Université de Montréal Université Bourgogne Franche-Comté

Variabilités climatiques, régimes de feux et dynamiques de la végétation le long d'un gradient longitudinal est-ouest en forêt boréale du Québec au cours des 8500 dernières années

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Résumé

Les feux, le climat et leurs interactions sont des facteurs clés de la dynamique des forêts boréales. Dans un contexte où les changements climatiques en cours augmentent les risques d'incendies, une hausse de la fréquence des feux constitue une menace pour les populations locales (qualité de l'air, risques sanitaires, décès, etc.), les ressources forestières (déforestation, baisse de volume bois, etc.) et l'environnement (perte d'habitats naturels, hausse des émissions de CO_2, pollution diverse, etc.). Comprendre les dynamiques passées aidera à gérer durablement les forêts boréales et à anticiper les effets des changements climatiques futurs.

A l'aide d'analyses paléoécologiques multiproxies (chironomes, charbon de bois, pollen) de trois carottes sédimentaires (lacs Mista et Adèle (est du Québec), Aurélie (Ouest du Québec)), nous avons documenté les interactions à long terme entre le climat, le feu et la végétation le long d'un gradient longitudinal est-ouest du Québec au cours des 8500 dernières années.

Nos résultats suggèrent l'existence d'un fort contraste de températures estivales entre l'est et l'ouest du Québec avant 7000 ans AA (avant l'actuel). Dans l'est, durant cette période, l'influence indirecte des vestiges de l'Inlandsis Laurentidien et les conditions de surface de l'océan contrebalancent l'insolation maximale pour induire des conditions estivales plus fraîches. La température estivale maximale n'est atteinte qu'entre 6000 et 5000 ans AA. L'ouest du Québec est peu ou pas affecté par ces influences et l'évolution des températures semble parallèle à la diminution de l'insolation pendant l'été, avec un maximum de températures autour de 7500 ans AA.

Les changements de températures estivales ne semblent pas jouer un rôle prépondérant sur la dynamique de la végétation et des feux à l'est du Québec. La dynamique à long terme de la pessière à mousses de l'est est contrôlée, entre autres, par la taille et la fréquence des feux. Au lac Adèle, la pessière à mousses s'est ouverte vers 3000 ans AA. Mais le seuil de résilience de *Picea mariana* a probablement été dépassé vers 1500 ans AA, conduisant à la transformation de la pessière à mousses en pessière à lichens. Des incendies récurrents à intervalles rapprochés semblent être le principal mécanisme de déclenchement. Au lac Mista, la pessière à mousses s'est ouverte vers 2000 ans AA, mais elle s'est probablement redensifiée au cours des 300 dernières années. Bien que la pessière à mousses semble résiliente, elle reste dans un état d'équilibre précaire car la fréquence des incendies pourrait augmenter dans le contexte du changement climatique et déclencher la transformation de la pessière à mousses en pessière à lichens.

A l'opposé des sites à l'est du Québec, à Aurélie (ouest du Québec), les feux semblent moins récurrents avec le refroidissement de la température estivale. Il existe une relation entre les variations de température estivale et la végétation. Il y a donc un contraste entre l'est et l'ouest sur les processus de contrôle de la dynamique de la végétation.

Mots clés : Chironomidae, changement climatique, interactions climat-incendie-végétation, est du Canada, histoire des incendies, Holocène, histoire postglaciaire de la végétation, fonction de transfert.

Abstract

Fire, climate and their interactions are key factors in the dynamics of boreal forests. In a context where the ongoing climate change is increasing fire risk, a rise in fire frequency poses a threat to local populations (air quality, health risks, deaths, etc.), forest resources (deforestation, drop in timber volume, etc.) and the environment (loss of natural habitats, rise in CO_2 emissions, various types of pollution, etc.). Understanding past dynamics will help to manage boreal forests sustainably and anticipate the effects of future climate change.

Using multiproxy paleoecological analyses (chironomids, charcoal, pollen) of three sediment cores (lakes Mista and Adèle (eastern Quebec), Aurélie (western Quebec)), we have documented the long-term interactions between climate, fire and vegetation along a longitudinal east-west gradient in Quebec over the past 8500 years.

