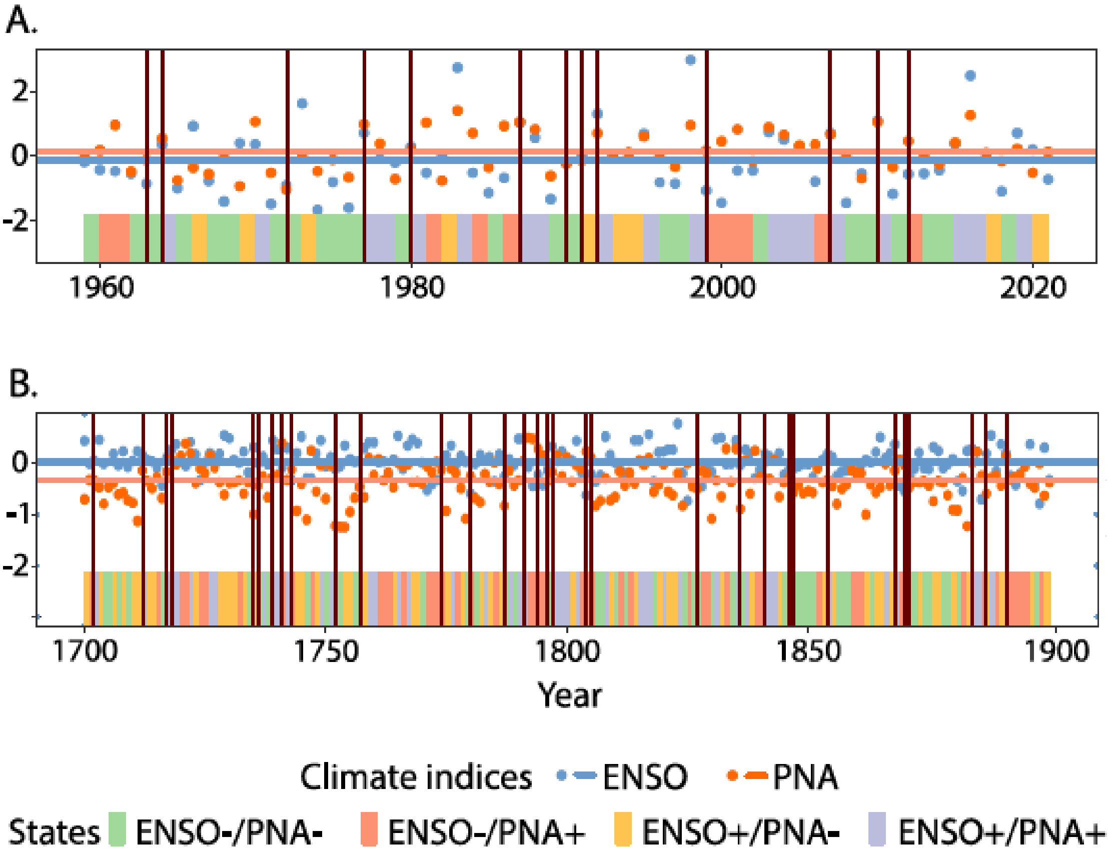

Figure 1.2.
Contingency analysis of the climate states, classified into positive and negative phases, of ENSO and PNA and high fire activity years (HFAYs) for (A) 1959-2021 and (B) 1700-1900. The maroon vertical lines represent the HFAYs. The scatter blue points represent the ENSO values and the red points represent the PNA values. The blue horizontal lines represent the mean of the ENSO chronology, and the red horizontal lines represent the mean of the PNA chronology. The color bars code the combinations ENSO-/PNA-, ENSO-/PNA+, ENSO+/PNA-, and ENSO+/PNA+.

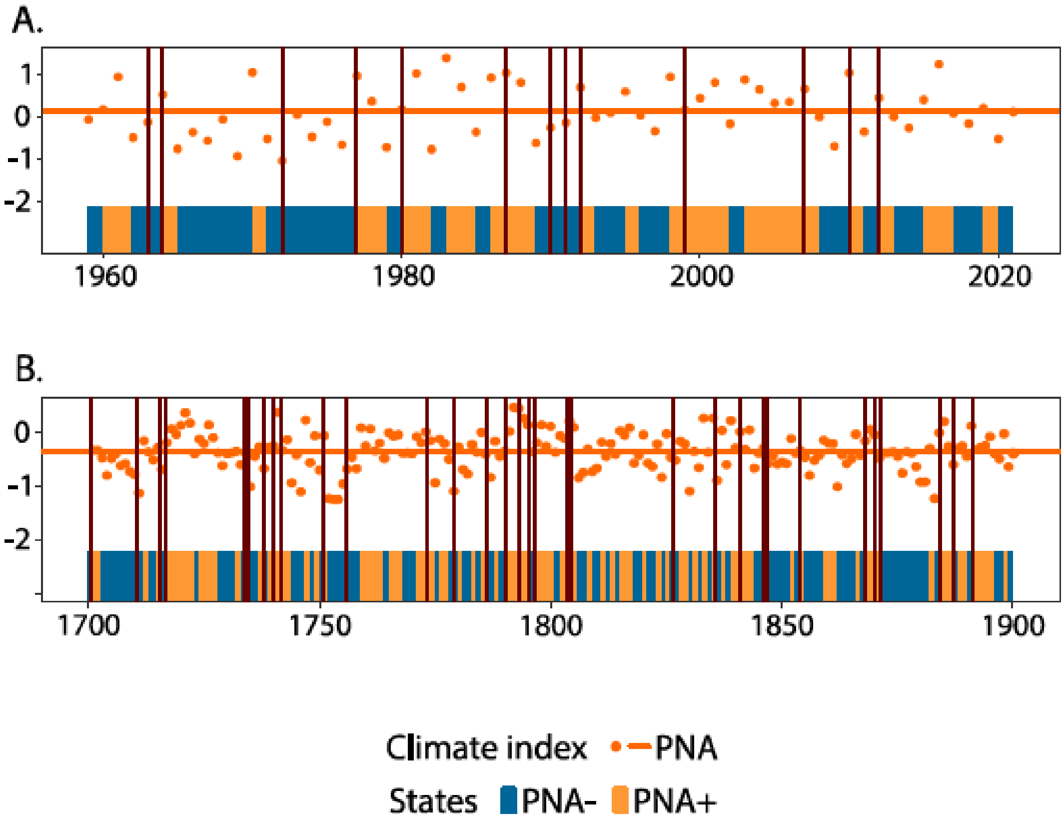

Figure 1.3.
Contingency analysis of the climate states, classified into positive and negative phases, of PNA during high fire activity years (HFAYs) for (A) 1959-2021 and (B) 1700-1900. The maroon vertical lines represent the HFAYs, the scatter points represent the PNA values, with the horizontal line representing the mean of the PNA chronology. The color bars code the states PNA- and PNA+

Both ENSO+/PNA+ (Fig. 1.5) and PNA+ (Fig. 1.6) were associated with high fire hazard weather. Specifically, during ENSO+/PNA+ years, mid-troposphere ridging prevailed over northern areas with troughing in the south during January-April, transitioning to widespread ridging during May-August. Positive temperature anomalies were mainly observed in western areas for January-April but expanded across the region during May-August. Negative precipitation anomalies exhibited a more coherent pattern during January-April than during May-August. Negative

PDSI anomalies were concentrated in the northwest areas during both periods, January-April and May-August (Fig. 1.5).

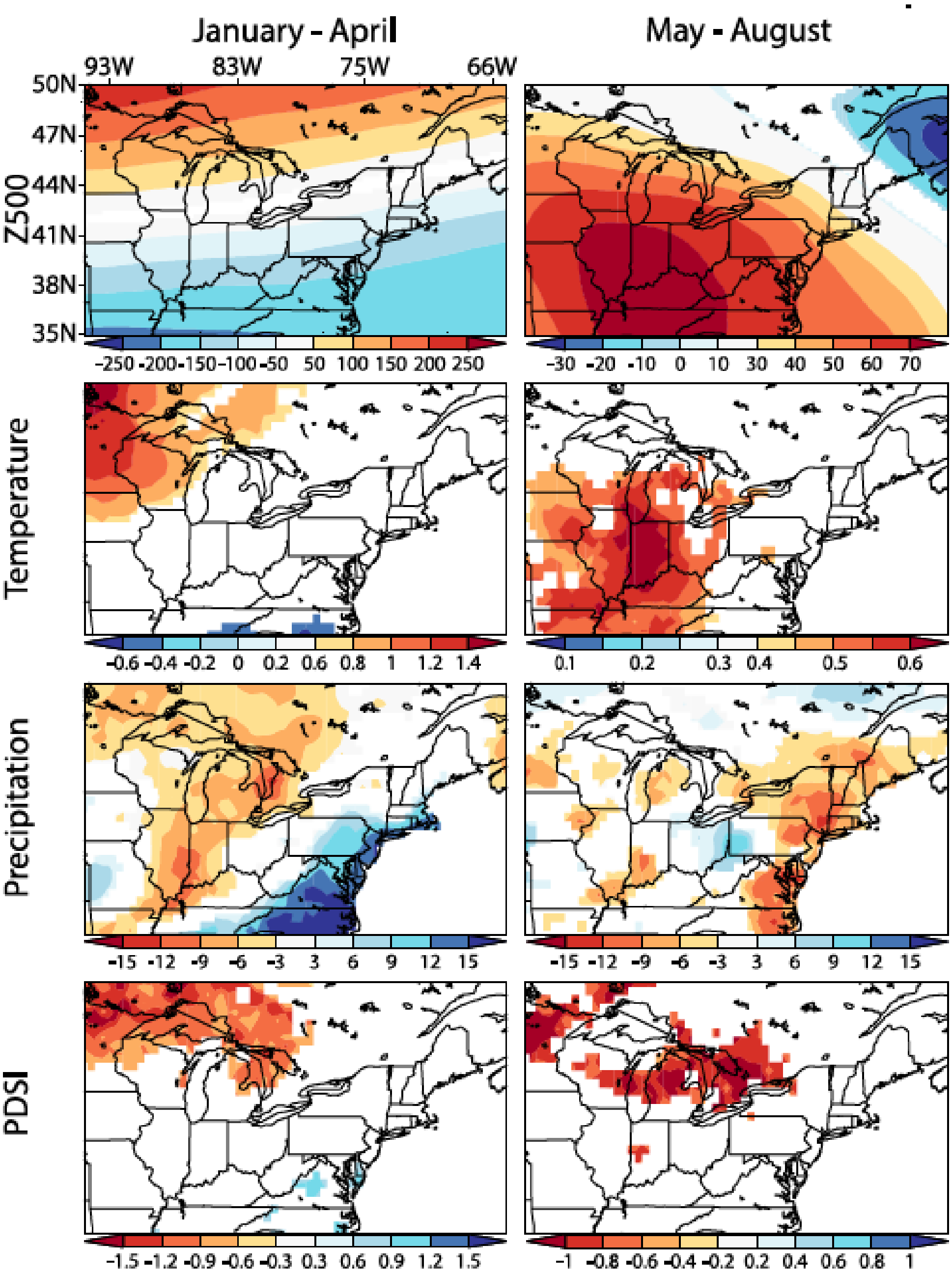

Figure 1.4.
Spatial composite analyses of local climate conditions during the fire-prone state ENSO+/PNA+ years (1950-2021). Fields are the 500 hPa geopotential height (Z500, m2/s2), temperature (°C), precipitation (mm/month), and PDSI (unitless). Significant anomalies (p < 0.10) from the 1950-2021 averages are shown as colored contours. Results are presented for early spring (January-April), and late spring-summer (May-August).

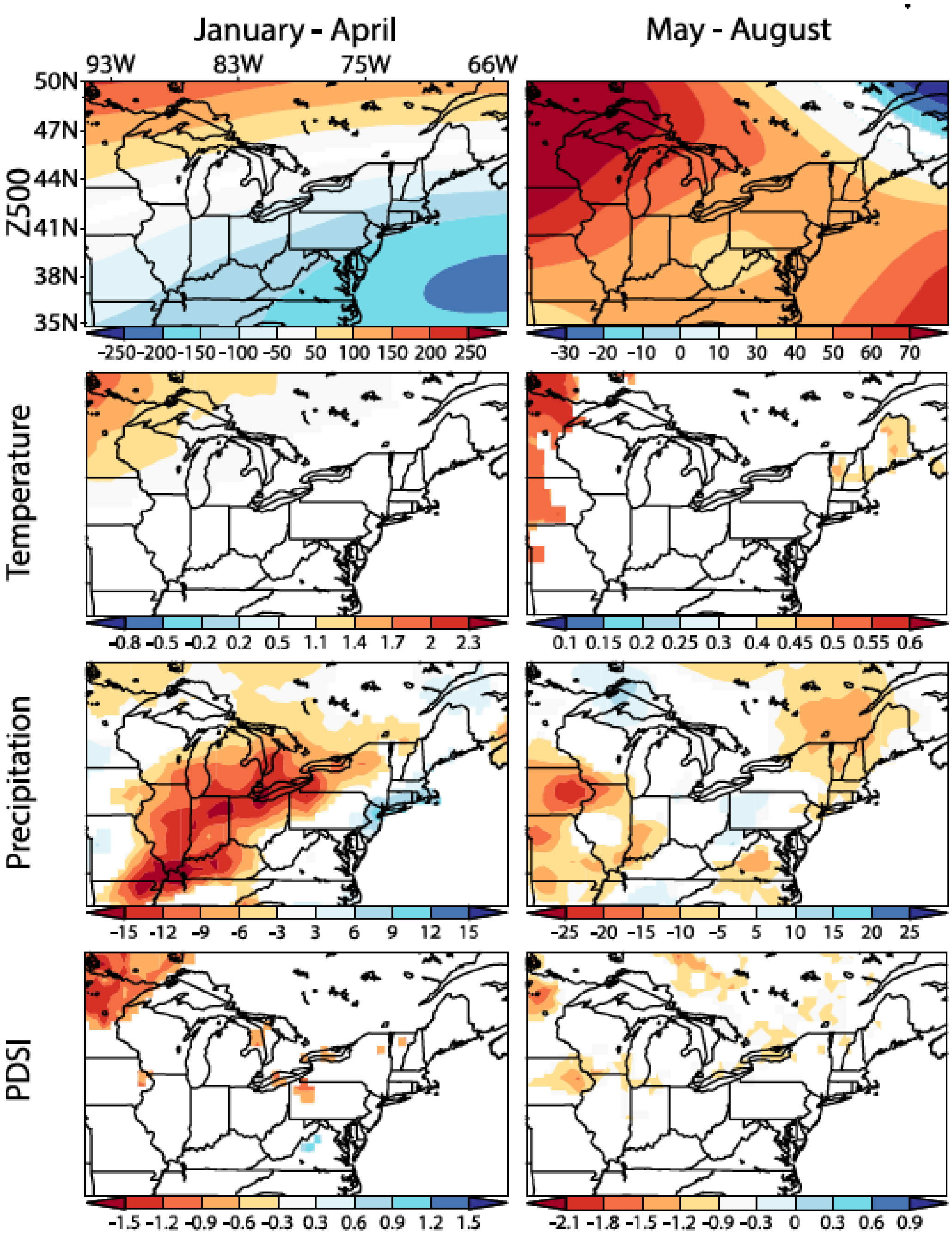

Figure 1.5.
Spatial composite analyses of local climate conditions during the fire-prone state PNA+ years (1950-2021). The fields are the 500 hPa geopotential height (Z500, m2/s2), temperature (°C), precipitation (mm/month), and PDSI (unitless). Significant anomalies ($p < 0.10$) from the 1950-2021 averages are shown as colored contours. Results are presented for winter-early spring (January-April), and late spring-summer (May-August).

State PNA+ exhibited a similar Z500 field pattern, with ridging in the north and troughing in the south for January-April, transitioning to widespread ridging during

May-August (Fig. 1.6). However, the coherence of positive temperature anomalies, negative precipitation and PDSI anomalies was lower for this state than for ENSO+/PNA+. Notably, the negative precipitation anomaly during PNA+ years was coherent during January-April but patchier during May-August (Fig. 1.6).

1.5.4. Long-term trends of fire-prone states

The fire-prone climate state ENSO+/PNA+ was frequent from the oldest part of the chronologies until around the mid-1700s and from around 1985 to around 2020. However, from 1750 to 1985, its frequency was low (Fig. 1.7). The climate state PNA+ was frequent from the 1750s until just before the 1850s, and then again from after the 1900s until 2021 (Fig. 1.7). Around 1990, PNA+ became even more frequent. Consequently, from the 1850s to the 1900s, the two fire-prone climate states were at a low frequency. In general, from the oldest part of the chronology until just before 1850 and then from after 1900s to 2021, at least one of these two fire-prone climate states was in a high-frequency mode (Fig. 1.7).

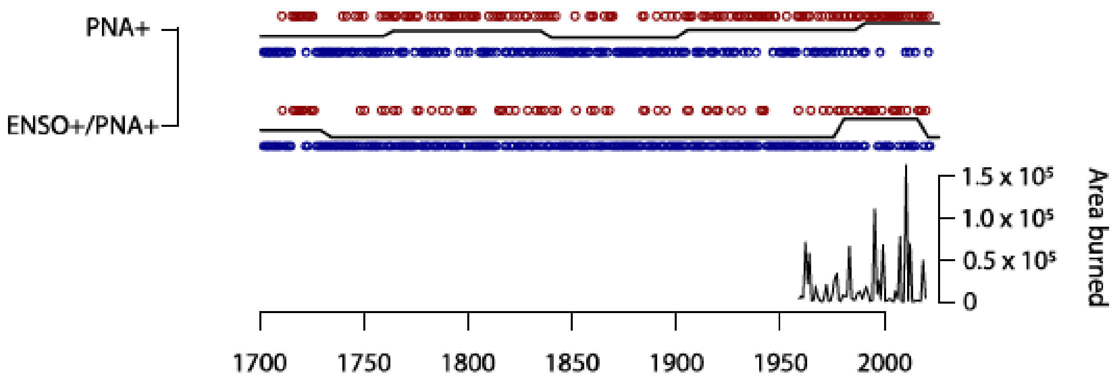

Figure 1.6.
Regime shift analysis for each fire-prone climate state for the period 1700-2021. Red circles represent years with fire-prone states of climate indices, and the blue circles are the years with non-fire-prone conditions. The thick black lines marks climate regimes, which are defined based on the proportion of fire-prone vs. non-fire prone states for a specific circulation index. A higher position of the black line for a specific index indicates a regime with a higher frequency of fire-prone states. Note that the vertical position of black lines in relation to circles is chosen with the only purpose to facilitate visibility of graphical elements. The black line is the observed area burned in Canada for the period 1959-2021, based on the data from the Canadian National Fire Database (CNFDB).

1.6. Discussion

In this study, we explored the effect of large-scale modes of atmosphere-ocean variability over the Pacific domain upon fire activity in the red pine forests of eastern North America. We detected fire-prone climate states, represented by climate indices (H1). These climate states were associated with a fire-conducive surface climate (H2). Our results suggested a decline in frequency of fire-prone climate towards the end of the LIA. However, such states became more frequent in the 1900s, and further increased around 1990. This pattern prevented us from drawing a definite answer to H3. Since the climate-driven changes in fire activity likely affect other ecosystems of this part of the North American continent, our results may have implications beyond mixed pine forests.

1.6.1. Reconstructed fire activity and local climate

The reconstructed HFAYs were associated with fire-conducive weather (mid-troposphere ridging and warm temperatures) during the 1836-1900 period (Fig. 1.2). The association with the summer PDSI over the whole reconstructed period (1700-1900) was modest and limited to the western parts of the study area. Inherent limitations of the reconstructed PDSI record might explain this result. First, the Midwest and northern New England were the weakest calibration areas of the PDSI grid of the contiguous U.S. due, possibly in part, to poor quality and coverage of tree-ring data in these regions (Cook et al., 1999). Second, the NADA's PDSI in our region has a weak to absent winter precipitation signature (St. George et al., 2010). Thus, important processes for the fire season that occur during the cold season, i.e., the dynamics of recharge of soil water reserves, are possibly not accounted for by this reconstruction the RPDA.

1.6.2. Fire-climate associations

At the annual scale, climate states characterized by two indices had a statistically stronger effect upon fire activity of the RPDA than states described by single climate indices. For example, while ENSO+ was not identified as fire-prone in the reconstructed record, it was identified as a fire-prone climate state when in combination with other climate indices (ENSO+/PNA+). These results further highlighted the value of looking at composite climate states, i.e., those represented by a combination of teleconnections (P. M. Brown, 2006; Sibold & Veblen, 2006). In our region, a study of teleconnections associated with the dynamics of Great

Lakes ice cover found that even when the single indices, that included ENSO and PDO, showed no significant associations with ice cover, their effect in combination was significant (J. Wang et al., 2018).

The historical and modern fire-prone climate states consistently involved the positive state of both ENSO and PNA (Table 1.2). During EP El Niño events, the AL deepens and is also displaced eastwards to the Gulf of Alaska (Rodionov and Assel 2003). This leads to a PNA configuration with an eastwards-displaced ridge closer to the RPDA, resulting in milder winters and springs in the region (Rodionov and Assel 2003). In line with these dynamics, our analysis identified the combination ENSO+/PNA+ in the reconstructed and the modern record (Fig. 1.3) as a fire-prone climate state and the state that had the most coherent patterns with fire-conducive local climate in the region (Fig. 1.5). However, in the subperiod 1800-1900 and the whole period (1700-1900), the combination ENSO-/PDO+ was also associated with HFAYs (Table 1.2). This result might be explained by the ENSO diversity phenomenon.