Our results suggest the existence of a strong contrast in summer temperature between eastern and western Quebec prior to 7000 years BP (before present). In the east, during this period, the indirect influence of the remnants of the Laurentide Ice Sheet and ocean surface conditions offset maximum insolation to induce cooler summer conditions. Maximum summer temperatures were only reached between 6000 and 5000 cal yr BP. Western Quebec is little or unaffected by these influences, and the evolution of temperatures parallels the decrease in insolation during summer, with a temperature maximum around 7500 cal yr BP.

Changes in summer temperatures are probably not the main factor controlling fire and vegetation dynamics in eastern Quebec. The long-term dynamic of the eastern spruce-moss forest is controlled, among other things, by the size and frequency of fires. At Lake Adèle, the spruce-moss forest opened around 3000 cal yr BP. But the resilience threshold of *Picea mariana* was probably exceeded around 1500 cal yr BP, leading to the transformation of the spruce-moss forest into a lichen woodland. Recurrent fires at short intervals seem to be the main triggering mechanism. At Lake Mista, the moss forest opened around 2000 cal yr BP, but has probably redensified over the last 300 years. Although the spruce-moss forest seems resilient, it remains in a precarious state of equilibrium, as the frequency of fires could increase in the context of climate change, triggering the transformation of the spruce-moss forest into a lichen woodland.

In contrast to the sites in eastern Quebec, in Aurélie (western Quebec), fires seem to recur less frequently as summer temperatures cool. There is a relationship between summer temperature variations and vegetation. There is therefore a contrast between east and west in terms of the processes controlling vegetation dynamics.

Keywords: Chironomidae, climate change, climate-fire-vegetation interactions, eastern Canada, fire history, Holocene, postglacial vegetation history, transfer function.

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AA	Avant aujourd'hui
AD	Anno domini
ADN	Acide désoxyribonucléique
AMS	Accelerator mass spectrometry
BB	Individual biomass burned
bCHAR	CHAR background
c-à-d	C'est à dire
Cal yr BP	Calibrated years before present
CAZ	Chironomid assemblage zones
CCA	Canonical correspondence analysis
CHAR	Charcoal accumulation rate
C/N	Carbon to nitrogen ratio
CONISS	Constrained incremental sum of squares
DACP	Dark Age Cold Period
DCA	Detrended correspondence analysis
e.g.	For example
FAO	Food and agriculture organization
FF	Individual fire frequency
FRI	Fire return interval
FS	Individual fire size index
GIEC	Groupe d'experts intergouvernemental sur l'évolution du climat
HTM	Holocene thermal maximum
i.e.	That is

IPCC	Intergovernmental Panel on Climate Change
kyr^{-1}	per thousand years
LIS	Laurentide ice sheet
LIA	Little ice age
LOESS	Locally weighted scatterplot smoothing
m.a.s.l.	meters above sea level
MWP	Medieval warm period
PAR	Pollen accumulation rate
PAZ	Pollen assemblage zones
PCA	Principal component analysis
p.ex.	Par exemple
RMSE	Root mean square error
RMSEP	Root mean square error of prediction
RWP	Roman warm period
eSEP	Sample-specific estimated standard error of prediction
SD	Standard deviation
smPeak	Frequency fire occurrence per thousand years
smFRIs	Fire return interval per thousand years
SNI	Signal to noise index
TBE	Tordeuse de bourgeons de l'épinette
TOC	Total organic carbon
TN	Total nitrogen
WAPLS	Weighted average partial least square

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Avant-propos

Cette thèse est structurée sous la forme de cinq chapitres, dont un chapitre introductif, suivi de trois chapitres sous forme d'articles, et d'une synthèse et perspectives. Le chapitre 2 (article) est publié dans la revue *Ecoscience* (DOI : 10.1080/11956860.2023.2292354). Les chapitres 3 et 4 (articles) seront soumis sous peu pour publication. Des redondances d'informations peuvent être observées dans chacun des chapitres, en raison du format de la thèse qui est par articles.

Je suis le premier auteur de chacun des chapitres de ce manuscrit.

Chapitre 1

Introduction générale

1.1 Contexte et problématique

1.1.1 La forêt boréale : écosystème à enjeu au devenir incertain

Les forêts boréales constituent le plus grand biome terrestre du monde (Fig.1.1), avec une superficie d'environ 19,6 millions de km^2 qui s'étend du nord de l'Eurasie et l'Amérique du Nord (Burton et al., 2010 ; Gauthier et al., 2023). Elles fournissent des services écosystémiques essentiels (Gauthier et al., 2015a) et contiennent le plus grand réservoir de carbone terrestre stocké dans le sol et les tourbières (Pan et al., 2011 ; Walker et al., 2019 ; Ameray et al., 2021 ; Girona et al., 2023a). Au niveau mondial, les industries forestières boréales produisent 33 % du bois scié et 26 % du papier sur le marché, et génèrent plus d'un million d'emplois directs (Burton et al., 2010).

Au Canada, la forêt boréale couvre environ 5,5 millions de km^2, ce qui représente à peu près 30% de la superficie mondiale de forêt boréale (Burton et al., 2010). Un cinquième des forêts boréales canadiennes, soit près de 1,1 millions de km^2, se trouve au Québec (Fig.1.1). Elles génèrent environ 45000 emplois directs et indirects (Burton et al., 2010). Trois quarts des peuples autochtones du Canada habitent dans ces régions forestières (Ressources Naturelles Canada, 2021). Les forêts boréales sont culturellement et économiquement importantes pour ces peuples autochtones. Elles constituent des destinations touristiques et de loisirs pour de nombreux habitants et visiteurs du Canada (Ressources Naturelles Canada, 2021).

Dans un contexte de réchauffement climatique, les prédictions à l'échelle mondiale annoncent une hausse des températures de l'ordre de 2 à 4°C d'ici le prochain siècle (Overpeck et al., 1991 ; GIEC, 2014), et une altération graduelle des régimes de précipitations (Trenberth, 2011 ; GIEC, 2014). Avec le réchauffement climatique, les évènements extrêmes comme les sécheresses, les inondations (Trenberth et al., 2014 ; Spinoni et al., 2020 ; Tabari, 2020 ; Rodell et Reager, 2023) et les feux de forêts (Stocks et al., 1998 ; Jones et al., 2022 ; Pimont et al.,

2022) seront de plus en plus récurrents. Le changement climatique pourrait constituer une menace pour la biodiversité au cours du siècle prochain (Overpeck et al., 1991 ; Davis et Shaw, 2001 ; Weltzin et al., 2003 ; Parmesan et Yohe, 2003 ; Urban, 2015 ; Román-Palacios et Wiens, 2020).

Figure 1.1 Carte des forêts boréales du monde (d'après Ressources naturelles Canada, 2008).

Dans l'hémisphère nord, et plus particulièrement en zone boréale, les hausses du taux de CO_2 atmosphérique et des températures, de l'ordre de 4 à 5°C d'ici l'an 2100 (Price et al., 2013), pourraient affecter l'ensemble du fonctionnement de ces écosystèmes forestiers boréaux (Gauthier et al., 2014), dont la fonction écologique et les rôles économique et sociaux sont bien documentés (Pan et al., 2011 ; Gauthier et al., 2015a). Dans ce contexte changeant, la gestion durable de ces écosystèmes afin de garantir la fourniture des biens et services associés est un enjeu majeur pour les experts et les décideurs (Gauthier et al., 2014 ; GIEC, 2014 ; Gauthier et al., 2015b ; Girona et al., 2023b).

Divers scénarii de l'altération des régimes de précipitations, marqués notamment par une répartition non uniforme et des contrastes géographiques remarquables, sont prévus à travers le globe selon les prédictions de plusieurs modèles climatiques (Trenberth, 2011 ; GIEC, 2014 ;

Spinoni et al., 2020 ; Tabari, 2020). Au Québec, la continentalité et la direction des vents dominants font que l'intérieur des terres reçoit moins de précipitations et d'humidité atmosphériques que la côte (Villeneuve, 1959 ; Saucier et al., 2009 ; Jobidon et al., 2015 ; Couillard et al., 2019). La hausse annoncée des températures d'ici l'an 2100, couplée à celle des précipitations au Québec, et sur la côte atlantique en particulier, sont susceptibles de contribuer à l'accroissement de la productivité forestière à l'est du Canada (Price et al., 2013 ; D'Orangeville et al., 2016, 2018 ; Danneyrolles et al., 2023).