The consistent identification of the positive phase PNA as a fire-prone state, whether alone or in combination with other climate indices (Table 1.2), can also be explained by its impact on the midlatitude jet stream, the PFJ. The PNA pattern forces a meridional jet stream flow, which results in fewer Pacific-derived winter storm tracks and dry anomalies primarily in western North America (Rodysill et al., 2018). This effect may extend to our study area and bring drought conditions. The PNA pattern is also out-of-phase with the Tropical Northern Hemisphere (TNH) pattern, which features a deep trough over Hudson Bay associated with cold and moist conditions over eastern North America (Mo & Livezey, 1986; Soulard et al., 2019). Thus, the positive PNA entails a negative TNH, preventing formation of the trough and associated wetter conditions in our study area.

In the reconstructed record, the fire-prone climate states involving the PDO predominantly featured the PDO in its positive state (PDO+, ENSO-/PDO+, and PDO+/PNA+) except for one (PDO-/PNA+). The positive PDO phase is associated with a deeper AL (Mantua et al., 1997), and thus with the PNA pattern, which brings milder winter conditions to the RPDA. However, in the modern record, the identified fire-prone climate states only featured the PDO in its negative state (PDO- and

PDO-/PNA+). This discrepancy might be due to the relatively short length of the modern fire record, spanning only 60 years, potentially insufficient to capture PDO cycles. Another factor that might contribute to the lack of consistency between results obtained on the reconstructed the modern records could be a less significant PDO effect at the annual scale as this index is known for its decadal periodicities (Mantua et al., 1997).

1.6.3. Fire-prone climate states and local climate

Years with fire-prone climate states were characterized by a fire conducive local climate in the modern record (1950-2021). The fire prone climate states ENSO+/PNA+ and PNA+ were associated with high fire hazard, as indicated by positive mid-troposphere height and temperature anomalies, and low precipitation and PDSI anomalies for the winter-early spring and the late spring-summer season periods (Fig. 1.5 and 1.6). However, mid-tropospheric ridging especially in the late spring-summer season was the most widespread over the area and thus the strongest pattern for all three climate-state combinations. A mild winter-early spring season as well as a warm and dry late spring-summer season resulting from mid-troposphere ridging. Atmospheric ridges block zonal air flow, generating a warmer and drier climate. These conditions are favorable for the drying of fuels (Fauria & Johnson, 2008). A warm and dry late-spring-summer season featuring blocking ridges, high temperatures, and low precipitation also augment the fire risk. The formation as well as the breakdown of high-pressure blocking systems augment fire risk during the fire season. The formation of blocking ridges create warm, dry conditions (see above), and the breakdown of these systems is linked to enhanced lightning, strong surface winds, and limited rain to moisten fuels (M. D. Flannigan & Wotton, 2001; Skinner et al., 2002). Lightning provides the natural source of ignition in high latitude forests that is responsible for most of the area burned therein (Skinner et al., 2002; Veraverbeke et al., 2017), while strong winds increase fire spread (M. D. Flannigan et al., 2000).

1.6.4. Low frequency trends in occurrence of fire-prone states

Regime shift analysis spanning from 1700 to 2021 revealed a decline in the frequency of fire-prone climate states at the end of the LIA, around 1850 (Fig. 1.7). This result supported H3 and the earlier interpretation of the decrease in fire activity in the northern periphery of the RPDA in eastern Canada starting in 1850 as a climate-driven phenomenon (Bergeron et al. 2001; Bergeron, Flannigan, et al. 2004). However, we observed a resurgence of high-frequency regimes for PNA+ after the 1900s, with a notable further increase around the 1990s, which contradicts H3. Contrary to this pattern, the decrease in fire activity in eastern Canada continued and became more pronounced after 1920 (Bergeron et al. 2001). Fire suppression measures have been proposed as factors contributing towards a decline in fire activity during the 20th century (Nowacki & Abrams, 2008). However, fire suppression has been shown to be of limited importance at least at the northern fringes of RPDA, where climate remains the dominant control of the fire regime (Bergeron et al. 2001; Danneyrolles, Cyr, et al. 2021). A decrease in traditional subsistence practices has been proposed to explain the decrease in fire activity in the 20th century for some areas in the Great Lakes (Kipfmueller et al. 2021). More research is clearly needed to explain why the observed low levels of fire activity in eastern Canada (Bergeron et al. 2001) and in the rest of the RPDA (Drobyshev et al., 2008b) over the 20th century do not reflect the long-term patterns of the frequencies of fire-prone climate state (PNA+) reported here.

An atmospheric circulation pattern associated with drought conditions in the area became more frequent since 1985 (Girardin et al. 2006), which coincides with the shift to a higher frequency of ENSO+/PNA+ state around the 1980s (Fig. 1.7). This atmospheric pattern reported by Girardin et al. (2006), resembles the eastward displaced PNA pattern, which is forced by ENSO EP, the ENSO configuration we focused on in this study. Another atmospheric circulation pattern increasing its frequency since 1850 was a TNH-like pattern with a trough around the Hudson Bay, bringing wetness and a decline in fire activity in eastern and central Canada (Girardin et al. 2006). This configuration became more common during 1850s – 1990 (Girardin et al. 2006), which does not agree with the evolution of PNA+ reported here (Fig. 1.7).

1.6.5. Study limitations

We acknowledge several limitations of this work. We used frequency data as opposed to spatially explicit reconstructions, which may potentially compromise our view of large fire years, defined here as years with large burned areas. Although we assumed that the synchrony of fire occurrence is a legitimate proxy of fire size and, by extension, climate forcing upon fire activity (Drobyshev et al., 2014; Falk et al., 2011; Farris et al., 2010), frequency data may not fully capture the dynamics of the burned areas, which is a better proxy of landscape and region level fire activity. Spatial fire reconstruction on dendrochronological data, however, are largely missing over eastern North America.

Limiting analyses to combinations of two climate indices might oversimplify and potentially miss important interactions within the climate system. It is difficult to analyze more indices in a single analysis due to the low expected frequencies of three-state combinations in the contingency tables, effectively precluding such analyses with the available record. To overcome this obstacle, we would need to considerably expand the length of the regional fire chronology by at least 200-300 years. This is, however, problematic due to a limited residency time of dendrochronologically datable remnant wood on the forest floor of increasingly mesic forests. Finally, the use of the modern fire data for the Canadian part of RPDA might introduce another source of uncertainty. Although the choice of Canadian data was justified by the larger proportion of forested areas and longer fire records, we realized that the modern fire dataset might not be fully representative of the red pine range.

1.6.6. Dynamics of fire activity in the red pine forests and its ecological implications

The lower frequency of ENSO+/PNA+ during the 20th century could have facilitated successional development away from xeric mixed pine forests towards mesic forests dominated by deciduous trees, reported earlier across the American Midwest (Nowacki & Abrams, 2008). Fire suppression and infrequent use of prescribed fire have been viewed as the primary factors behind this conversion (Frelich et al. 2021). Our results, however, show that climate change likely also contributed to decreased fire activity starting in the 1850s, leading to mesophication of historically fire-maintained ecosystems and supporting the view of climate-driven disturbance regimes as having lasting legacy on regional species composition (Pederson et al., 2014).

The increase in the frequency of fire-prone climate states since the 1980s may foreshadow the anticipated increase in climatological fire hazard projected for eastern Canada in the future (Wang et al. 2017). Such an increase will likely interact with the legacies of the less fire-prone period, such as fuel load accumulation, further increasing probabilities for potentially large and high severity fires. Fires developing under the conditions of higher fuel loading, including ladder fuels, would likely increasingly be of higher severity and potentially stand-replacing. A similar effect of a "fire deficit" has been recently proposed for the modern Canadian boreal forest (Parisien et al., 2020). For the red pine, high-severity fires generally remove on-site seed sources and limits post-fire recovery (C. E. Van Wagner, 1971). Red pine has a limited seed dispersing capacity and, therefore, is highly dependent on the presence of scattered surviving individuals for recolonization after fires (Horton & Bedell, 1960). Scarcity of red pine seed banks and high fire severity would likely favor regeneration of more easily dispersed species. In the boreal and sub-boreal section of red pine range, jack pine will likely replace red pine (Nyamai et al., 2014). In fact, it is a change from surface to stand-replacing fire as the dominant fire type at the northern fringe of red pine distribution that has been attributed to the disappearance of red pine from the forest canopy (Bergeron & Brisson, 1990; M. d. Flannigan & Bergeron, 1998). To this end, prescribed fires could be a critical element in the conservation policies aiming to maintaining red pine forests during the transition to more fire-prone climate conditions of the present and future (Montour et al., 2020).

It is likely that the legacies of fire-free periods in shaping future disturbance regimes are not limited to red pine ecosystems. Human-related or climatically driven modification of successional pathways, leading to changes in fuel loads, may become increasingly important for the control of future disturbance regimes, and specifically – of the fire behavior. We speculate that the feedbacks in the climate-vegetation-fire system likely affect the strength of association between large-scale climate drivers and the properties of current and future disturbance regimes.

1.7. Acknowledgements

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2 - CHAPTER 2: 500-YEAR WILDFIRE HISTORY IN SWEDEN REVEAL CONSISTENT AND NON-MONOTONIC RELATIONSHIPS TO POPULATION DENSITY AND PRECIPITATION

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2.1. Résumé

La variabilité climatique et l'utilisation des terres par l'homme sont des facteurs critiques de l'activité des feux de forêt dans la zone boréale européenne, mais les évaluations à long terme sont limitées par des archives insuffisantes avec une résolution spatio-temporelle adéquate. Ici, nous démêlons les influences climatiques et humaines sur la dynamique des feux de 1559 à 2000 en utilisant un vaste réseau de reconstructions dendrochronologiques des feux à travers la Suède, des archives exceptionnellement longues des populations à l'échelle des municipalités, ainsi que des données maillées de précipitations estivales. Nos résultats ont indiqué que la densité de population humaine et les précipitations estivales influençaient significativement la survenue des feux, avec des effets dépendant des sous-périodes pour les deux variables, et des effets de densité de population soumis à des changements de phase. L'activité des feux était favorisée par de faibles densités de population, mais elle diminuait au-delà de seuils critiques de densité de population. De même, à mesure que les précipitations estivales diminuaient, l'activité des feux diminuait. Ces seuils sont restés relativement constants au cours des 500 dernières années, soulignant leur rôle persistant dans la détermination de l'activité des feux. Les précipitations estivales ont continué d'exercer un effet significatif sur l'activité des feux durant les périodes plus récentes, remettant en question l'idée selon laquelle l'influence humaine croissante a totalement éclipsé les contrôles climatiques. Nous avons trouvé un fort gradient sud-nord dans l'apparition de la période sans feux due à la suppression des incendies, mettant en évidence une variabilité spatiale prononcée des contrôles humains sur l'activité historique des feux.

Mots-clés : Feux de forêt historiques, zone boréale européenne, densité de population humaine, précipitations estivales, dendrochronologie.

2.2. Abstract

Climate variability and human land use are critical controls of forest fire activity across the European boreal zone, yet long-term assessments remain limited by sparse records with adequate spatiotemporal resolution. Here, we disentangle climatic and human influences on fire dynamics from 1559 to 2000 using an extensive network of dendrochronological fire reconstructions across Sweden, exceptionally long municipality-level population records and gridded summer precipitation data. Our results indicated that both human population density and summer precipitation significantly influenced fire occurrence, with subperiod-dependent and phase-shifting population density effects. Fire activity was favored by low population densities but declined beyond critical population density thresholds. As low summer precipitation increased, fire activity decreased. The population density thresholds remained relatively consistent over the last 500 years, emphasizing their persistent role in shaping fire activity. Summer precipitation continued to exert a significant effect on fire activity in more recent periods, challenging the idea that increasing human influence completely overshadowed climatic controls. We found a strong south-to-north gradient in the onset of the fire-free period due to fire suppression, highlighting a pronounced spatial variability of human controls of historical fire activity.

Keywords: Historical wildfire, European boreal zone, human population density, summer precipitation, dendrochronology.

2.3. Introduction

Wildfire is the most important natural disturbance agent in the European boreal forests, defining successional pathways (Carcaillet et al., 2007; Goldammer & Furyaev, 2013; Remy et al., 2023), contributing to global biogeochemical cycles (Bowman et al., 2009), and promoting landscape heterogeneity that supports biodiversity (Berglund & Kuuluvainen, 2021; Kuuluvainen, 2002; Turner, 2010). Wildfires exert a substantial impact on the global climate by influencing nutrient cycles, surface energy budgets, and the land surface albedo (Ward et al., 2012). Fire activity in contemporary Northern European boreal forests is markedly lower than it was during the 1500s-1800s, primarily due to highly effective fire suppression and the disappearance of agricultural and pastoral forest burning practices (Wallenius, 2011). In Fennoscandia, the average annually burnt area is currently less than 0.01% of the forested land (Granström, 2001), and the fire cycles, i.e., period required to burn an area equivalent to the study area (C. Van Wagner, 1987), have significantly increased. In Sweden, the modern fire cycle is 10^3 to 10^4 years (Drobyshev, Niklasson, et al., 2012). This reduction in fire activity has led to declines in fire-adapted species in both northern (Granström, 2001; Wikars & Schimmel, 2001) and southern (Lindbladh et al., 2003) Swedish forests.

Climate and human land-use practices are the major drivers of fire activity in European boreal forests. Climate has been the dominant factor controlling fires in Fennoscandian forests throughout the Holocene (Carcaillet et al. 2007; Drobyshev et al. 2016; Aakala et al. 2018). Key climatic conditions that promote fire include persistent positive geopotential height anomalies (ridges) in the mid-troposphere, which disrupt zonal air flow, leading to warmer, drier conditions that enhance fuel drying (Fauria & Johnson, 2008). The formation of these ridges over Sweden is largely controlled by the North Atlantic Oscillation (NAO), a major driver of tropospheric circulation and regional climate patterns across Northern Europe (Deser et al. 2017), with notable implications for fire activity (Drobyshev et al., 2016). The NAO reflects variations in sea level pressure (SLP) between its action centers, the Icelandic Low and Azores High, which control storm tracks and the jet stream over the Europe-North Atlantic sector (Hurrell, 1996; Hurrell & Deser, 2010). The location and intensity of action centers vary from seasonal to multi-decadal scales, causing non-stationarity in the NAO's local manifestation (Comas-

Bru & McDermott, 2014; Moore et al., 2013). During the warm season, the NAO dipole contracts and shifts poleward, positioning the southern node over northern Europe rather than over the Azores islands. This configuration results in a high-pressure cell aloft Scandinavia, leading to dry and warm conditions (Folland et al., 2009) that promote fire hazard (Högbom, 1934). Indeed, fire activity in Sweden and across the European boreal zone has been linked to the summer NAO (Drobyshev et al., 2015, 2021).

In Scandinavia, two important fire regime shifts coincided with major socio-economic transitions. The first shift occurred around the 1600s with the expansion of permanent settlements and the associated increase in anthropogenic fires. This shift was characterized by a reduction in fire size, and increased fire frequency and early-season fires (Niklasson & Drakenberg, 2001; Niklasson & Granström, 2000; Rolstad et al., 2017). The second shift, marked by a drastic decline in fire activity, is generally ascribed to improvements in agricultural techniques and the growing importance of the forest as a timber source. This shift is conventionally dated to the early 1700s to early 1800s in southern Sweden (< 60°N) (Niklasson & Drakenberg, 2001; Pinto, Niklasson, et al., 2020) and to the mid- to late 1800s in the north (Granström & Niklasson, 2008; Niklasson & Granström, 2000). The abandonment of agricultural and pastoral burning practices followed by the introduction of fire suppression policies contributed to a significant decline of fire activity across the whole European boreal domain (Rolstad et al., 2017; Ryzhkova et al., 2022; Wallenius, 2011).

Quantitatively assessing the contributions of climatic and anthropogenic drivers on fire activity over long historical periods is challenging due to the scarcity of records with adequate temporal and spatial resolution. Previous multi-century fire studies have typically analyzed these two drivers qualitatively, often isolating their effects independently. To isolate the climate signal, studies have treated the human factor as “noise” masking the climate signal in fire chronologies (Granström and Niklasson 2008; Drobyshev et al. 2015). These studies have focused on large fire years (LFYs), or years when extensive areas burned regions (e.g., Drobyshev et al. 2015; Drobyshev et al. 2016; Rolstad et al. 2017; Aakala et al. 2018; Ryzhkova et al. 2020; Drobyshev et al. 2021), which illustrate the role of the climate as a topdown control, with atmospheric circulation anomalies creating fire-prone conditions over extensive regions (Falk et al., 2011). Conversely, to discern the human signal, studies have relied on comparing fire regime shifts to known changes in land-use patterns (Pinto et al. 2020a; Ryzhkova et al. 2020; Ryzhkova et al. 2022). However, integrating both climate and anthropogenic drivers into a single quantitative framework is essential to build on these qualitative insights and provide a more nuanced understanding of historical fire dynamics.

To address this knowledge gap, we conducted a quantitative assessment of both climatic and anthropogenic drivers of historical fire activity in Sweden from 1559 to 2020. We relied on the largest synthesis of dendrochronological fire reconstructions developed for Sweden, along with municipality-level human population records (Palm, 2000) and gridded summer precipitation reconstructions (Pauling et al., 2006). We used a Generalized Additive Model (GAM) framework, as it allows for the estimation of non-linear relationships between predictors and fire activity, providing the flexibility to learn these functions directly from the data while quantifying the independent contribution of each driver. As the proxy of fire activity, we used fire occurrence reconstructed dendrochronologically. Unlike previous studies that predominantly focused on LFYs to explore climate forcing within the European boreal region (e.g., Drobyshev et al. 2021), our approach utilized complete annually-resolved fire chronologies from single locations within a network. This allowed us to capture both extreme fire years and smaller events, providing a more comprehensive view of fire dynamics over time. Our study spanned the boreo-nemoral and boreal biogeographical zones and periods with significant climatic and socio-economic variability with associated changes in land-use practices. We tested three hypotheses: (H1) Human population dynamics and climate variability exercised temporally consistent thresholds upon fire activity; (H2) Increasing human population over time and its influence on forests diminished the relative role of climate variability in controlling fire activity, which resulted in a declining influence of climate upon fire during 1559-2000 AD; and (H3) The timing of the onset of the fire suppression period correlated with site latitude, with more northerly sites exhibiting a more recent onset of fire suppression.

2.4. Methods

2.4.1. Study area

Our study area covered most of Sweden (except for the nemoral and alpine domains) and encompassed a network of 49 sites distributed across 36 Swedish municipalities. The latitudinal extent of the study area ranged from 56.46° to 66.58° N (Fig. 1). Our dataset also included a single site near Oslo in Norway (59.65° N 9.32° E), bringing the total number of sites in our network to 50. The study area exhibits large gradients in temperature, precipitation, and the length of the growing and fire seasons. The southernmost site, located in the Tingsryd municipality (56.46° N), has an average annual temperature of 7.57° C, an average maximum July temperature of 25.82° C, and an average minimum January temperature of -12.57° C. In contrast, the corresponding temperatures for the northernmost site, located in Jokkmokk (66.58° N), are -0.72° C, 23.74° C, and -32.63° C, as recorded by nearby meteorological stations for the 1995-2022 period (*Swedish Meteorological and Hydrological Institute SMHI*, n.d.). The study area exhibits an east-west precipitation gradient that is most pronounced in the south (Crespi et al., 2018; Johansson & Chen, 2003). The average annual precipitation in the westernmost site in the study area, located in Norway (59.65° N 9.32° E), is 733 mm yr^{-1} (Norwegian Centre for Climate Services, n.d.), while the easternmost site in southern Sweden, located in Nybro (57.02° N 16.02° E), receives an average of 573 mm annually (*Swedish Meteorological and Hydrological Institute SMHI*, n.d.). The length of the growing season, or the number of days with the mean temperature above 5° C, is 170-200 days in the south and 130-170 in the north (Raab & Vedin, 1995).