En forêt boréale québécoise, le cycle et la fréquence des feux varient avec le régime des précipitations (Saucier et al., 2009 ; Ali et al., 2012 ; Aakala et al., 2023). Du continent vers la côte, les feux sont moins fréquents, et leurs cycles tendent à s'allonger (Gauthier et al., 2001 ; Cyr et al., 2007 ; Gauthier et al., 2015b ; Portier et al., 2016). A l'intérieur des terres, la baisse des précipitations (fréquence et quantité) contribue à rendre les feux déjà fréquents, plus sévères (*sensu* Keeley, 2009), ce qui entraine le rajeunissement du couvert forestier (Boucher et al., 2003 ; Parisien et Sirois, 2003). La sévérité d'un feu est la manifestation des effets de l'incendie sur des organismes vivants, communautés ou des écosystèmes (White et Pickett, 1985 ; Keeley, 2009). Proche de la côte, le climat océanique, caractérisé par des précipitations plus importantes en fréquence et quantité, rend les feux peu fréquents et peu sévères (*sensu* Keeley, 2009), avec pour conséquence le vieillissement du couvert forestier (Flannigan et al., 1998 ; Kneeshaw et Bergeron, 1998 ; Bergeron et al., 2004a ; Cyr et al., 2009 ; Bergeron et Fenton, 2012), important pour la préservation de la biodiversité et des fonctions écologiques (Kneeshaw et Gauthier, 2003 ; Bergeron et Fenton, 2012 ; Watson et al., 2018). Au Canada, la saison des feux est de plus en plus longue (Wotton et Flannigan, 1993 ; Hanes et al., 2019), les sols s'assèchent plus tôt (début précoce de la saison) et le restent plus longtemps (fin tardive de la saison), ce qui rend le milieu de saison encore plus sec que par le passé, augmentant ainsi le risque de feux plus sévères. On observe également un raccourcissement de la période de recouvrement du sol par la neige, qui va fondre plus tôt que par le passé, rendant les territoires plus vulnérables à l'embrasement. Les feux devenant de plus en plus sévères (Flannigan et al., 2013 ; Gauthier et al., 2014 ; Guindon et al., 2021), les gestionnaires forestiers s'efforcent d'adapter les systèmes d'aménagement forestier au régime naturel des perturbations dans un contexte où des incertitudes demeurent sur la variabilité de ce régime dans le futur ainsi que sur le devenir de ces écosystèmes forestiers boréaux (Gauthier et al., 2014 ; Gauthier et al., 2023 ; Girona et al., 2023b).

1.1.2 Problématique générale : comprendre les dynamiques passées de la forêt boréale pour gérer durablement et anticiper les effets des changements climatiques futurs

Ne sachant pas avec exactitude si les précipitations augnmenteront ou pas avec la hausse des températures (Seager et al., 2012), et encore moins jusqu'à quel seuil la hausse des précipitations ne pourrait plus compenser les effets de l'augmentation des températures sur l'évapotranspiration et la variabilité des régimes de feux (Wotton et Flannigan, 1993 ; Girardin et Mudelsee, 2008 ; Flannigan et al., 2016), il est important d'analyser tous les scénarii climatiques envisageables afin de préparer des réponses adéquates aux changements futurs (Price et al., 2013 ; Gauthier et al., 2014 ; Hof et al., 2021). C'est partant de ces constats, auxquels s'ajoute la complexité des régimes de perturbation et de la dynamique successionnelle subséquente en forêt boréale (Cyr et al., 2007 ; De Grandpré et al., 2008 ; Bergeron et Fenton, 2012 ; Molina et al., 2022), que ce projet de thèse a été conçu sur la base d'un transect climatique.

La compréhension des processus affectant les changements climatiques n'est possible que si nous sommes en mesure de retracer ces changements. Pour cela, nous avons besoin d'informations sur les transformations provoqués par des variables naturelles sur de longues séquences temporelles. L'Holocène reste un bon référentiel temporel car les fluctuations de températures futures seront probablement analogues à celles observées au début de l'Holocène et de l'Holocène moyen (11000 - 6000 ans AA (AA signifie avant aujourd'hui, i.e. par convention avant 1950), Renssen et al., 2012 ; Marcott et al., 2013). Par ailleurs, des doutes subsistent quant à savoir si les régimes de feux qu'induiront les changements climatiques demeureront sous la même gamme de variabilité qu'au cours de l'Holocène (Bergeron et al., 2010 ; Ali et al., 2012 ; Hennebelle et al., 2018).