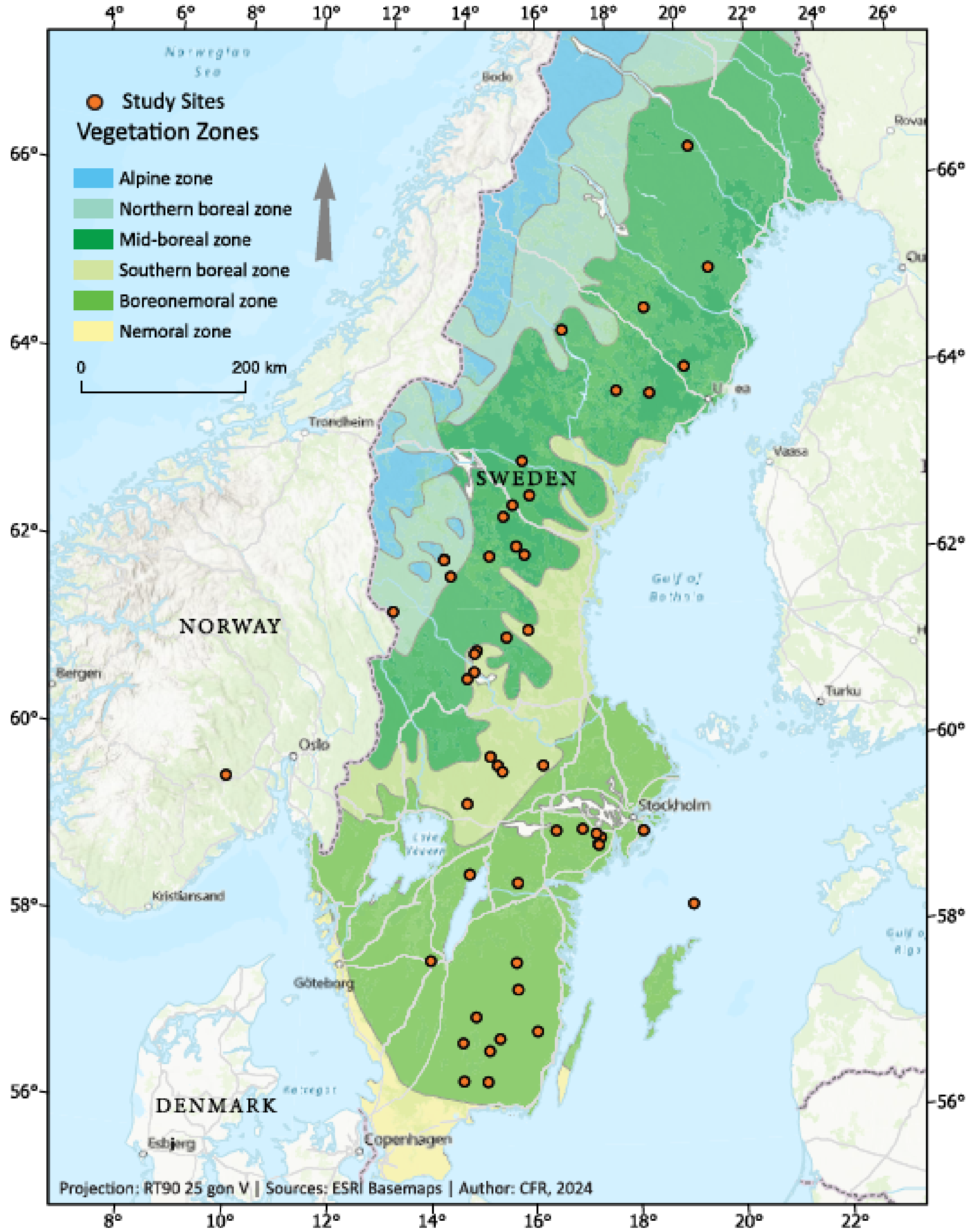

Figure 2.1.
Geographical distribution of the site network across the bioclimatic zones in Sweden.

The forest ecosystems in Sweden stretch from nemoral forests in the south to northern-boreal forests in the north. South Sweden (Götaland, 55°N–58.7°N) belongs mostly to the nemoral (temperate) and boreo-nemoral (hemiboreal according to Ahti et al. 1968) vegetation zone (Fig. 1). This region features a natural mixture of broadleaved and coniferous forest (Ahti et al., 1968). However, due to intensive forestry, Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.) dominate, constituting approximately 44% and 33% of the total volume, respectively (Lindbladh et al., 2014). Broadleaved species present in the boreo-nemoral zone include *Quercus robur* L., *Ulmus glabra* Huds., *Fraxinus excelsior* L., *Acer platanoides* L., *Tilia cordata* Mill.; and with more restricted distribution: *Carpinus betulus* L. in the southern parts, *Fagus sylvatica* L. in the southern and southwestern parts, *Quercus petraea* (Matt.) Liebl. in the western parts, and *Ulmus minor* Mill. in Oland and Gotland islands in the Baltic (Diekmann, 1994).

Central Sweden (Svealand, 58.7°N–63.5°N) and North Sweden (Norrland, 63.5°N–68.3°N) belong mostly to the southern boreal and middle boreal vegetation zones, respectively (Ahti et al., 1968). Within these zones, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate forest canopies in roughly equal proportions (Loman, 2004).

2.4.2. Human impact on Swedish forests

Logging, agriculture, mining activities and animal husbandry all affected Swedish forests. The onset of substantial human-induced alteration began in southern Sweden since the Viking Age (800-1000 AD) and the early Middle Ages (1000 AD) (Lindbladh et al., 2000). Land-use practices included forest clearance through burnings or tree cutting to establish meadows, fields, and pastures. Slash-and-burn agriculture and deliberate burnings in forests to improve fodder production were also part of the land-use regime. The reliance on fire by local populations altered the natural fire regimes (Niklasson & Granström, 2000).

Land use directly altered the vegetation composition, particularly in southern Sweden. Deciduous forests that once dominated the region have been replaced by Norway spruce and Scots pine due to land use (Björse & Bradshaw, 1998; Lindbladh et al., 2000). Norway spruce likely spread due to its lower palatability to grazing animals (Lindbladh & Bradshaw, 1998). The expansion of Scots pine from southeastern Sweden into western regions was likely facilitated by anthropogenic fires (Lindbladh et al., 2000). Norway spruce was also favored by the cessation of slash-and-burn agriculture during the agrarian revolution (1700-1879), the implementation of fire suppression, and artificial regeneration (Lindbladh et al., 2014; Niklasson & Drakenberg, 2001).

In northern Sweden, human impact was generally low and spatially constrained until the onset of industrial logging in the mid-nineteenth century (Östlund & Norstedt, 2021). The native Sami people that inhabited the interior of the region for millennia follow a nomadic lifestyle with minimal influence on forest composition (Östlund & Norstedt, 2021). While agrarian colonization occurred in coastal areas as early as 50 BC, the northern interior was not settled until the late eighteenth century (Andersson et al., 2005).

Historical logging practices in Sweden varied regionally but converged during the twentieth century. In southern and central Sweden, the "German forestry" model, introduced in the early eighteen century (Eliasson & Törnlund, 2018), emphasized clear-cutting and forest cultivation (Lundmark et al., 2013). In contrast, in the north, selective cutting with natural regeneration was preferred (Andersson et al., 2005). In this region, logging focused on large-diameter pine due to its high commercial value, which could offset the high costs of logging in the region's harsh climate and underdeveloped infrastructure (Lundmark et al., 2017). Over time, clear-cutting spread to northern Sweden due to concerns about economic sustainability (Lundmark et al. 2013).

Logging shifted forest composition and fire regimes. In the north, logging reduced old forest trees, and replaced many multi-storied stands with even-aged stands (Ostlund et al., 1997). In the south, deciduous forests were replaced by even-aged stands of spruce or pine (Eliasson & Törnlund, 2018). Fire suppression practices, introduced to protect timber, altered fire regimes and favored spruce (Niklasson & Drakenberg, 2001).

2.4.3. Data sources

2.4.4.1. Historical climate data

We collected summer (June-August) precipitation data for each site based on coordinates, using gridded (0.5° x 0.5°) multi-proxy annual summer precipitation reconstructions (Pauling et al., 2006). Summer precipitation has been identified as a strong predictor of fire in the European boreal zone (Aakala et al. 2018; Drobyshev et al. 2021).

2.4.4.2. Historical fire data

We compiled a dataset of 50 annual fire chronologies available from the archive of the Dendrochronological laboratory of the Swedish University of Agricultural Sciences (SLU) in Alnarp, Sweden (Table SI 2.1, in Supplementary Information, SI). The fire reconstructions relied on dendrochronological dating of fire scars in living trees and dead wood of Scots pine, see Niklasson and Granström (2000) for a comprehensive presentation of the chronology development methods. Data collection took place between 1996 and 2022 and varied greatly in the amount of sampling effort per site, specific scope, and amount of associated metadata. Area of sites varied from 386.56 km^2 to 19 492.25 km^2, each site represented by five to more than a hundred sampling locations (Table SI 2.1). All sites provided frequency data, i.e., annual data on the occurrence of fires.

Although fires on some sites were dated with seasonal resolution, we opted for using annual resolution in all our analyses for the sake of a more homogenous dataset and better comparability of results across time and space.

2.4.4.3. Data on human population dynamics

We utilized population census data recorded at the municipal level (Palm, 2000), spanning from 1571 to the present day. The data featured a non-uniform distribution of census events in time. We addressed the difference between census intervals by interpolation of population data points, designed to fill the largest time gaps in the dataset. We added data points for 1595, 1660, and 1934 to bridge three gaps: the 79-year gap between the censuses of 1620 and 1699, the 68-gap between 1900 and 1968, and the 49-year gap between 1571 and 1620. Following the addition of these new points, the mean interval between population observations became 24.85 (SD: ±8.34) years. For the interpolation, we assumed exponential population growth and used the function `approx()`, part of the R *base* package (R Core Team, 2023).

In cases where our sites were situated in municipalities without available human population data, we assigned to the site the population data from the nearest municipality with an available record. This was the case for six sites, including one in southeastern Norway, which was assigned the human census data of the nearest Swedish municipality.

2.4.4. *Statistical analyses*

2.4.4.1. Pre-treatment of fire data

We pretreated the fire occurrence data using an adjustment algorithm (Drobyshev et al., 2022; Ryzhkova et al., 2020) to address the "fading record problem". This issue arises when the replication at the older parts of the reconstruction gradually declines, compromising comparisons of fire activity along the period covered by the chronology (Swetnam et al. 1999). The adjustment method involved recalibrating the count of recorded fire years by examining the relationship between the number of recorded fire years and the number of locations recording fire for a given site. For the period covering the section of the fire chronology with a declining trend, we assumed that changes in the number of recording locations was the only factor driving variation in the number of fire years among 20-year temporal bins. For each bin, we calculated the ΔS, representing the difference between the maximum number of recording locations over the whole study period and the location replication for a focal time segment. This ΔS was used as an input for a regression, with the number of fire years as the dependent variable:

$$Number\ of\ fire\ years = \beta_0 + \beta_1 \Delta S$$

The regression outcome provided an estimate of the missing fire years, capturing the disparity between expected and observed fire years. The missing years were randomly placed within their respective 20-year segments. This algorithm offered a conservative solution to the fading record problem as it assumed a uniform "process density" throughout the study period. This adjustment procedure was applied to the fire chronologies of 25 sites that had the fading record problem.

2.4.4.2. Binning of data for the historical fire occurrence model

To align the fire, human population density, and climate datasets to the same temporal scale, we implemented a data binning procedure. Our approach involved (a) creating bins of varying lengths reflecting intervals between human population censuses, and (b) applying this binning to the fire and the climate variables' datasets. We calculated the length of each bin as a sum of two periods: (a) half the interval between the focal human population observation and the preceding observation, and (b) half the interval between the focal observation and the subsequent observation. For the earliest human population observation (year 1571), we subtracted half the interval between year 1571 and the subsequent observation to determine "the start year" of the first bin. Conversely, for the most recent observation (1997), we added half of the interval between it and the preceding observation to determine "the end year" of the last bin. This adjustment resulted in the human population chronology extending from 1559 to 2000.

We used these temporal bins to aggregate the fire and the climate data. For the fire occurrence data, we counted the number of fire years for each bin for each site. For the climate data, we averaged the climate values falling in the lowest 25th percentile of the distribution for each bin and each site (see next subsection). For the human population data, we assumed that the population count at the focal year (i.e., the year of census) represented the population for the entire period covered by the respective bin. We then converted the data into population densities using the surface area for the corresponding Swedish municipalities.

2.4.4.3. Historical fire occurrence model

To assess the influence of climatic factors and anthropogenic factors on the historical fire activity (fire occurrence) to test H1 and H2, we used a Generalized Additive Model (GAM) (Hastie and Tibshirani 1987; Wood 2006). Previous studies leveraging GAMs have successfully modeled fires in European forests using charcoal-based records (Feurdean et al., 2020) and contemporary records (Zumbrunnen et al., 2011). GAMs extend the capabilities of Generalized Linear Models (GLMs), allowing for more flexible relationships between the response variable and covariates. Unlike GLMs, GAMs do not assume a predefined form for the relationship between response and predictors, such as linearity (on the link scale). Instead, GAMs use smooth functions to represent the effects of covariates on the response (Hastie and Tibshirani 1987). These smooth functions are parameterized using penalized splines, where the penalties balance the trade-off between maximizing fit to the data and model complexity.

In considering the main covariates of climate and human factors, we used thin plate smooth functions with the default penalty on the second derivative of the spline representing its curvature (Simpson, 2018; Wood, 2003). For the human effect, we used the human population density log-transformed to enhance interpretability and address skewness. For the climate factor, we used Low Summer Precipitation (LSP). We defined LSP as the average of the lowest 25th percentile of the summer precipitation values within each temporal bin. Our selection of the 25th percentile was guided by experimentation with other percentiles, including the 30th and the 10th. Ultimately, we selected the 25th percentile because it had robust explanatory power and included a sufficient number of observations, given the average bin length of 24.85 years.

During the preliminary model development stages, we identified a strong temporal pattern in the data. To address the temporal pattern, we introduced time periods we called subperiods as a categorical unordered factor in the GAM to explore the covariates' effects on the response variable across different time segments. We delineated these subperiods to span approximately 50 years between successive human population census years. As a result, the binned data were segmented into the following subperiods: 1559-1640, 1641-1708, 1709-1765, 1766-1817, 1818-1872, 1873-1951, and 1952-2000.

We addressed both the dependency among observations from the same site and the variability in bin lengths. To account for the nested structure of our data and accommodate for the inherent correlations among observations originating from the same site, we incorporated site-level variability as a random effect in our model. To account for the different bin lengths, we added bin length as an offset argument in the GAM.

We included the coordinates of the sites as covariates to account for spatial patterns. We used a tensor product smoother, which is a smooth function of more than one variable, to capture the interaction effect between latitude and longitude. Despite this covariate having a moderate significance of $p = 0.08$, we retained it in the model, considering the subsequent analyses that evaluated the model's predictive performance. These analyses involved excluding single sites from the training dataset and testing the model on these individual sites (see next subsection). By keeping the coordinates as a covariate, the model remained capable of capturing spatial patterns in the testing data (i.e., data used for model parameterization), even when excluding individual sites. This ensured that the model's predictions were informed by the broader spatial context, facilitating accurate predictions for single sites excluded from the training data.

We used the Poisson error distribution which is well-suited for modelling fire occurrence counts per bin. We used the restricted maximum likelihood (REML) smoothing parameter selection method (Wood, 2011) to estimate model coefficients and smoothing parameters. We fitted the model using the gam() function available in R package *mgcv* (Wood, 2011). Diagnostic information and model fitting were assessed using residual plots generated by the appraise() function from the R package *gratia* (Simpson, 2024).

In summary, the model we built to test H1 and H2 was expressed as follows:

$$fire\ count_{ij} \sim Poisson(\mu_{ij})$$

$$log(\mu_{ij}) = \beta_0 + Site_i + Subperiod_j + s(\log(human\ population\ density_{ij})) + s(low\ summer\ precipitation_{ij}) + log\ (BinLength)$$

Where $fire\ count_{ij}$ is the number of fire years per bin for Site i during subperiod j. $Poisson(\mu_{ij})$ indicates that the fire count at each site and subperiod followed a Poisson distribution with mean μ_{ij}. $log(\mu_{ij})$ is the logarithm of the expected value of the fire count. β_0 is the intercept. $Site_i$ is the random effect for site i. ($Subperiod_j$) is a categorical unordered factor representing different ~50-year time periods. $s(\log(human\ population\ density_{ij}))$ is the smooth function of the log-transformed human population density for each site and for each subperiod, $s(Low\ Summer\ Precipitation_{ij})$ is the smooth function of the LSP for each site and for each subperiod. $log\ (BinLength)$ is the offset term to adjust for the different bin lengths.

2.4.4.4. Model evaluation

To assess the predictive performance of the GAM model, we used h-block cross-validation. This approach involved withholding a randomly selected site from the training dataset used to develop the GAM. This excluded site was then used to test the model and predict fire occurrence. For a robust evaluation, we employed non-parametric bootstrapping, repeating the process 1 000 times. During each iteration, a random site was selected with replacement. This approach generated multiple variations of the GAM-predicted fire occurrence values based on the training data. We compared these predicted fire count values with the observed fire value by performing a linear regression analysis.

2.4.4.5. Onset of the fire-free period in Sweden

To test H3, we examined the variation in the onset of the fire-free period across the network of sites. To this end, we conducted regime shift analyses on the smoothed annual chronology of fire occurrence for each site, using Rodionov's sequential *t*-test algorithm (S. N. Rodionov, 2004). We set the Loess smoothing parameter to 0.15, the moving timeframe (L parameter) to 10 years, the Hubert weight parameter to 1, and the significance value (α) to 0.05. We extracted the year of the last regime shift towards reduced fire activity for each site and mapped these years to evaluate progression of fire suppression in time and space.

2.5. Results

2.5.1. Historical fire occurrence model

The historical fire occurrence GAM explained 72% of the deviance in historical fire occurrence. Both human population density and average low summer precipitation (LSP) had significant effects on the historical fire occurrence with variations across subperiods. The linear regression between predicted and observed fire occurrence indicated a strong correlation ($R^2 = 0.55$) (Table 2.1 and Fig 2.2). The model tended to under-predict the true values for higher fire counts (Fig. 2.2).

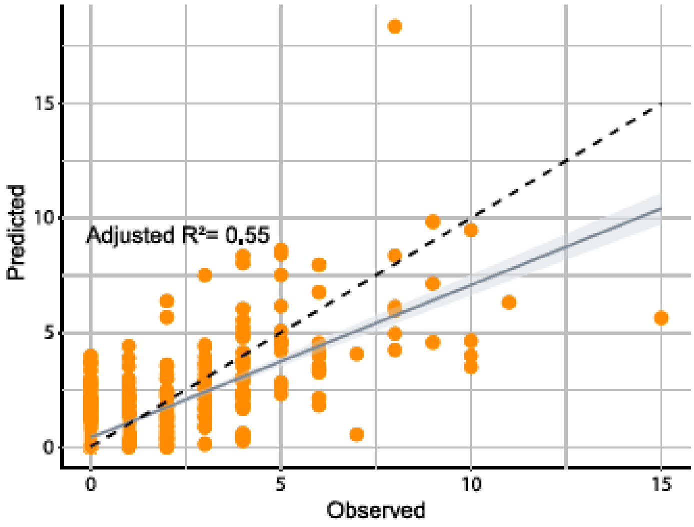

Figure 2.2.
Verification of the GAM model based on comparison of observed and modelled data (H-block cross-verification). The shaded area is the 95% confidence interval. The dashed line represents perfect agreement and the solid line indicates the fitted linear regression.

Tableau 2.1.
Statistical details of the linear regression model of the fire counts predicted by the generalized additive model (GAM) of historical fire occurence based on the observed fire data. Std. Error is the standard errors.

Predictor	Coefficient	Std. Error	t-value	*p*-value
(Intercept)	0.41	0.06	7.28	< 0.0001
Fire observation	0.67	0.02	27.11	< 0.0001

Adjusted R-squared: 0.55

F-statistic: 734.8 on 1 and 600 degrees of freedom, p-value < 0.0001

Human population density had a significant ($p < 0.001$) effect on fire occurrence across five of the seven subperiods examined (Table 2.2 and Fig. 2.3): 1559-1640, 1709-1765, 1766-1817, 1818-1872, and 1873-1951. An additional visualization of the human population density's effect on fire occurrence with the y-axis back-transformed to its original scale is provided in Supplementary Information (Fig. SI 2.1).

Tableau 2.2.
Summary of the significant smooth terms for the main covariates, log-transformed human population density and summer precipitation during LSPY (low summer precipitation years) during different subperiods. Edf and Ref. edf are the estimated and reference degrees of freedom, respectively. Chi-sq is the chi-square statistics.

Subperiod	Covariate	edf	Ref. edf	Chi-sq	p
1559-1640	Low summer precipitation	2.15	2.66	1.60	0.49
	Log(Population density)	2.67	3.23	11.89	0.01
1641-1708	Low summer precipitation	2.06	2.57	1.76	0.42
	Log(Population density)	1.00	1.00	1.73	0.19
1709-1765	Low summer precipitation	1.08	1.15	0.58	0.53
	Log(Population density)	3.28	4.00	13.12	0.01
1766-1817	Low summer precipitation	2.85	3.58	11.29	0.01
	Log(Population density)	3.53	4.33	41.13	< 0.001
1818-1872	Low summer precipitation	2.89	3.62	21.36	< 0.001
	Log(Population density)	4.28	5.03	56.35	< 0.001
1873-1951	Low summer precipitation	2.44	3.09	16.82	0.001
	Log(Population density)	3.02	3.77	23.68	< 0.001
1952-2000	Low summer precipitation	1.53	1.90	0.61	0.76
	Log(Population density)	3.38	4.07	6.36	0.16

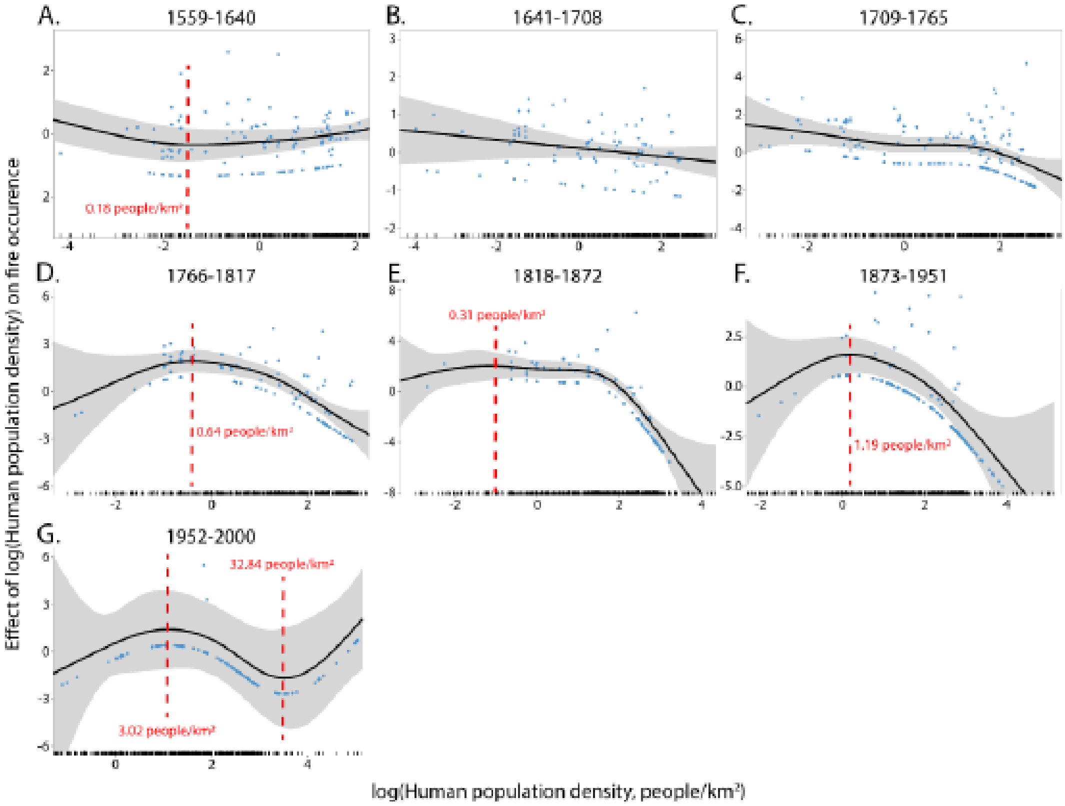

Figure 2.3.
Partial effects of log(human population density) on fire occurrence during different ~50-year subperiods. Note that the y-axis is in the log scale as the GAM used a Poisson distribution with a log-link function. Population density had a significant effect on fire occurrence for subperiods: 1559-1640 (A), 1709-1765 (C), 1766-1817 (D), 1818-1872 (E), and 1873-1951 (F). The red dashed lines mark population densities associated with changes in the partial effects, i.e., changes in the direction of the effect, with the corresponding human population density in the original scale (people/km^2). The gray shaded areas are the estimated 95% confidence intervals. The small vertical lines along the x-axis show the distribution of data points along the gradient of log(human population density).

For the earliest subperiod (1559-1640), the estimated partial effect of population density was negative at the lowest end of the gradient and became positive beyond 0.18 people/km2 (-3.14 in the log scale) (Fig. 2.3A). However, data were sparse at the lowest end of the population density distribution, where the negative effect was observed, leading to high uncertainty for this trend. In contrast, the positive effect at higher population densities was supported by more data, lending greater credibility to this trend.

For the subsequent two subperiod 1641-1708 and 1709-1765, the partial effect of population density on fire occurrence was negative (Fig. 2.3B, 2.3C). For 1641-1708, the negative effect on fire occurrence was linear but was not statistically significant (Table 2.2). For subperiod 1709-1765, the negative effect became more pronounced at higher population densities, i.e., the downward slope became steeper (Fig. 2.3C).

For the subperiods between 1766 and 1951, the relationship between population density and fire occurrence followed a consistent pattern: the effect was positive at low population densities and became negative beyond a threshold, which varied by subperiod. Specifically, the effect transitioned from positive to negative at approximately 0.64 people/km² (-0.45 on the log scale) for 1766–1817 (Fig. 2.3D), 0.31 people/km² (-1.17 on the log scale) for 1818–1872 (Fig. 2.3E), and 1.19 people/km² (0.17 on the log scale) for 1873–1951 (Fig. 2.3F). However, data were sparse at the lowest population densities, where the effect was positive, and at the thresholds, leading to greater uncertainty.

During the most recent subperiod (1952-2000), population density followed a similar pattern to the subperiods between 1766 and 1951 (described above), with a positive effect on fire occurrence at low densities, followed by a negative effect beyond a threshold of approximately 3.02 people/km2 (1.11 on the log scale). However, the effect reached a trough at approximately 32.84 people/km2 (3.49 in the log scale), beyond which it became positive again (Fig. 2.3G). This effect was not significant (Table 2.2).

2.5.2. Effect of low summer precipitation on fire occurrence

For the three earliest oldest subperiods between 1559 and 1765 (1559-1640, 1641-1708, and 1709-1765), summer precipitation had no significant effect on fire occurrence (Table 2.2), and the trend lines remained flat close to zero (Fig. 2.4A, 2.4B, 2.4C). An additional visualization of the Low Summer Precipitation's effect on fire occurrence with the y-axis back-transformed to its original scale is provided in Supplementary Information (Fig. SI 2.2).

For the three subsequent subperiods between 1766 and 1951, summer precipitation had a significant ($p > 0.01$, Table 2.2) negative effect on fire occurrence as indicated by downward-slope trend lines (Fig. 2.4D, 2.4E, 2.4F).

For the most recent subperiod 1952-2000, summer precipitation had a negative effect on fire occurrence, as indicated by a generally downward slopping trend line (Fig. 2.4G), however, the effect was not significant (Table 2.2).

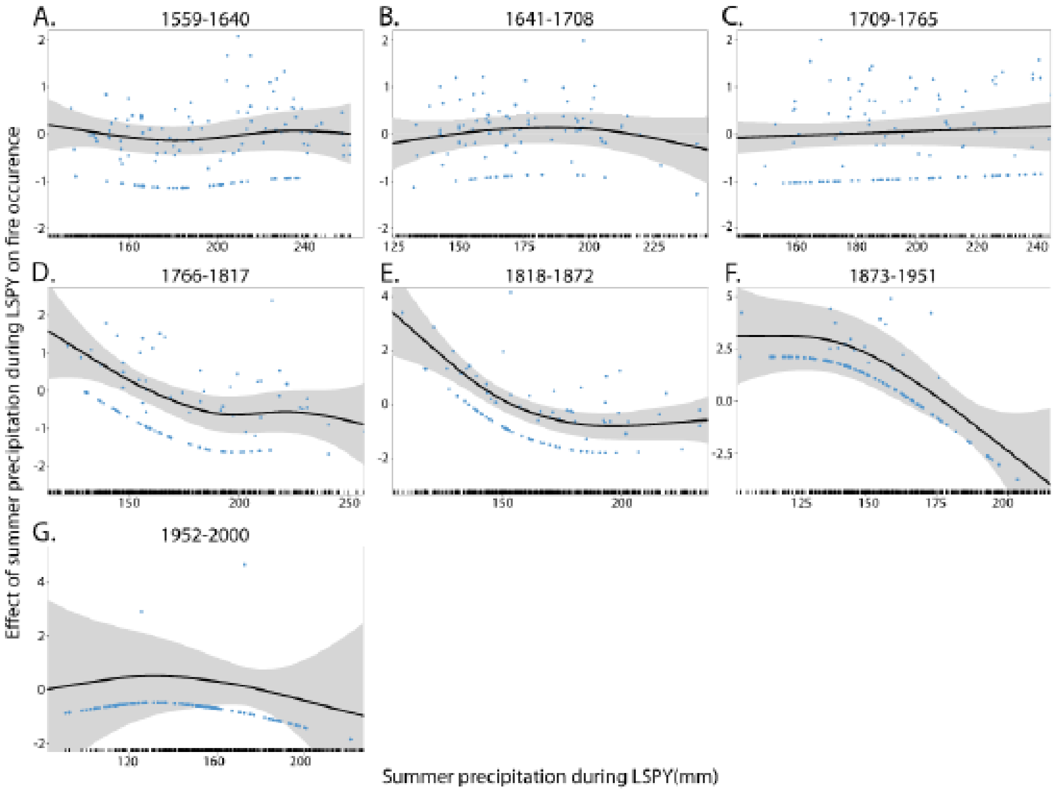

Figure 2.4.
Partial effects of LSP (low summer precipitation) on fire occurrence during different ~50-year subperiods. LSP had a significant effect on fire occurrence for subperiods 1766-1817 (D), 1818-1872 (E), and 1873-1951 (F), while its effect on the other subperiods (plots A, B, C, and G) was not significant. The gray shaded areas are the estimated 95% confidence intervals. The small vertical lines along the x-axis indicate distribution of data point along the precipitation gradient.

2.5.3. Spatial patterns and onset of the fire-free period in Sweden

Geographical position of the study locations influenced fire occurrence at a significance level of $p = 0.08$. Increase in latitude was associated with lower fire occurrence while the longitude effect was less clear (Fig. 2.5).

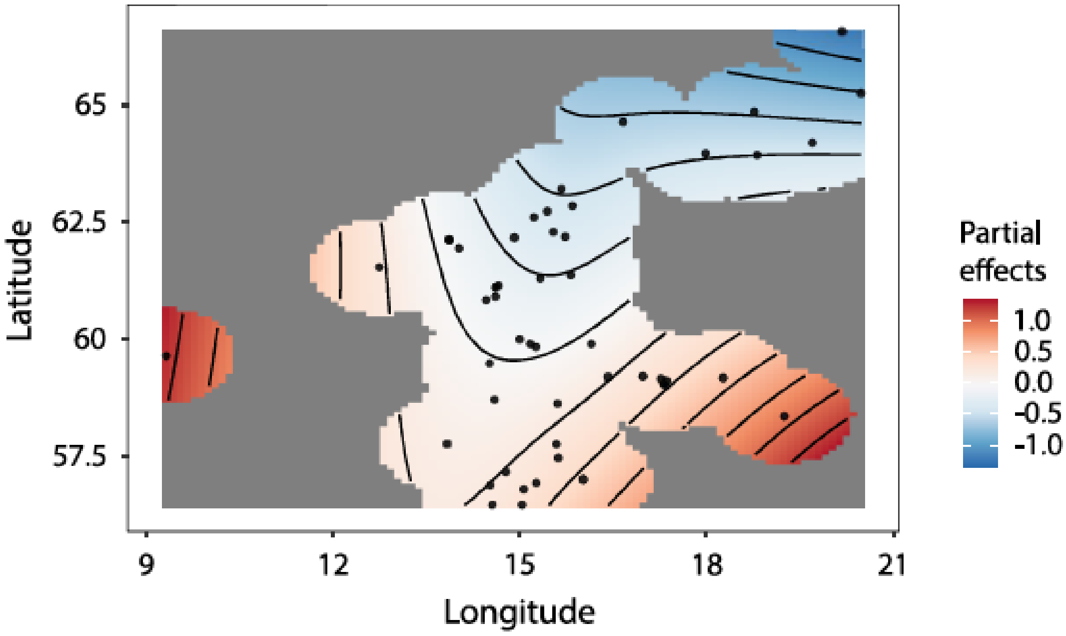

Figure 2.5.
Partial effect of the geographical coordinates on historical fire occurrence.

The most recently observed fire regime shift marked a transition towards the lowest level of fire activity throughout the entire chronology for most sites (n = 45) (Fig. SI 2.3). Southern sites showed an earlier onset of the fire free period than northern sites (Fig. 2.5). Notably, around latitude 60° N, a transition point emerged, with southern sites (n = 25) experiencing the onset of the fire-free period between 1660 and 1860 (mean and SD: 1752 ± 62 years), and northern sites between 1730 and 2000 (1868 ± 59 years). Within the southern sites, those near the capital, Stockholm, showed the earliest onset of the fire-free period.

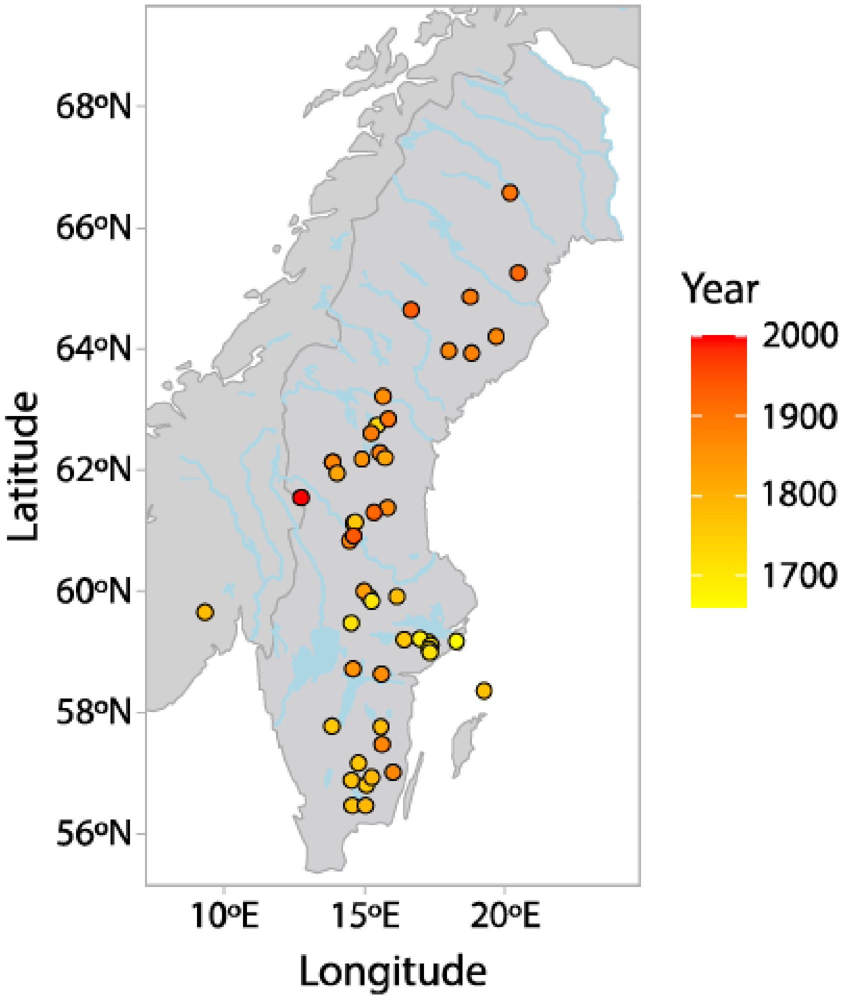

Figure 2.6.
Onset of fire suppression across the network of studied dendrochronological reconstructions. Color of the circles reflect the onset of the fire suppression as assessed through Rodionov's regime shift analysis (2004) on the fire occurrence data for each site.

2.6. Discussion

Relying on the largest synthesis of dendrochronologically reconstructed fire histories in boreal Europe, we quantified the complex interplay between anthropogenic and climatic drivers shaping historical fire occurrence in Sweden. Although both summer precipitation and human population density significantly affected fire occurrence, their influences were subperiod-dependent. In general, human population density positively influenced fire activity at low densities, but beyond population density thresholds of around 0.64, 0.31, and 1.19 people/km^2, the effect became negative (Fig. 2.3). These thresholds were of similar magnitudes across the different subperiods, supporting H1. Increasing levels of Low Summer Precipitation (LSP) had a negative impact on fire occurrence. Significant summer precipitation effects were observed in both early (1766-1817) and more recent (1873-1951) subperiods, but not in the earliest subperiods analyzed (those between 1559 to 1765). This result did not support the idea that the relative role of climate in controlling fire activity progressively declined over the study period (H2). Instead, it highlights that climate has remained an important driver of fire activity even during recent subperiods characterized by significant human effect on fire. This underscored the robustness of our methodology in capturing the combined effect of both fire drivers. We documented a strong south-to-north gradient in the onset of the fire-free period, reflecting the earlier introduction of forestry and fire suppression practices in the south, supporting H3. Despite the earlier fire suppression onset in the south, our historical fire occurrence model showed higher fire activity in the south, reflecting more favorable climatic conditions and more anthropogenic ignitions. In contrast, fires in the north are fewer, but burn larger areas, illustrating the spatial complexity of fire regimes that our model did not fully capture as it focused exclusively on fire occurrence. Nonetheless, our study represents an advancement in the quantitative assessment of the drivers of fire activity over long temporal scales.

The partial effect of human population density on fire occurrence showed an inverted U-pattern between 1766 and 1951 (Fig. 2.3D, 2.3E, 2.3F). Population density had a positive effect on fire occurrence, but this effect plateaued and became negative beyond population densities of approximately 0.64 people/km^2 (for 1766-1817), 0.31 people/km^2 (1818-1872), and 1.19 people/km^2 (1873-1951). This phase-shifting pattern reflected the two primary ways in which the human influence manifests on fire occurrence: (1) by increasing fire ignitions and (2) by decreasing ignitions and suppressing fires (Granström & Niklasson, 2008). As human population density increased, initial settlement activities increased fire ignitions (Drobyshev et al., 2024). However, as human population grew and technology advanced (particularly in agricultural productivity), fire activity decreased due to abandonment of agricultural burnings and the expansion of settlements and road network that reduced fuel availability and increased forests fragmentation. Fire suppression further augmented this trend. This pattern aligns with our results for subperiods between 1766 and 1951 showing an inverted U-trend, and supports the notion that both intense human activity and the near absence of humans are associated with fewer fires, with the effect of human population density on fire reaching a peak at intermediate population densities (Syphard et al., 2007). However, it is important to note that this pattern may not occur in other contexts. For example, in the boreal forests of northeastern North America, increasing population densities did not show a negative effect on burned areas and fire suppression did not reduce burned areas (Danneyrolles, Cyr, et al., 2021).

Remarkably, the thresholds in human population density affecting fire activity, documented by this study, align closely to a previously reported. The threshold below which population density had an increasingly positive effect on fire activity varied across the three subperiods that exhibited this stage (1766-1817, 1818-1872 and 1873-1951), but remained within a similar magnitude: 0.64, 0.31 and 1.19 people/km^2. These thresholds are very similar to the one reported by Guyette et al.'s (2002) of 0.64 people/km^2. Although there is considerable uncertainty around the thresholds reported by this study and Guyette et al.'s (2002) and they are merely indicative of the order of magnitude, similarities are notable considering the major differences in spatiotemporal scale and methodologies.

The maximum positive partial effect occurred at a higher population density for 1873-1951, 1.46 people/km^2, compared to 0.31 and 0.64 people/km^2 for earlier subperiods (1818-1872 and 1766-1817, respectively). This increase may reflect significant demographic and socio-economic transformations in Sweden between 1873 and 1951. During the 1870s, Sweden experienced a declining rural population, which was in part due to the crop failures in 1868 and 1869 that caused substantial emigration during the subsequent six decades (Widgren & Pedersen, 2011). During the late 1800s, Sweden also transitioned from an agrarian society to an industrial nation (Widgren & Pedersen, 2011). Migration of the population away from rural areas towards urban centers likely reduced human ignitions, increasing the population density threshold required to sustain fire activity in the landscape.

Some subperiods did not exhibit the inverted U-shaped pattern in the pattern in the relationship between population density and fire occurrence. For the earliest subperiod 1559-1640 (Fig. 2.3A), the effect of population density displayed a U-shaped trend. However, there were fewer data points at the lowest end of the population density gradient, which introduces uncertainty in interpreting the negative effect observed in this range. In contrast, the segment of the trend representing an increasing positive effect had a greater number of data points, lending more credibility to this part of the trend. The increasing positive effect highlights the role of land-use practices involving fire (e.g., slash-and-burn cultivation and charcoal production) that made humans positive net contributors to the total pool of effective ignitions.

The effect of population density on fire occurrence for subperiods 1641-1708 and 1709-1765, was negative (Fig. 2.3B, 2.3C), although it was not significant for period 1641-1708 (Table 2.2). The negative effect suggests that the typical inverted U-shaped relationship between human population density and fire occurrence can vary, highlighting a context-dependent nature of this dynamic.

We identified a significant climatic influence on historical fire occurrence between 1766 and 1951 (Table 2.2), a period marked by a strong anthropogenic influence on fire activity. Increasing summer precipitation had a negative effect on fire occurence. This has also been documented at both annual and decadal scales with Finnish data (Aakala et al. 2018). In contrast to Aakala et al. (2018) that focused on large fire years (LFYs), our study demonstrated this effect by operating on complete fire chronologies (i.e., not only LFYs). This result highlighted the importance of precipitation variability as a key control of fire occurrence even outside periods marked by severe climatic anomalies. Earlier research has linked summer drought and historical fire activity in European boreal forests, although these studies did not isolate climatic factors from human impacts within a unified quantitative framework (Pinto et al. 2020; Ryzhkova et al. 2020; Drobyshev et al. 2021; Ryzhkova et al. 2022).

While LSP significantly influenced fire occurrence during 1766 to 1951, it did not emerge as a significant predictor for the earliest subperiods, from 1559 to 1765, contradicting H2. Initially, we had anticipated a stronger climate signal in the oldest period due to lower population densities and technological limitations, which potentially could allow climate to exert a greater influence on fire occurrence. At least three factors could explain the lack of significance in these early subperiods. First, the reduced reliability of the precipitation reconstruction for these earlier periods might have played a role. Uncertainty of the reconstruction is markedly higher between 1500 to 1750 compared to later years (Pauling et al., 2006). Second, the methodology we employed could have played a role. By using complete fire chronologies aggregated at an above-annual scale, our analysis may have been less sensitive to detecting climatic effects, compared to previous studies focused on LFYs, which are strongly climate-driven (Aakala et al., 2018; Drobyshev et al., 2015; Falk et al., 2011; Robles et al., 2024). Indeed, LFYs from 1500s to 1900s in northern Sweden (> 60° N) have been associated with positive summer temperatures and negative precipitation anomalies (Drobyshev et al., 2014). Finally, the broader climatic context of the 1600s, the coldest period of the LIA, may have played a role. The LIA was associated with very dry and sunny conditions with clear skies (Gagen et al., 2011; G. H. F. Young et al., 2012), which enhanced fire risk (Drobyshev et al., 2015). In this highly fire-prone climatic context of the 1600s, the influence of extreme low summer precipitation on fire activity may have been diminished, as conditions were already conducive to fire. Our protocol that averaged the lowest 25th percentile of summer precipitation for each ~ 25-year bin, might have reduced the sensitivity of the analysis, as fire occurrence during these fire-prone period could have been common even outside of extreme precipitation anomalies.

Two subperiods (1641-1708 and 1952-2000) in our analysis stand out for lacking significant effects from either one of the two main covariates. For 1641-1708, the lack of a discernible climatic or anthropogenic effect may be attributed to the unique climatic and sociopolitical conditions during this time. Climatically, the 1600s were the coldest part of the LIA, which, as discussed earlier, could have reduced the sensitivity of our protocol. Sociopolitically, this subperiod coincided with war, agricultural crisis, and depopulation which likely disrupted anthropogenic fires. This period coincided with Sweden's military involvement in The Thirty Years' War (1618-1648), which began in 1630 (Davis, 2017). The annual conscripting of adult male peasants could have impacted agricultural production (Stoffel et al., 2022), diminishing agricultural burnings. The 1641-1708 subperiod also coincided with agricultural crises triggered by volcanism-caused cooling (D'Arrigo et al., 2020). Crop failure in 1641 led to increased grain prices, impoverishment, famine, migration, epidemic diseases, and failing birth rates in Sweden (Huhtamaa & Helama, 2017; Stoffel et al., 2022). Southern Sweden, in particular, suffered from hunger-related diseases such as typhoid fever and typhus (Stoffel et al., 2022). This period culminated in the Great Famine of 1695-1697, marked by impoverishment, epidemics, and high mortality rates (Lappalainen, 2014). The combined effects of war, famine, and depopulation likely diminished human-driven fire activity, thereby decoupling dynamics of human population upon fire occurrence.

On the other hand, for the most recent subperiod, 1952-2000, our GAM did not detect a significant LSP or population density effect probably due to minimal fire incidents to operate on. Nonetheless, the drastic decline in fire occurrence was a result of human land-use practices, specifically, effective fire suppression (Niklasson & Granström, 2000; Ryzhkova et al., 2020; Wallenius, 2011). Climate could have contributed to the decline of fire occurrences since there were less fire-prone conditions in Scandinavia after the LIA (Drobyshev et al., 2016). A less fire-prone climate after the end of the LIA, accompanied by a drastic decrease in fire activity, has also been reported for eastern North America (Bergeron et al. 2001; Martin P Girardin et al. 2006; Chavardès et al. 2022). Despite low fire activity in the 1900s, mid-tropospheric ridging, large-scale atmospheric circulation patterns, and drought, have been associated to twentieth-century observational fire records (Drobyshev et al., 2021; Drobyshev, Niklasson, et al., 2012).

We observed a modest (p = 0.08) influence from geographical coordinates on historical fire occurrence in the GAM. Lower latitudes (< 60° N) exhibited a positive effect on fire activity, while higher latitudes (> 60° N) had a negative effect (Fig. 2.5). This spatial pattern likely reflected climate variability and historical land-use differences across Sweden. Southern Sweden features a higher density of lightning ignitions (Granström, 1993) and a longer fire season (Drobyshev, Niklasson, et al., 2012; Wastenson et al., 1995). Southern Sweden is also more densely populated, increasing the potential for human ignitions. Southern Sweden experienced a more pronounced anthropogenic influence earlier in time, whereas the human impact in the north remained relatively limited until the nineteenth century, with the arrival of industrial logging (Östlund and Norstedt 2021). Even though higher infrastructure density in the south is associated with more fragmented forests, it could contribute to more fire activity as forest fragmentation increases human access and anthropogenic ignition potential (Pinto, Rousseu, et al. 2020)

The onset of the fire-free period occurred one to two centuries earlier in southern (< 60° N) Sweden than in its northern part, with onset years ranging from 1660 to 1860 in the south, and from 1730 to 2000 in the north (Fig. 2.6). This gradient aligns with historical land-use transitions, particularly the shift from traditional livelihoods reliant on frequent fires to modern agriculture and the introduction of forestry, which introduced fire suppression measures to protect timber sources (Wallenius, 2011). Forestry began in the eighteenth century in the southern Sweden (Eliasson & Törnlund, 2018). The timber industry then expanded northward in response to growing demand for coniferous timber, leading to the introduction of commercial forestry in northern Sweden in the early nineteenth century (Östlund, 1995). This progression accounts for the earlier onset of the fire-free period in the south compared to the north.

Notably, the earliest onset years in southern Sweden occurred in sites near the capital, Stockholm, highlighting the importance of proximity to administrative centers for forest management and resource access. The higher human population densities in sites close to the capital and in southern Sweden in general are associated to denser road networks, which could improve fire suppression capabilities (Pinto et al. 2020). However, the effectiveness of fire suppression may vary in other contexts. For example, fire suppression in eastern Canadian boreal forests did not lead to a decrease in area burned (Danneyrolles, Cyr, et al., 2021).

The observed spatial gradient in the initiation of the fire-free period did not align with the effect of the coordinates on fire occurrence captured by our GAM (Fig. 2.5). In the most recent subperiods analyzed in our GAM, fire occurrence data primarily corresponded to northern sites, where fire suppression was implemented later in time compared to the south. Consequently, a positive effect of latitude on fire activity was expected for these most recent subperiods. However, the higher latitudes had a negative association with fire occurrence whereas lower latitudes had a positive association with fire occurrence (Fig. 2.5). We did not observe the expected positive latitude effect, which would have been possibly apparent only in the most recent subperiods, since we opted not to analyze the partial effect of geographic coordinates across different subperiods to maintain model parsimony. Additionally, although fire occurrence observations during the most recent subperiods were predominantly from northern sites, the fire regime in northern Sweden is characterized by fewer fire occurrences but larger burned areas compared to the south (Niklasson & Granström, 2000). Thus, the most recent subperiods may have featured a low number of fires in northern regions, but large burned areas, suggesting that a positive latitudinal effect could have been apparent in terms of area burned rather than fire occurrence. However, our model did not detect this effect since it solely focused on fire occurrence and did not analyze area burned.

Our quantitative assessment of historical fire occurrence in Sweden over the past 500 years demonstrates the significant roles of both human population density and summer precipitation in shaping fire activity. The non-monotonic relationship between population density and fire highlights the importance of understanding regional socio-economic transformations and their effects on fire regimes. The persistent effect of summer precipitation highlights the resilience of climate as a key driver of fire dynamics, even amid growing human interventions. As future climate change is expected to increase fire risk (Lehtonen et al., 2016; Yang et al., 2015), quantitative understanding of the fire activity drivers across long temporal scales remains essential for guiding management strategies.

2.7. Acknowledgments

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3 - CHAPTER 3: 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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3.1. Résumé

La composition de la végétation des forêts de du nord-est de l'Amérique du Nord a subi des changements significatifs depuis les périodes précoloniales, avec une réduction marquée des peuplements dominés par les conifères ainsi que de la diversité taxonomique et fonctionnelle. Ces changements ont été attribués aux modifications du régime des feux, à l'exploitation forestière et aux changements climatiques. Dans cette étude, nous avons dissocié les effets individuels de ces facteurs sur la composition forestière du sud-ouest du Québec entre 1830 et 2000, en menant une modélisation rétrospective à l'aide du modèle de simulation des paysages forestiers LANDIS-II. Le modèle a été exécuté en se basant sur des reconstructions de la composition forestière précoloniale, des historiques de feux, des archives historiques de récolte de bois et des données de réanalyse climatique.

Nos résultats ont indiqué que l'exploitation forestière a eu le plus grand impact sur la dynamique des forêts au cours des derniers siècles. En l'absence d'exploitation forestière, les abondances des espèces précoloniales étaient en grande partie maintenues, préservant ainsi des traits fonctionnels clés tels que la tolérance au feu et à l'ombre, qui contribuent à la résilience des écosystèmes. L'augmentation de l'activité des feux a favorisé l'accroissement des espèces pionnières comme le peuplier faux-tremble (*Populus tremuloides* Michx.), mais c'est l'exploitation forestière qui a joué le rôle dominant. L'exclusion des feux n'a eu aucune influence sur la composition de la végétation, suggérant que le processus de mesophication se déroule sur des échelles de temps plus longues que celles capturées dans cette étude. Les impacts des changements climatiques sur la dynamique des peuplements ont eu un effet mineur sur les changements de végétation, car l'augmentation des précipitations a peut-être atténué les effets néfastes de la hausse des températures. Cependant, les changements climatiques futurs devraient devenir un facteur plus significatif dans la composition forestière. Ces résultats soulignent l'importance de la restauration forestière et de la poursuite des recherches sur la dynamique passée des forêts pour mieux comprendre les changements actuels et futurs, afin d'orienter les stratégies de gestion.

Mots-clés : changement de composition de la végétation, composition pré-colonisation, nord-est de l'Amérique du Nord, changement climatique, récolte de bois, modification du régime des feux, période de colonisation, période d'exclusion des feux.

Abstract

The vegetation composition of northeastern North American forests has significantly changed since pre-settlement times, with a marked reduction in conifer-dominated stands and taxonomic and functional diversity. These changes have been attributed to fire regime shifts, logging, and climate change. 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. 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 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* Michx.), 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: vegetation composition change, pre-settlement composition, northeastern North America, climate change, timber harvesting, fire regime shift, settlement era, fire exclusion era.

3.2. 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 (B. N. Shuman et al., 2009), causing rapid shifts in vegetation composition (B. Shuman et al., 2004; Williams et al., 2002; Z. 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 & White, 1985; White & Jentsch, 2001). Forests often exhibit resilience to natural disturbance regimes (Johnstone et al., 2016) due to adaptive traits shaped by long-term exposure (Keeley et al., 2011; Sousa, 1984). 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 & 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 (Danneyrolles et al., 2019; Ojima et al., 1994; Seidl et al., 2017; Thom et al., 2018).

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 (L. 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.) (Danneyrolles et al., 2016a; Dupuis et al., 2011; Friedman

& Reich, 2005; Schulte et al., 2007; Terrail et al., 2019). These shifts contributed to the homogenization of taxonomic and functional diversity (Danneyrolles, Vellend, et al., 2021; Dupuis et al., 2011; Hanberry et al., 2012; Jackson et al., 2000; Schulte et al., 2007).

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., 2008b). Low- to moderate-severity fires created conditions essential for pine regeneration by reducing the soil organic layer (Nyamai et al. 2014; Stambaugh et al. 2019), 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. 2019). 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 (Stambaugh et al., 2018; Terrail et al., 2020; Weir & Johnson, 1998). 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 (Cardil et al., 2019; Gauthier et al., 2008; Lauzon et al., 2007).

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 & 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 (M.-P. 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 (Chavardès et al., 2022; Drobyshev et al., 2017). 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 & 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 (Archambault et al., 2009; Kenefic et al., 2005). 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 & Nowacki, 2015; Brice et al., 2019, 2020; Danneyrolles et al., 2019; Liang et al., 2018, 2023; Nowacki & Abrams, 2015). 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.

3.3. Methods

3.4.1. Study area

The study area extended over 1 300 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 (J.-L. Brown, 1981; Vincent & Hardy, 1977). 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.

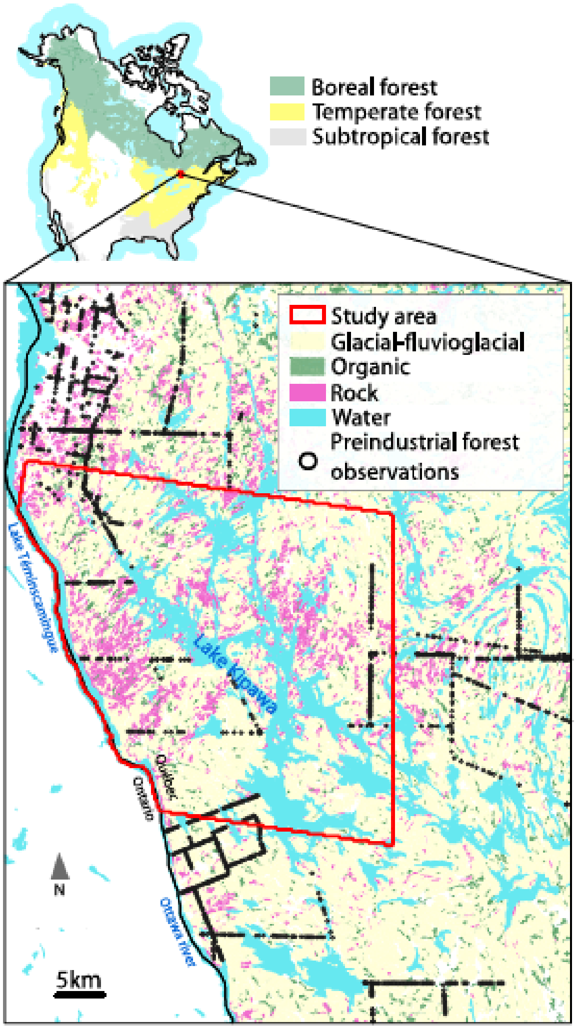

Figure 3.1.
Pre-industrial species lists point observations (black circles and lines, N = 1 474) located within our study area (perimeter shown as red-outlined polygon) and within a 20 km buffer area surrounding the study area that we used to populate our initial vegetation landscape raster based on the surface deposit class.

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 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 & Royall, 1995; Munoz & Gajewski, 2010). However, this perspective has been a subject of debate among other scholars (Campbell & McAndrews, 1995; Danneyrolles et al., 2016a; Munoz et al., 2014).

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-20th 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).

3.4.2. Data

3.4.2.1. 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 reanalysis 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.

3.4.2.2. 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 1 474 of these georeferenced pre-settlement vegetation plots located both within our study area and within a 20 km buffer surrounding it (Fig. 3.1).

3.4.2.3. 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 significantly longer, at > 3 000 years (Boulanger et al., 2014).

3.4.2.4. 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 3.1. Detailed descriptions of timber harvest data processing, including diameter limits, volume conversions, and assumptions made are provided in SI 3.1.

Tableau 3.1.
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	

3.4.3. 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.

LANDIS-II has been used extensively to study the effect of disturbances and their interactions on the vegetation composition under climate change (Lucash et al., 2018; Molina et al., 2021, 2022). However, only a few studies have used it for retrospective analyses (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.

3.4.3.1. Model parameterization

Our study area was represented as a grid of 20 800 cells, each with an area of 6.25 ha (250 x 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: fluvioglacial and glacial (11 257 cells), organic (769), and rock (2 961). The remaining 5 723 cells were water (Table 3.2.). We ran the simulations in 10-year time steps.

Tableau 3.2.
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	No. cells	Surface Deposit	Altitude (in meters)			Slope (in degrees)		
			Range	Mean	SD	Range	Mean	SD
1	11257	Fluvio-glacial 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						

3.4.3.2. 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 = 1 474) (Fig. 3.1, subsection *Forest composition data* 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 1 000 years using the Base Fire extension of LANDIS-II (H. S. He & 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 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 *2.2.1 Climate data* subsection above) and kept these conditions constant for the whole duration of the spin-off simulation.

3.4.3.3. Climate change impacts on stand-level forest dynamic

To account for climate change impacts on stand-level forest dynamic from the pre-settlement to the present time, we used the Biomass Succession extension for LANDIS-II (Scheller & 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 & 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 & 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, maxANPP, and maxAGB were extracted from these simulations following (Boulanger et al., 2017).

3.4.3.4. Fire regime shifts

We simulated changes in fire regime using the Base Fire extension (H. S. He & 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 subsection *2.2.3. Fire regime data* above) at ±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.

3.4.3.5. 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 pixels 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 pixels sampled, we determined the number of harvestable pixels equivalent to the harvested biomass and the percentage of affected pixels 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 pixel (6.25 ha).
In simulating historical timber harvesting, we did not include plantations, fertilization, thinning, or other forms of intensive forest management.

3.4.3.6. 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 & 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 & He, 1999) to simulate wind events with a recurrence interval of 2 500 years.

3.4.4. Modelling scenarios

We modelled six scenarios, all spanning from 1830 to 2000 (Fig. 3.2) 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 subsection *3.4.5. Analysis* 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.
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.

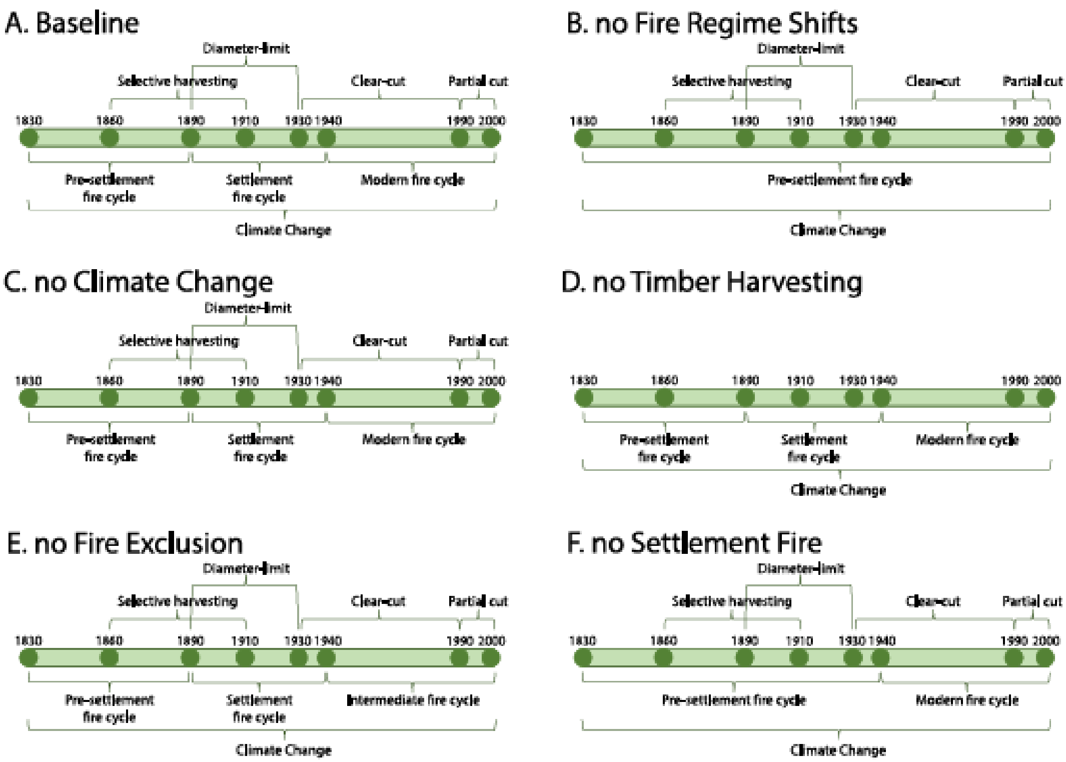

Figure 3.2.
Timeline of all scenarios simulated: (A.) Baseline scenario (BL) that included all disturbances that historically affected the landscape, (B.) Succession without Fire Regime Shifts scenario (noFRS), (C.) Succession without Climate Change scenario (noCC), (D.) Succession without Timber Harvesting scenario (noTH), (E.) Succession without Fire Exclusion scenario (noFE), (F.) Succession without Settlement Fire scenario (noSF).

3.4.5. 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).

3.4. Results

3.5.1. 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 3.3). The model overestimated aspen biomass while underestimating yellow birch.

Tableau 3.3.
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

3.5.2. 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. 3.3, Table 3.4). 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. 3.3). Red maple's relative abundance increased from ~ 3% to 13%, and its cumulative abundance from 2 to 8 tons/ha (Fig. 3.3). Paper birch's relative abundance increased from ~ 3% to 8%, and its cumulative abundance from 3 to 5 tons/ha (Fig. 3.3).

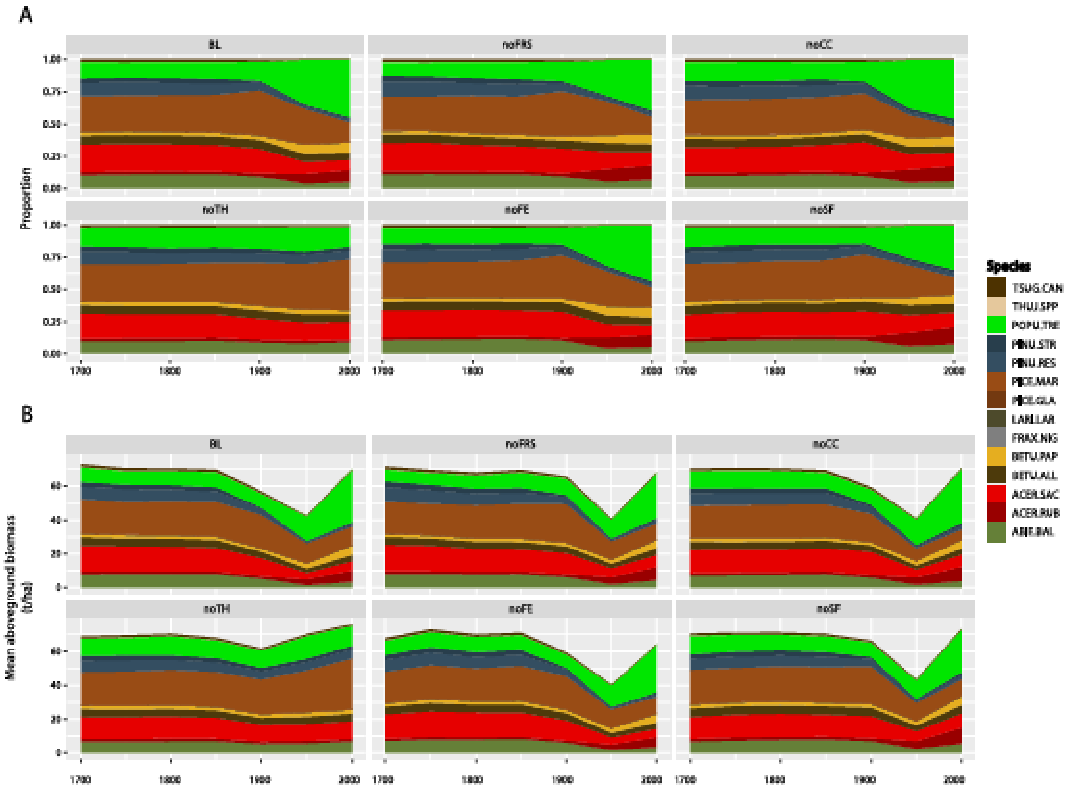

Figure 3.3.
(A) Relative abundance of each species over time and (B) Cumulative biomass over time under the baseline scenario (BL) and each of the counterfactual scenarios: Without Fire Regime Shifts scenario (noFRS), Without Climate Change scenario (noCC), WithoutTimber Harvesting scenario (noTH), Without Fire Exclusion scenario (noFE), Without Settlement Fire scenario (noSF).

Tableau 3.4.
Comparison of composition changes per species in the baseline scenario of this study and those reported by (Danneyrolles et al., 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%		

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. 3.3). 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. 3.3). 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. 3.3). 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. 3.3).

3.5.3. 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. 3.4). Unlike the BL and the other counterfactual scenarios, the noTH showed relatively stable species abundance over time (Fig. 3.3). 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. 3.3). 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. 3.3). 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. 3.3A). 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. 3.3B).

3.5.4. 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. 3.4). 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. 3.4). Similarly, the noFRS, controlling for fire regime shifts, showed an increase in R^2 beginning in 1900 reaching 0.30 by 2000 (Fig. 3.4). 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. 3.3).

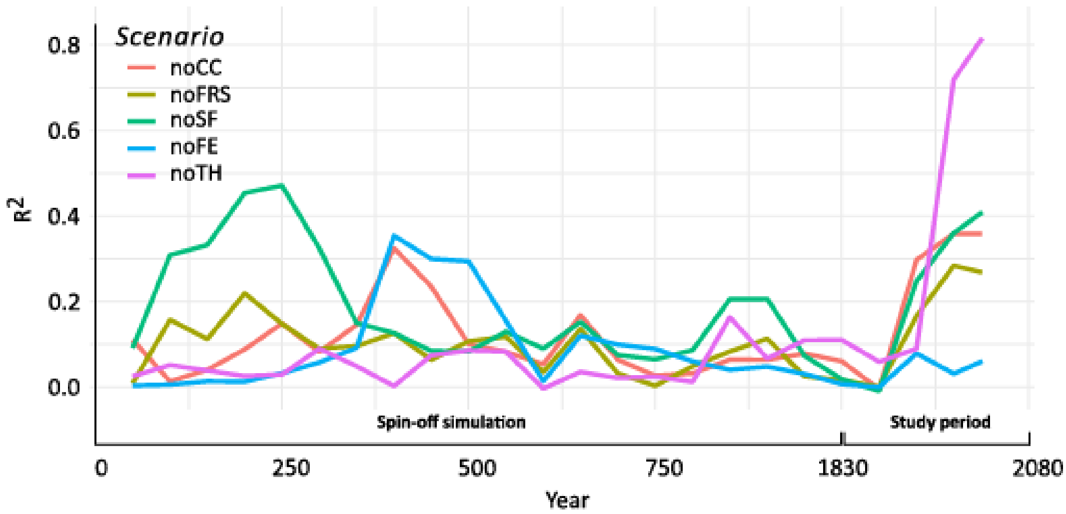

Figure 3.4.
PERMANOVA of the forest composition matrices between the historical baseline scenario (BL) and each of the counterfactual scenarios: Without Fire Regime Shifts scenario (noFRS), Without Climate Change scenario (noCC), Without Timber Harvesting scenario (noTH), Without Fire Exclusion scenario (noFE), Without Settlement Fire scenario (noSF). Shown is the spin-off simulation of 1000 years followed but our study period (1830-2000).

3.5.5. 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. 3.4). The overall evolution of species composition under the noCC closely resembled that of the BL. However, the decline in black spruce observed under the BL was slightly more pronounced under the noCC.

3.5. 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 (Danneyrolles et al., 2016a; Jackson et al., 2000), 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 vegetation composition shifts, 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 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 (Danneyrolles et al., 2016a; Dupuis et al., 2011; Friedman & Reich, 2005; Schulte et al., 2007; 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.

3.6.1. 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. 3.3, Table 3.4). In general, these results were consistent with previous studies of forest dynamics from pre-settlement to modern times (Danneyrolles et al., 2016a; Dupuis et al., 2011; Friedman & Reich, 2005; Jackson et al., 2000; Schulte et al., 2007; 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. 3.3A).

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 & 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. 3.3A). 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 & Abrams, 2008) like aspen and paper birch, showed a remarkable fourfold increase in relative abundance, from 3% to 13% (Fig. 3.3A). 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, maturating 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. 3.3A). 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 3.2).

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 (C. D. Brown & Johnstone, 2012). This vulnerability likely contributed to a decrease in black spruce's relative abundance from 32% to 18% (Fig. 3.3A). 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 (C. D. Brown & 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 (Danneyrolles et al., 2016a; Dupuis et al., 2011). Notably, Danneyrolles et al. (2016b) 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).

3.6.2. 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. 3.4). 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. 3.3). 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., 2000). The decrease of spruce and pine in eastern Quebec (Dupuis et al., 2020), and the widespread increase in red maple in the region (Fei & 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 & Bergeron, 1998), a pattern observed in old temperate hardwood forests under natural disturbance regimes in the region (L. E. Frelich & 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).

3.6.3. 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 3.4). 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. 3.4), 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 (L. E. Frelich et al., 2021; Nowacki & Abrams, 2008). 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.

3.6.4. 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 (J. 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. 3.4), 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 (M. P. Girardin et al., 2009). The noSF had the second strongest effect on the vegetation composition (Fig. 3.4) and contributed to some extent to the increase of aspen (see subsection *Controlling for fire regimes* 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 (M. P. 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 & Bernier, 2005; Soja et al., 2007), and the increased fire activity in northwestern North America (Chavardès et al., 2022; Hanes et al., 2018). 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).

3.6.5. 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 (Buma, 2015; Kulakowski et al., 2003).

3.6.6. 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). 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.

3.6. Acknowledgements

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4 - CHAPTER 4: GENERAL CONCLUSIONS

My research underscores the persistent role of climate as an important driver of fire activity in northern forests even as anthropogenic influences have become increasingly important in moderating forest fire dynamics. My study in Scandinavian suggests that the anthropogenic effect on fire activity is non-monotonic and exhibits thresholds. My analysis of the various drivers of forest composition in eastern North America suggests that timber harvesting had the strongest influence on driving forest vegetation changes from pre-settlement times to the present compared to climate change and fire regime shifts. Below, I detail these findings.

4.1. Climate as a persistent driver of fire activity amid strong anthropogenic influence

Both Chapter 1 and Chapter 2 demonstrate that climate has remained an important driver of fire dynamics in the studied regions in the temperate and boreal zones over the last centuries, despite a strong anthropogenic influence upon forest disturbance regimes. In Chapter 1, the analysis of the fire history of eastern North American red pine forest revealed the influence of large-scale modes of atmospheric-ocean variability on fire activity from 1700 to 1900. Specifically, the fire-prone “climate states” were the positive phases of the Pacific North American (PNA) pattern and of the El Niño-Southern Oscillation (ENSO) as they were associated with large fire years, i.e., years when more sites in the region burned synchronously than expected due to chance. These climate states were also associated with fire-prone climatic conditions in the study area, including positive height anomalies in the mid-troposphere and higher temperatures.

Similarly, Chapter 2 confirmed a significant climatic effect on landscape-level fire occurrence across a large network of sites over Sweden over the last five centuries. The model developed to examine historical fire occurrence quantified the contributions of climatic and anthropogenic drivers. Showing that low summer precipitation was associated with higher fire activity, but beyond 159.20 to 177.38 mm of precipitation, the association became negative. Low summer precipitation was a significant driver of fire occurrence from 1766 to 1951, during a period with strong anthropogenic activity, highlighting its enduring influence on fire occurrence.

4.2. Anthropogenic effects on fire are non-monotonic

Chapter 2 revealed that human population density exerted a non-monotonic effect on fire occurrence. At lower human population densities, initial settlement activities increased fire ignitions. This positive effect plateaued at population densities of 0.64 to 1.46 people/km^2. However, as human population grew and technology advanced (particularly in agricultural productivity), fire activity decreased due to abandonment of agricultural burnings and the expansion of settlements and road network that increased forests fragmentation. Fire suppression further augmented this trend. The effect became increasingly negative above 6.93 people/km^2 to 8.53 people/km^2. Remarkably, these thresholds in population density aligned closely with previous studies.

In northeastern North America, fire regime shifts from pre-settlement times to the present further illustrated the non-monotonic human impact. During the Euro-American-settlement (1890-1940), fire activity increased mainly driven by increased anthropogenic fires from land clearing and agricultural activities. However, from 1940 to the present, the fire cycle lengthened to > 3 000 years (Boulanger et al., 2014). This drastic decrease is largely attributed to 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 (Cardil et al., 2019; Gauthier et al., 2008; Lauzon et al., 2007).

However, it is important to acknowledge the role of climate in these historical fire regime shifts. Drought conditions during the 1910s and 1920s could have exacerbated the settlement-related fire activity (M.-P. Girardin et al., 2004). Changes in atmospheric circulation patterns since the end of the Little Ice Age 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 (Chavardès et al., 2022; Drobyshev et al., 2017).

4.3. Timber harvesting contributed the most to the forest composition shifts from pre-settlement to present times

In Chapter 3, I disentangled the individual effects of fire regime shifts, logging, and climate change on forest composition changes in temperate mixedwood forests of northeastern North America from pre-settlement to modern times. Simulations showed that timber harvesting had the greatest influence on the forest composition changes, favoring fast growing broadleaf species, including aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyfera* Marsh.), and red maple (*Acer rubrum* L.), and reducing late-successional, long-lived conifers such as red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.), and late-successional species like black spruce (*Picea mariana* (Mill.)) and balsam fir (*Abies balsamea* (L.) Mill.). When simulations controlling for timber harvesting, aboveground biomass of all species remained relatively stable through time, preserving the functional traits present during the pre-settlement period (e.g., fire tolerance and shade tolerance) and thus maintaining ecosystem resilience.

Fire regime shifts and climate change had modest effects on forest composition. Although increased fire activity during the settlement period contributed to the rise of aspen, timber harvesting had a dominant effect on regional forest composition. In contrast, climate change had a modest impact on forest composition. The increase in temperature from the pre-settlement to the present of 0.47°C benefited the growth of black spruce, given that the increase in temperature was accompanied by an increase in precipitation (1.66%) that could have mitigated the adverse effects of evapotranspiration.

4.4. Significance of my thesis

My thesis provides several important contributions to our understanding of wildfire and forest dynamics. By upscaling the examination of fire history to a large regional scale and by focusing on large-scales modes of climate variability, Chapter 1 elucidated the climatic effect on fire activity, which has been obscured by unique characteristics of single sites and human ignitions. Reporting that large-scale modes of climate variability have affected fire activity in eastern North American red pine forests (Ch.1), even during periods where the anthropogenic effect was substantial, is important considering future climate change. More research is needed to have a more nuanced understanding of large-scales modes of variability and their impact on disturbances. Our understanding of climate indices such as ENSO has particularly been expanding in recent decades (C. Wang, 2018);

however there are still many unknowns. Further research is needed to improve predictive models and enhance management strategies.

The quantitative historical fire occurrence model developed in Chater 2 goes beyond qualitative assessments of fire dynamics over multi-centennial scales and integrates both population density and climate variability into the same analytical framework. This approach allows for a more rigorous understanding of the interplay between climate and anthropogenic drivers of fire activity. As climate change is expected to increase fire risk in northern European boreal forests (Lehtonen et al., 2016; Yang et al., 2015), understanding these dynamics across long temporal scales is essential for guiding management strategies.

Chapter 3 highlights the lasting impact of historical land use, primarily timber harvesting, on forest composition of northeastern North America. Given that climate change is projected to further alter forest composition, my study highlights the importance of restoring forests with a diversity of functional traits to enhance their resilience to future disturbances (Boulanger et al., 2018). 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.

4 - CHAPITRE 4 : CONCLUSIONS GÉNÉRALES

Ma recherche souligne le rôle persistant du climat en tant que facteur clé de l'activité des feux de forêt dans les forêts nordiques, même si les influences anthropiques sont devenues de plus en plus importantes pour modérer cette dynamique. Mon étude en Scandinavie suggère que l'effet anthropique sur l'activité des feux n'est pas monotone et présente des seuils. Mon analyse des différents moteurs de la composition forestière en Amérique du Nord orientale indique que l'exploitation forestière a eu l'influence la plus marquée sur les changements de végétation forestière depuis l'époque précoloniale jusqu'à aujourd'hui, comparativement aux changements climatiques et aux modifications du régime de feux. Ci-dessous, je détaille ces résultats.

4.5. Le climat comme facteur persistant de l'activité des feux de forêt malgré une forte influence anthropique

Les chapitres 1 et 2 montrent que le climat est resté un moteur important de la dynamique des feux dans les régions étudiées des zones tempérées et boréales au cours des derniers siècles, malgré une forte influence anthropique sur les régimes de perturbations forestières. Dans le chapitre 1, l'analyse de l'historique des feux dans les forêts de pins rouges de l'est de l'Amérique du Nord a révélé l'influence des modes de variabilité atmosphérique-océanique à grande échelle sur l'activité des feux entre 1700 et 1900. Plus spécifiquement, les « états climatiques » favorables aux feux étaient les phases positives de la configuration pacifique nord-américaine (PNA) et de l'oscillation El Niño–Sud (ENSO), qui étaient associées aux années de grands feux, c'est-à-dire des années où davantage de sites de la région brûlaient simultanément que ce que le hasard aurait prédit. Ces états climatiques étaient aussi associés à des conditions favorables aux feux dans la région d'étude, incluant des anomalies pression positive dans la mi-troposphère et des températures plus élevées.

De même, le chapitre 2 confirme un effet climatique significatif sur présence des feux à l'échelle du paysage dans un large réseau de sites en Suède au cours des cinq derniers siècles. Le modèle développé pour examiner les feux historiques a quantifié les contributions des effets climatiques et anthropiques, montrant qu'une faible précipitation estivale était associée à une activité accrue des feux, mais au-delà de 159,20 à 177,38 mm de précipitations, l'association devenait négative.

Cette faible précipitation estivale a été un facteur significatif des feux entre 1766 et 1951, pendant une période d'activité anthropique importante, soulignant son influence durable sur les feux.

4.6. Les effets anthropiques et climatiques sur les feux n'ont pas été constants

Le chapitre 2 a révélé que la densité de la population humaine exerçait un effet non constant sur la présence des feux. Aux densités de population plus faibles, les activités d'installation initiales augmentaient les déclenchements de feux. Cet effet positif a plafonné à des densités de population de 0,64 à 1,46 personnes/km². Cependant, à mesure que la population humaine augmentait et que la technologie progressait (notamment dans la productivité agricole), l'activité des feux diminuait en raison de l'abandon des brûlis agricoles et de l'expansion des établissements et du réseau routier, augmentant la fragmentation des forêts. La suppression des feux a renforcé cette tendance, l'effet devenant de plus en plus négatif au-delà de 6,93 à 8,53 personnes/km². Remarquablement, ces seuils de densité de population correspondent étroitement à ceux trouvés dans des études précédentes.

Dans le nord-est de l'Amérique du Nord, les changements de régime de feux depuis l'époque précoloniale jusqu'à aujourd'hui illustrent encore l'impact non constant de l'activité humaine. Pendant la colonisation euro-américaine (1890-1940), l'activité des feux a augmenté, principalement en raison des feux anthropiques provoqués par le défrichement des terres et les activités agricoles. Cependant, de 1940 à nos jours, le cycle des feux s'est allongé à plus de 3 000 ans (Boulanger et al., 2014). Cette baisse drastique est largement attribuée à la conversion des forêts en terres agricoles et à l'aménagement des infrastructures (R. P. Guyette et al., 2002; Stambaugh et al., 2018), ainsi qu'à la suppression active des feux mise en place au début du XXe siècle, devenue de plus en plus efficace dans les années 1970 (Cardil et al., 2019; Gauthier et al., 2008; Lauzon et al., 2007).

Il est toutefois important de reconnaître le rôle du climat dans ces changements historiques de régime de feux. Les conditions de sécheresse dans les années 1910 et 1920 ont pu exacerber l'activité des feux liée aux colonisations (Girardin et al. 2004). Les changements de circulation atmosphérique depuis la fin du Petit Âge glaciaire ont entraîné une diminution de la sévérité des sécheresses, une augmentation de l’activité cyclonique et l'afflux de masses d'air humides (Girardin et al. 2006), contribuant à l’allongement des cycles de feu dans l'est de l'Amérique du Nord (Chavardès et al., 2022; Drobyshev et al., 2017).

4.7. L’exploitation forestière a été le moteur le plus important des changements de composition forestière depuis la période précoloniale jusqu'à aujourd'hui

Dans le chapitre 3, j’ai décomposé les effets individuels des changements de régime des feux, de l’exploitation forestière et du changement climatique sur les modifications de la composition forestière des forêts mixtes tempérées du nord-est de l’Amérique du Nord, de la période précoloniale jusqu'à l'époque moderne. Les simulations ont montré que l'exploitation forestière avait l'influence la plus marquée sur les changements de composition forestière, favorisant les espèces de feuillus à croissance rapide, notamment le peuplier faux-tremble (Populus tremuloides Michx.), le bouleau à papier (Betula papyrifera Marsh.) et l'érable rouge (Acer rubrum L.), tout en réduisant les conifères et à longue durée de vie, tels que le pin rouge (Pinus resinosa Ait.), le pin blanc (Pinus strobus L.) et de fin de succession comme l’épinette noire (Picea mariana (Mill.)) et le sapin (Abies balsamea (L.) Mill.). Dans les simulations contrôlant l'impact de l'exploitation forestière, la biomasse aérienne de toutes les espèces est restée relativement stable au fil du temps, préservant les traits fonctionnels présents durant la période précoloniale (comme la tolérance au feu et à l’ombre) et, par conséquent, maintenant la résilience de l’écosystème.

Les changements de régime des feux et le changement climatique ont eu des effets modestes sur la composition forestière. Bien que l’augmentation de l’activité des feux durant la période de colonisation ait contribué à l'essor du peuplier faux-tremble, l'exploitation forestière a eu un effet dominant sur la composition régionale des forêts. En revanche, le changement climatique a eu un impact modeste sur la composition forestière. L'augmentation de la température de 0,47 °C entre la période précoloniale et aujourd’hui a favorisé la croissance de l'épinette noire, l'augmentation des précipitations de 1,66 % ayant potentiellement atténué les effets néfastes de l'évapotranspiration.

4.8. Importance de ma thèse

Ma thèse apporte plusieurs contributions importantes à notre compréhension des dynamiques des feux de forêt et des écosystèmes forestiers. En élargissant l'examen de l'historique des feux à une échelle régionale étendue et en se concentrant sur les modes de variabilité climatique à grande échelle, le chapitre 1 met en lumière l'effet climatique sur l'activité des feux, souvent obscurci par les caractéristiques uniques de certains sites et par les ignitions humaines. La démonstration que ces modes de variabilité climatique ont influencé l'activité des feux dans les forêts de pins rouges de l'est de l'Amérique du Nord (chapitre 1), même lorsque les effets anthropiques étaient substantiels, revêt une grande importance dans le contexte du changement climatique futur. Des recherches supplémentaires sont nécessaires pour obtenir une compréhension plus nuancée de ces modes de variabilité et de leurs impacts sur les perturbations. Notre compréhension des indices climatiques comme l'ENSO s'est particulièrement développée au cours des dernières décennies (C. Wang, 2018); cependant, de nombreuses incertitudes subsistent. De futures recherches sont essentielles pour améliorer les modèles prédictifs et renforcer les stratégies de gestion.

Le modèle quantitatif d'occurrence historique des feux développé dans le chapitre 2 va au-delà des évaluations qualitatives de la dynamique des feux sur des échelles multi-centennales, en intégrant la densité de population et la variabilité climatique dans le même cadre analytique. Cette approche permet une compréhension plus rigoureuse de l'interaction entre les facteurs climatiques et anthropiques de l'activité des feux. Comme le changement climatique devrait accroître le risque de feux dans les forêts boréales de l'Europe du Nord (Lehtonen et al., 2016; Yang et al., 2015), comprendre ces dynamiques sur de longues échelles temporelles est essentiel pour orienter les stratégies de gestion.

Le chapitre 3 souligne l'impact durable de l'usage historique des terres, principalement l'exploitation forestière, sur la composition des forêts de l'est de l'Amérique du Nord. Étant donné que le changement climatique devrait encore modifier la composition forestière, mon étude met en avant l'importance de restaurer les forêts avec une diversité de traits fonctionnels pour accroître leur résilience face aux perturbations futures (Boulanger et al., 2018). Distinguer les effets des différents facteurs de changement global sur la dynamique des écosystèmes forestiers restera un sujet de recherche clé pour garantir que les forêts puissent continuer à fournir leurs fonctions et services écosystémiques essentiels.

ANNEXE A – SUPPLEMENTARY INFORMATION FOR CHAPTER 1

Tableau SI 1.1.
Geographical information about all the sites included in the synthesis and their sources.

Source	Sites	Site Code	Area	Area Code	State or Prov.	Coordinates	
						Lat.	Long.
(Bergeron & Brisson, 1990)	Lac Duparquet	Duparquet	Abitibi	Duparquet	QC	48.50	-79.30
(Brose et al., 2013, 2015; Stambaugh et al., 2018)	Long Branch Hill	LBH	Pine Creek Gorge (Pennsylvania Grand Canyon)	PCG	PA	41.56	-77.45
(Brose et al., 2013, 2015; Stambaugh et al., 2018)	Slate Run	SLR	Pine Creek Gorge (Pennsylvania Grand Canyon)	PCG	PA	41.5	-77.56
	Upper Dry Run	UDR	Pine Creek Gorge (Pennsylvania Grand Canyon)	PCG	PA	41.39	-77.50
(D. Dey & Guyette, 2000; R. P. Guyette et al., 1995)	Bracebridge	BRB	Town of Bracebridge	AlgonquinE	ON	45.81	-77.80
(D. C. Dey & Guyette, 1996c; D. Dey & Guyette, 2000)	Jocko River	JKO	Jocko Rivers Provincial Park	TEM	ON	46.60	-79.22
(Dey & Guyette, 1996a; Dey & Guyette, 2000)	Papineau Lake	PPU	Papineau Lake	PPU	ON	45.35	-77.80
(Dey & Guyette, 1996b; D. Dey & Guyette, 2000)	Seguin Falls	SGN	Parry Sound District, Central Ontario	ParrySound	ON	45.40	-79.65
(Dey & Guyette, 2000; Guyette & Dey, 1995b)	Basin Lake	BSL	Algonquin Park	AlgonquinE	ON	45.80	-77.79

Tableau SI 1.1.
Geographical information about all the sites included in the synthesis and their sources (Continuation).

(D. Dey & Guyette, 2000; R. Guyette & Dey, 1995a)	**Costello Creek**	**COS**	**Opeongo Lookout, Algonquin Park**	**AlgonquinW**	**ON**	**45.62**	**-78.35**
Igor Drobyshev (not previously published)	Temiscamingu e	TEM	Temiscamingu e	TEM	QC	46.93	-79.22
	Temiscamingu e	TEMEM	Temiscamingu e	TEMEM	QC	46.93	-76.80
	Verendrye	Verendrye	Verendrye National Park	Verendrye	QC	47.39	-77.39
(Drobyshev et al., 2008b; Drobyshev, Goebel, et al., 2012a)	Seney National Wildlife Refuge	Seney	Seney National Wildlife Refuge	Seney	MI	46.18	-86.03
(Frissell, 1973)	Itasca Park	Itasca	Itasca Park	Itasca	MN	47.00	-95.00
(Larson & Green, 2017)	Castle Mound Pine Forest State Natural Area	CMPF	Castle Mound Pine Forest State Natural Area	CMPF	WI	44.28	-90.82
(Guyette et al., 2010)	Grindle Lake	GLR	Chequamegon -Nicolet National Forest	CNNF	WI	45.23	-88.36
(Guyette et al., 2010, 2016)	Waube Lake	WBL	Chequamegon -Nicolet National Forest	CNNF	WI	45.36	-88.44
(Guyette et al., 2015)	Norway Beach Site	NWB	Chippewa National Forest	Chippewa	MN	47.37	-94.52
(Guyette et al., 2015)	Cass Lake	CAS	Chippewa National Forest	Chippewa	MN	47.55	-94.09
(Guyette et al., 2015)	Turkey Tail Lake	TTL	Jo-Mary Lakes	JoMary	ME	45.62	-68.93
(Guyette et al., 2015; Guyette et al., 2016)	Moquah Barrens	MOQ	Chequamegon -Nicolet National Forest	CNNFWF	WI	46.60	-91.30
(Guyette et al., 2015)	Fourth Machias Lake	ML4	Machias Lake, Downeast Maine	Machias	ME	45.15	-67.98
(Guyette et al., 2015)	Wolf Lake	WFL	Manistee National Forest	Manistee	MI	44.00	-85.85
(Guyette et al., 2010; Muzika et al., 2015)	Burnt Mountain	BRT	Huron Mountains Club	Huron	MI	46.83	-87.92
(Guyette et al., 2010; Muzika et al., 2015)	Pine Lake and River	PLK	Huron Mountains Club	Huron	MI	46.87	87.92

Tableau SI 1.1.
Geographical information about all the sites included in the synthesis and their sources (Continuation).

(Guyette et al., 2010; Muzika et al., 2015)	**Rush Lake**	**RSH**	**Huron Mountains Club**	**Huron**	**MI**	**46.88**	**87.90**
(Guyette et al., 2016)	Airport Road	AIR	Chequamegon -Nicolet National Forest	CNNF	WI	45.18	-88.33
(Heinselman, 1973)	Boundary Waters Canoe Area	Canoe	Boundary Waters Canoe Area	Canoe	MN	47.92	-91.25
(Hessl et al., 2011)	Pike Knob Preserve	PikeKnob	Pike Knob Preserve	PikeKnob	WV	38.67	-79.44
(Meunier et al., 2019; Meunier & Shea, 2020)	Camp Bird	CampBird	Chequamegon -Nicolet National Forest	CNNF	WI	45.26	-88.26
	Hiawatha Corner Lake	CornerLake	Seney National Wildlife Refuge	Hiawatha	MI	46.16	-86.59
	Fern and Onion Lakes	FOLakes	Seney National Wildlife Refuge	Hiawatha	MI	46.06	-86.56
	Off Road Valley	OffRoadV	Seney National Wildlife Refuge	Hiawatha	MI	46.13	-86.47
	Peck's Lake	Peck	Seney National Wildlife Refuge	Hiawatha	MI	46.29	-86.63
	Big Pine Overlook	PineOverlook	Seney National Wildlife Refuge	Hiawatha	MI	46.06	-86.86
	Hiawatha Plantation	Plantation	Seney National Wildlife Refuge	Hiawatha	MI	46.29	-86.63
	Steuben Lake	Steuben	Seney National Wildlife Refuge	Hiawatha	MI	46.20	-86.44
	Inch Lake	InchLake		CNNFWF	WI	46.50	-91.35
	Pine Bluff	PineBluff	Pine Bluff	PineBluff	WI	43.48	-89.61
	Totogatic	Totogatic	Totogatic	Totogatic	WI	46.06	-91.99
	Wildcat	Wildcat	Castle Mound Pine Forest State Natural Area	CMPF	WI	44.24	-90.59
	Bruce Mound	Brucemound	Castle Mound Pine Forest State Natural Area	CMPF	WI	44.45	-90.80
(Johnson & Kipfmueller, 2016)	Lac La Croix	BWCAW	Boundary Waters Canoe Area	BWCAW	MN	48.30	-92.06
(Kipfmueller et al., 2017)	Voyageurs National Park	VNP	Voyageurs National Park	VNP	MN	48.40	-92.61
(Marschall et al., 2019; Stambaugh et al., 2018)	Bald Hill	BAH	Tioga	Tioga	PA	41.86	-77.15
(Marschall et al., 2019)	Big Hill	BIH	Tioga	Tioga	PA	41.87	-77.10

Tableau SI 1.1.
Geographical information about all the sites included in the synthesis and their sources (Continuation).

(Marschall et al., 2019)	**Park Hill**	**PKH**	**Tioga**	**Tioga**	**PA**	**41.88**	**-77.10**
(Muzika et al., 2015)	Breakfast Roll	BKF	Huron Mountains Club	Huron	MI	46.85	-87.83
(Muzika et al., 2015)	Cranberry	CRN	Huron Mountains Club	Huron	MI	46.87	-87.82
(Muzika et al., 2015)	Homer Mountain	HOM	Huron Mountains Club	Huron	MI	46.86	-87.91
(Muzika et al., 2015)	Ives Lake	IVL	Huron Mountains Club	Huron	MI	46.85	-87.84

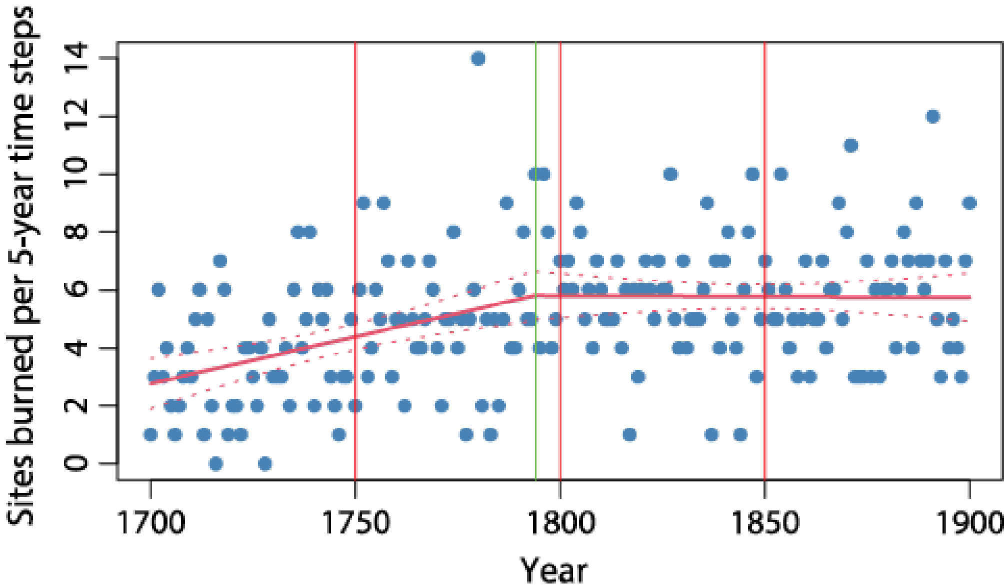

Figure SI 1.1.
Segmented regression of sites burned per 5-year time steps for the studied period 1700-1900. There is a change in the linear regression's trend during the year 1795 (shown with a green vertical line). The red vertical line shows 50-year time periods.

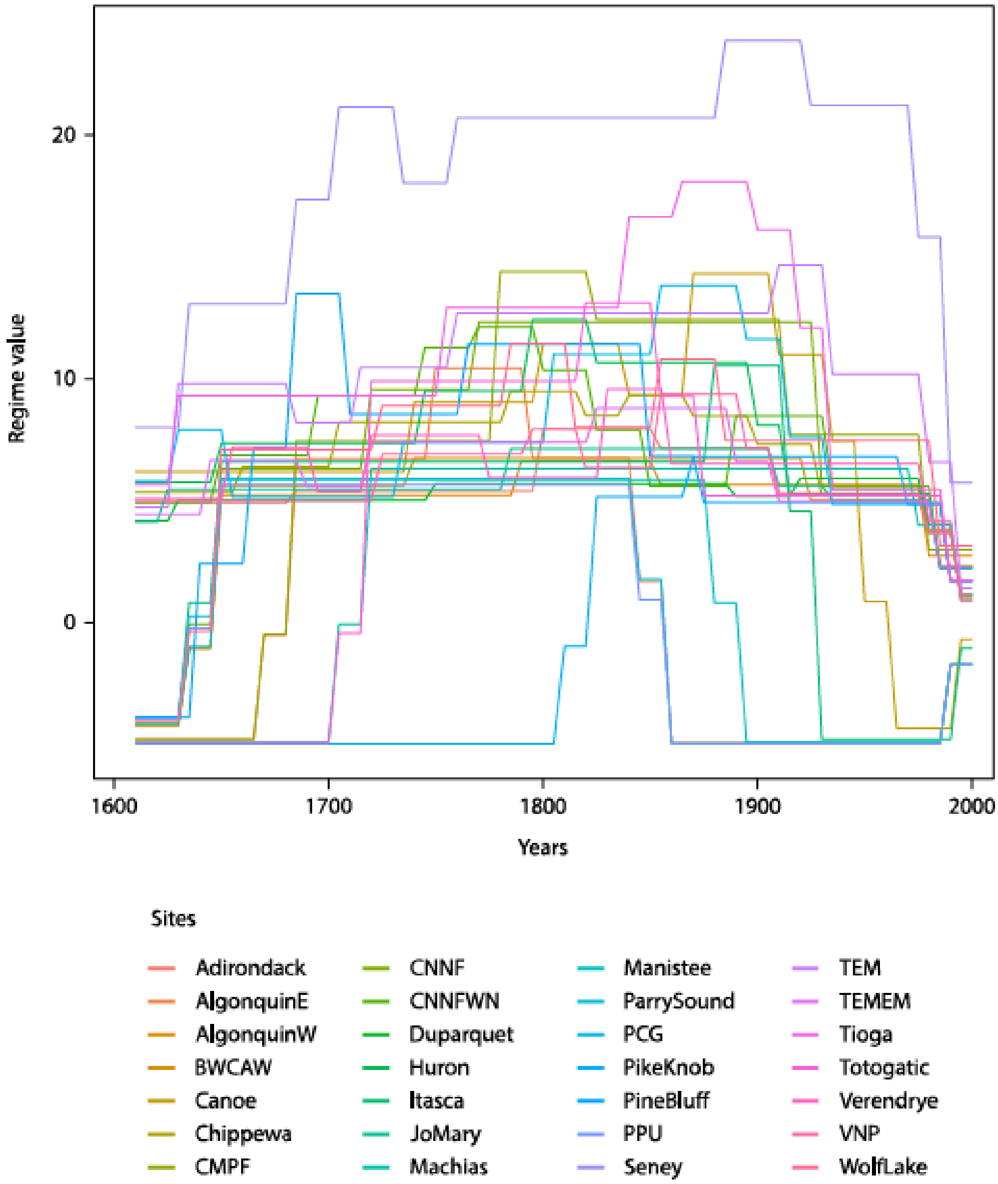

Figure SI 1.2.
Regime Shift Analysis conducted on all the sites to determine the reconstructed time-period for the study. The analysis used Rodionov's sequential t-test algorithm (Rodionov 2004), with a moving timeframe to 5 years, the Hubert weight parameter set to 1 and the significance level for the t-test set at 0.05.

Tableau SI 1.2.
Contingency analyses of years with high fire activity (HFAY) and circulation indices states for the reconstructed record (1700-1900). The climate index chronologies were classified into two states (+ or -) depending on whether or not the annual index value exceeded the mean for study period. Each cell presents the number of HFAYs/number of years with given climate state in the first row, observed/theoretical frequency of HFAYs in the second row, and the corresponding quantile. Color is based on the quantiles, with higher quantiles having a deeper color

State	ENSO+	ENSO-	PNA+	PNA-	PDO+	PDO-
ENSO+	15/101 0.15/0.16 0.42					
ENSO-		17/100 0.17/0.16 0.72				
PNA+	12/47 0.26/0.16 0.98	9/51 0.18/0.16 0.66	21/98 0.21/0.16 0.99			
PNA-	3/54 0.06/0.16 0.01	8/49 0.16/0.16 0.53		11/103 0.11/0.16 0.02		
PDO+	5/42 0.12/0.16 0.21	11/48 0.23/0.16 0.92	12/53 0.23/0.16 0.90	4/37 0.11/0.16 0.12	16/90 0.18/0.16 0.79	
PDO-	10/59 0.17/0.16 0.58	6/52 0.12/0.16 0.17	9/45 0.20/0.16 0.82	7/66 0.11/0.16 0.11		16/111 0.14/0.16 0.33

Tableau SI 1.3.
Contingency analyses of years with high fire activity (HFAY) and circulation indices states for the subperiod 1700-1800 of the reconstructed record. The climate index chronologies were classified into two states (+ or -) depending on whether or not the annual index value exceeded the mean for study period. Each cell presents the number of HFAYs/number of years with given climate state in the first row, observed/theoretical frequency of HFAYs in the second row, and the corresponding quantile. Color is based on the quantiles, with higher quantiles having a deeper color.

State	ENSO+	ENSO-	PNA+	PNA-	PDO+	PDO-
ENSO+	7/48 0.15/0.18 0.3					
ENSO-		11/53 0.21/0.18 0.84				
PNA+	6/22 0.27/0.18 0.91	6/28 0.21/0.18 0.71	12/50 0.24/0.18 0.97			
PNA-	1/26 0.04/0.18 0.02	5/25 0.20/0.18 0.68				
PDO+	2/21 0.10/0.18 0.14	7/25 0.28/0.18 0.94	6/29 0.21/0.18 0.64	3/17 0.18/0.18 0.51	9/46 0.20/0.18 0.75	
PDO-	5/27 0.19/0.18 0.58	4/28 0.14/0.18 0.30	6/21 0.29/0.18 0.96	3/34 0.09/0.18 0.07		9/55 0.16/0.18 0.46

Tableau SI 1.4.
Contingency analyses of years with high fire activity (HFAY) and circulation indices states for the subperiod 1800-1900 of the reconstructed record. The climate index chronologies were classified into two states (+ or -) depending on whether the annual index value exceeded its mean over the study period. Each cell presents the number of HFAYs/number of years with given climate state in the first row, observed/theoretical frequency of HFAYs in the second row, and the corresponding quantile in the third row. Color is based on the quantiles, with higher quantiles having a deeper color.

State	ENSO+	ENSO-	PNA+	PNA-	PDO+	PDO-
ENSO+	6/48 0.13/0.14 0.48					
ENSO-		8/53 0.15/0.14 0.75				
PNA+	5/22 0.23/0.14 0.92	4/25 0.16/0.14 0.65	9/47 0.19/0.14 0.95			
PNA-	1/26 0.04/0.14 0.05	4/28 0.14/0.14 0.57		5/54 0.09/0.14 0.13		
PDO+	4/23 0.17/0.14 0.74	6/28 0.21/0.14 0.87	8/27 0.30/0.14 0.99	2/24 0.08/0.14 0.20	10/51 0.20/0.14 0.98	
PDO-	2/25 0.08/0.14 0.18	2/25 0.08/0.13 0.21	1/20 0.05/0.14 0.09	3/30 0.10/0.14 0.27		4/50 0.08/0.14 0.07

Tableau SI 1.5.
Contingency analyses of years with high fire activity (HFAY) and circulation indices states for the modern record (1959-2021). The climate index chronologies were classified into two states (+ or -) depending on whether the annual index value exceeded its mean over the study period. The HFAYs are years with an area burned withing the upper 85th quantile. Each cell presents the number of HFAYs/number of years with given climate state in the first row, observed/theoretical frequency of HFAYs in the second row, and the corresponding quantile in the third row. Color is based on the quantiles, with higher quantiles having a deeper color.

State	ENSO+	ENSO-	PNA+	PNA-	PDO+	PDO-
ENSO+	8/28 0.29/0.21 0.94					
ENSO-		5/35 0.14/0.21 0.15				
PNA+	7/18 0.39/0.20 0.96	2/12 0.17/0.20 0.38	9/30 0.30/0.20 0.98			
PNA-	1/10 0.1/0.21 0.14	3/23 0.13/0.21 0.16		4/33 0.12/0.21 0.07		
PDO+	6/21 0.29/0.21 0.82	0/12 0/0.21 0.01	6/24 0.25/0.21 0.72	0/9 0/0.21 0.01	6/33 0.18/0.21 0.42	
PDO-	2/7 0.29/0.21 0.79	5/23 0.22/0.20 0.58	3/6 0.5/0.21 1.00	4/24 0.17/0.20 0.38		7/30 0.23/0.21 0.79

ANNEXE B – SUPPLEMENTARY INFORMATION FOR CHAPTER 2

Tableau SI 2.1
Geographical coordinates for all 50 sites used in this study.

Site ID	Site Name	Latitude	Longitude
AKER	Strängnäs	59.22	16.98
ALBA	Bräcke	62.85	15.85
ASA0	Växjö	57.17	14.78
BJOR	Nordmaling	63.97	17.99
BJUR	Nordmaling	63.93	18.81
BOTT	Jönköping	57.77	13.84
BRAC	Bräcke	62.74	15.44
BRAN	Skellefteå	65.26	20.48
BRAS	Ljusdal	62.20	15.73
ELDF	Arvika	59.65	9.32
ENSJ	Ljusdal	62.29	15.54
FAGE	Växjö	56.80	15.06
FGES	Tingsryd	56.46	15.04
FULU	Älvdalen	61.55	12.75
GASB	Rättvik	61.30	15.33
GERU	Ljusnarsberg	60.00	15.00
GET0	Ljusnarsberg	59.90	15.17
GETK	Hultsfred	57.47	15.62
GNES	Södertälje	59.05	17.31
GOSO	Gotland	58.37	19.25
GRYT	Ovanåker	61.38	15.82
HAGR	Härjedalen	61.95	14.03
HALI	Härjedalen	62.13	13.87
HARA	Katrineholm	59.20	16.42
HELL	Bräcke	62.61	15.23
HORB	Ragunda	63.22	15.67
HORO	Nybro	57.02	16.02
JOKK	Jokkmokk	66.58	20.17
KATA	Lycksele	64.86	18.77
LANG	Lindesberg	59.84	15.26
LILL	Umea	64.20	19.70
MURS	Karlskoga	59.48	14.52
NASS	Alvesta	56.88	14.53
NORK	Vimmerby	57.76	15.59
SALA	Sala	59.91	16.15
SIGG	Älmhult	56.47	14.57
SJUN	Södertälje	59.12	17.36

Tableau SI 2.1
Geographical coordinates for all 50 sites used in this study. (Continuation)

SOFR	Mora	60.92	14.62
SOLL	Mora	60.84	14.47
SORM	Södertälje	59.04	17.32
STOR	Uppvidinge	56.93	15.27
STRS	Finspång	58.63	15.61
SVEG	Härjedalen	62.13	13.87
TALL	Strängnäs	59.16	17.27
TIVE	Laxå	58.72	14.60
TYRE	Haninge	59.18	18.27
VARA	Orsa	61.15	14.66
VARM	Orsa	61.12	14.62
VILH	Åsele	64.64	16.67
YTTE	Härjedalen	62.18	14.91

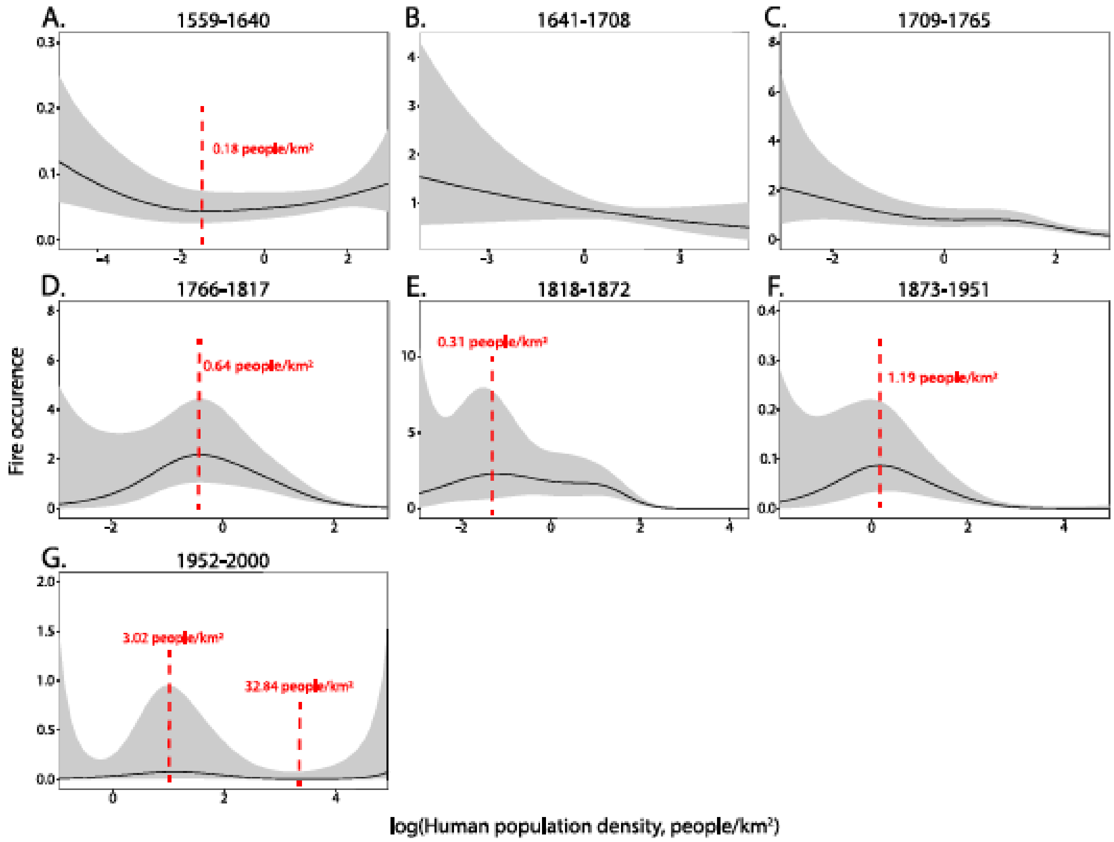

Figure SI 2.1.
Partial effects of human population density on fire occurrence during different ~50-year subperiods with the y-scale back-transformed to the scale of fire occurrence, the response variable.

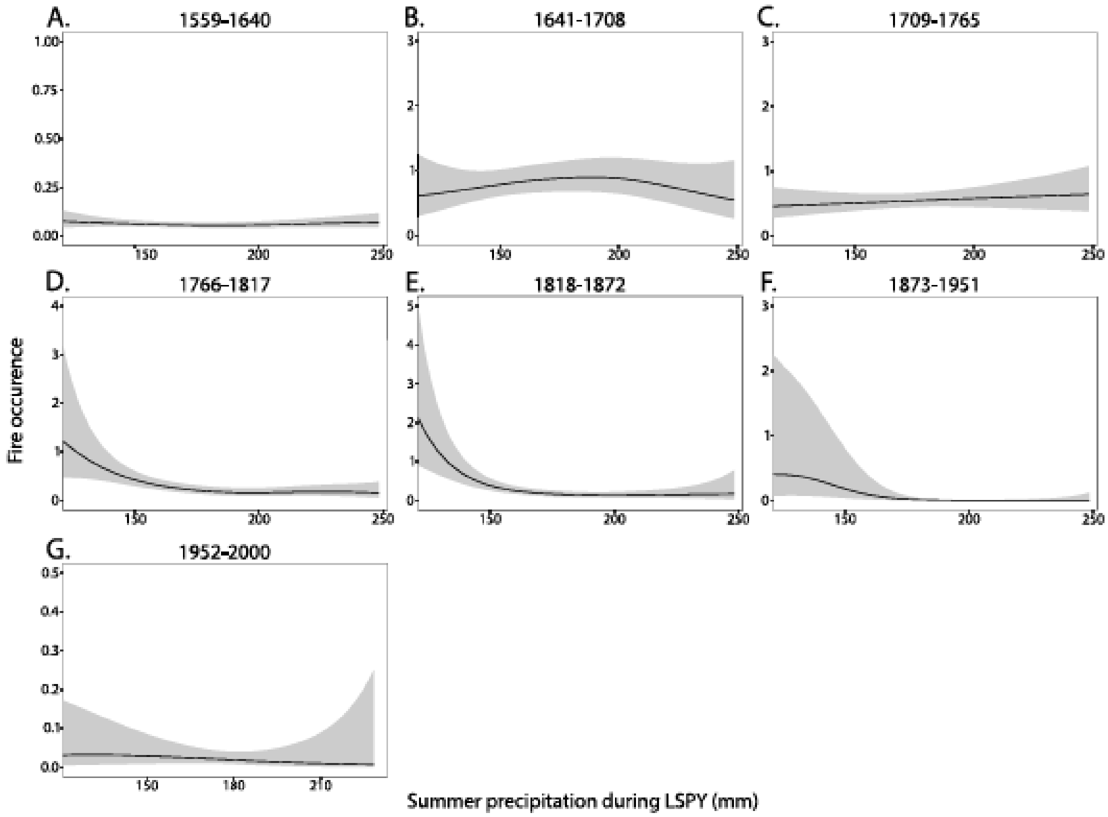

Figure SI 2.2.
Partial effects of LSP (low summer precipitation) on fire occurrence during different ~50-year subperiods with the y-scale back-transformed to the scale of fire occurrence, the response variable.

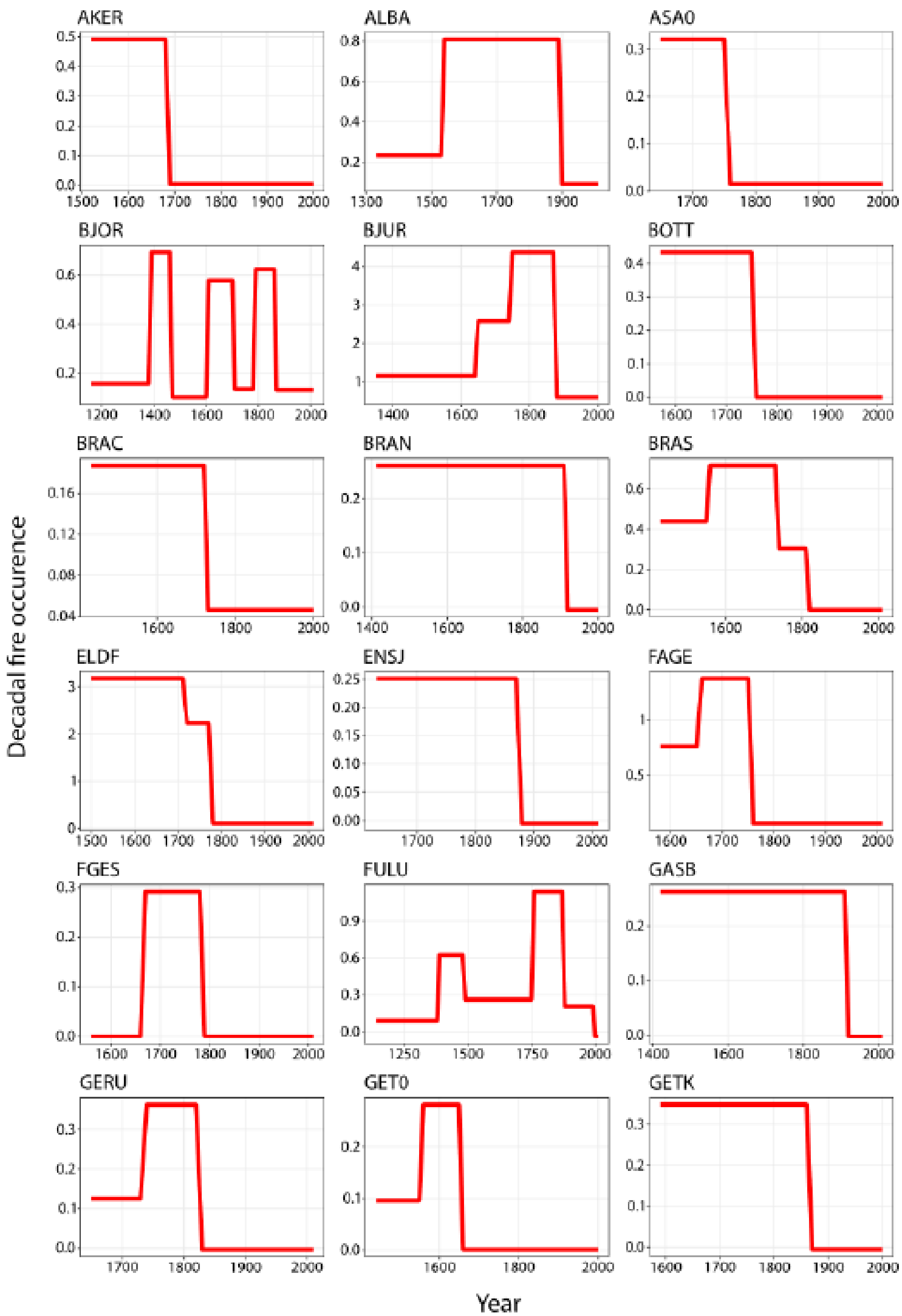

Figure SI 2.3.
Regime shifts in the fire occurrence for each site.

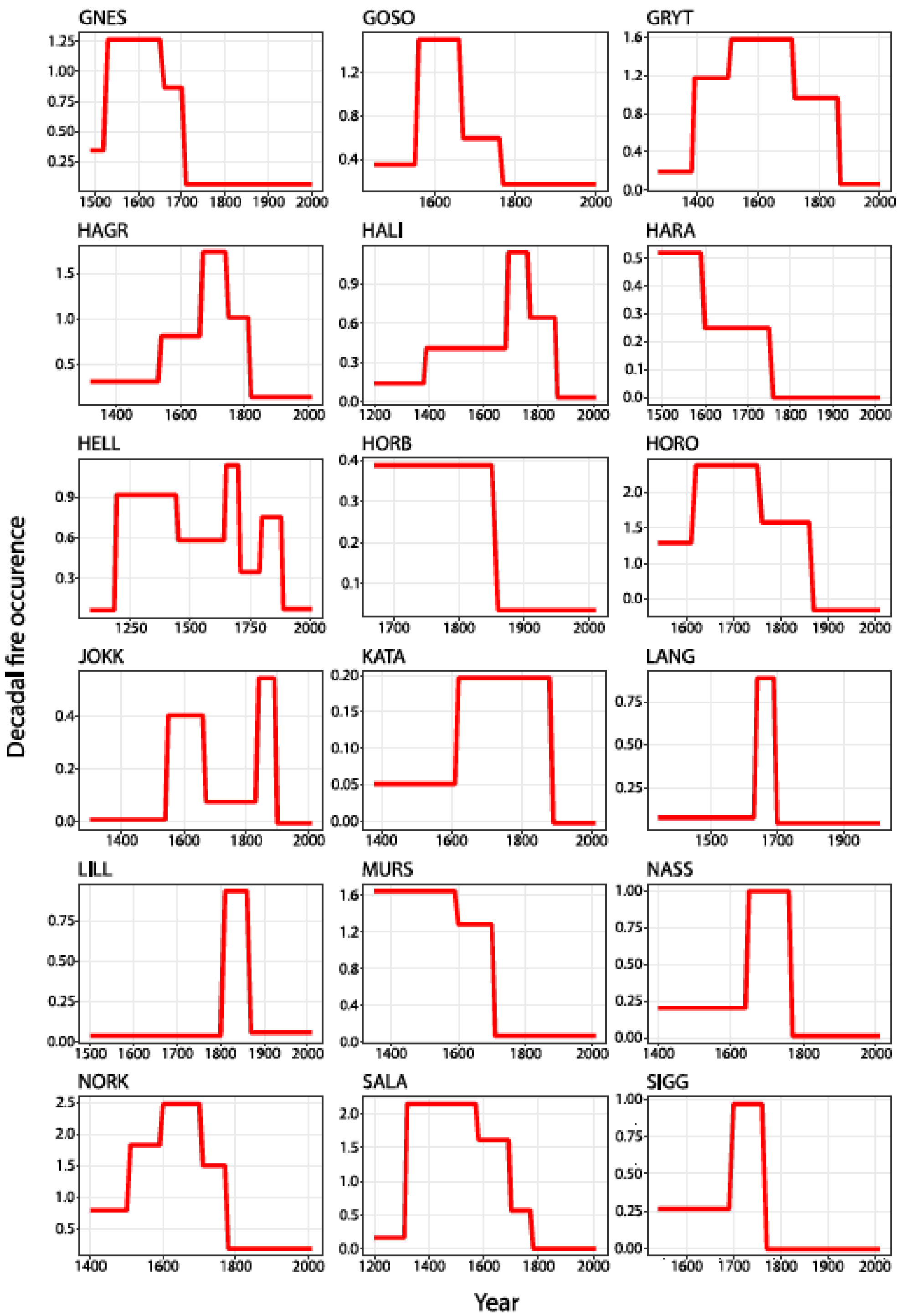

Figure SI 2.3.
Regime shifts in the fire occurrence for each site (Continuation).

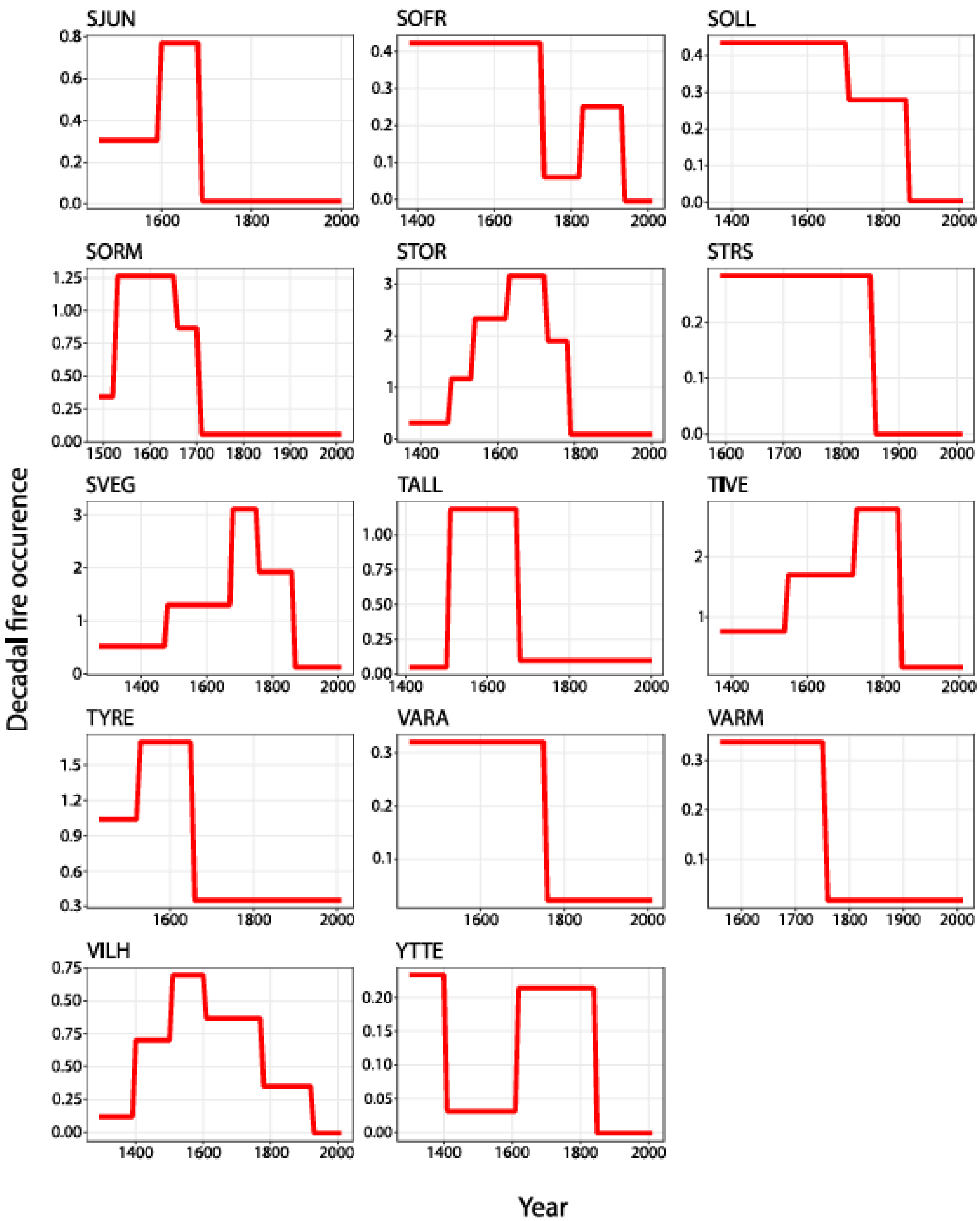

Figure SI 2.3.
Regime shifts in the fire occurrence for each site (Continuation).

ANNEXE C – SUPPLEMENTARY INFORMATION FOR CHAPTER 3

SI 3.1.
Timber Harvest Data Processing

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/). These reports included the surface area under license for the timber industry and the annual extracted volume for each species across different regions. 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.

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.

For (a), the extraction focused on the largest pines with a diameter at breast height (dbh) above 50.8 cm, corresponding to 200+ year old white pines (Pinchot & Graves, 1896) and 150+ year old red pines (Kipfmueller et al., 2021). For (b), we determined the minimum harvesting diameter for each species based on government regulations established in 1909. For the trees to be cut, these regulations recommended the minimum diameter at the stump (dsh), which we converted to dbh using the conversion table from the Direction of forestry inventories' report (Direction des inventaires forestiers, 2005). The resulting minimum dbh values were: 23.88 cm for white pine, 24.45 cm for red pine, 20.92 cm for white spruce, 17.56 cm for balsam fir, 17.83 cm for hemlock, 16.94 cm yellow birch, and 18.36 cm for aspen. These diameter limits roughly corresponded to the following age classes : ≥ 90 years for white pine (Pinchot & Graves, 1896), ≥ 130 years for red pine (Kipfmueller et al., 2021), ≥ 45 years for white spruce (Burgar, 1961), ≥ 45 years for balsam fir (Burgar, 1961), ≥ 60 years for hemlock (Lorimer, 1980), ≥ 50 years for yellow birch (Lorimer, 1980), and ≥ 80 for aspen (Nunifu, 2009). However, site conditions cause variation in dbh among trees of the same age (Chen et al., 2020), and these estimates are rough approximations.

For years where the commissioners' reports were missing, we interpolated extracted volumes by averaging the annual extracted biomass of previous and subsequent years. The commissioners' reports combined the harvested volume of red and white pine for square timber from 1900-1910. For this period, we assumed that the percentages of white and red pine volume were the average percentages for the 1860-1899 period, 91.23% and 8.77%, respectively.

The harvested volume for sawn timber in the commissioners' annual reports presented some inconsistencies. The unit of measurement for sawn timber varied over time, but we converted them to cubic feet using conversion tables in Gaudreau's (1986) and Ortuno et al.'s (2010). The reported volumes of white pine, red pine, and white spruce for sawn timber included combinations with other species. Considering that white pine, red pine, and spruce were the primary species of interest for sawn timber, it is reasonable to assume that a significant portion of the reported combined volumes consisted primarily of these three species. We used the volumes given by the reports for white and red pine, acknowledging the wasteful logging practices of the time that resulted in a significant volume being left behind in logged areas (Doyle, 1952). However, for white spruce, the pixels harvested had to include a combination of ≥ 3 species of white spruce, balsam fir, eastern hemlock, yellow birch, or aspen because the available biomass of white spruce alone in our landscape was insufficient to account for the extracted biomass reported. Despite some inconsistencies and necessary assumptions, these reports present the most comprehensive and official source of information available for historical logging.

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