Ainsi, reconstituer et comprendre comment le climat holocène a affecté et continue d'affecter les régimes de feux et la dynamique de la végétation à différentes échelles temporelles et spatiales, aide à une meilleure évaluation de la capacité de résilience des écosystèmes forestiers boréaux aux changements climatiques futurs. La variabilité des écosystèmes actuels étant semblable que dans le passé, l'approche paléoécologique permet, à partir des données empiriques issues des proxies tels les restes de chironomides, les charbons et les grains de pollen archivés dans des sédiments lacustres, de caractériser la variabilité climatique et des incendies, de décrire la dynamique à long terme des écosystèmes, d'appréhender leur comportement face aux changements climatiques passés, et en cours, et de prédire leurs réponses face aux changements climatiques futurs.

1.2 Un bref état de l'art : histoire climatique, régimes de feux et dynamique de la végétation postglaciaire au Québec

1.2.1 L'histoire climatique postglaciaire : facteurs de forçages et contrastes régionaux

Il y a plus de 22000 ans AA, la majeure partie du continent nord-américain était recouverte de glace (Dyke et al., 2002). A partir de 22000 ans AA (dernier maximum glaciaire, Webb et al., 1993 ; Clark et al., 2009), la hausse des températures a entrainé le retrait graduel de la calotte laurentienne qui prendra fin vers 6000 ans AA (Dalton et al., 2020). Quatre processus majeurs vont influencer le climat postglaciaire holocène : (i) la dynamique du retrait des calottes glaciaires (Dyke, 2004), (ii) la précession des équinoxes qui se traduira par des variations de l'insolation dans les hémisphères nord et sud (Berger et Loutre, 1991) avec une incidence sur les températures annuelles et saisonnières (COHMAP, 1988), (iii) les échanges océan-atmosphère-végétation (Renssen et al., 2009), puis (iv) les activités anthropiques et l'industrialisation sources potentielles des émissions des gaz à effet de serre (CO_2, CH_4 ; Bowman et al., 2009). A l'échelle régionale ou sous-régionale, la dynamique postglaciaire du climat résulte des équilibres et interactions entre ces différents forçages (Renssen et al., 2009), les effets des facteurs externes étant atténué ou exacerbés par des processus locaux.

En Amérique du nord, le retrait de la calotte laurentienne, couplé à la hausse de l'insolation estivale et du taux de CO_2 (Webb et al., 1993), furent à l'origine de la variabilité climatique du début de l'Holocène (11700 – 8200 ans AA *sensu* Walker et al., 2019), avec une tendance au réchauffement du climat (Mayewski et al., 2004). L'Holocène moyen (8200-4200 AA *sensu* Walker et al., 2019) coïncide avec la fin de la déglaciation (Dyke, 2004). Suite au forçage orbital, l'insolation (Bond et al., 2001) devient le principal facteur régulateur du climat (Bond et al., 2001 ; Mayewski et al., 2004 ; Renssen et al., 2012). Bien qu'une partie du Canada ne soit plus recouverte par la calotte laurentienne (Dalton et al., 2020), le climat de certaines régions du Québec a continué d'être influencé par les vestiges de l'Inlandsis laurentien (Kaufman et al., 2004 ; Renssen et al., 2012 ; Fréchette et al., 2021). Cette influence des conditions locales se traduit par des disparités territoriales et chronologiques de l'apparition du Maximum Thermique Holocène (HTM) qui suivant les régions du Québec se produit entre 11000 et 3000 ans AA (Viau et Gajewski, 2009 ; Renssen et al., 2012 ; Bajolle, 2018). Ces contrastes régionaux dans l'histoire climatique postglaciaire expliquent en partie des dynamiques régionalement distinctes de la colonisation végétale et de la migration graduelle des arbres (Davis et Shaw, 2001 ; Dyke, 2005 ; Blarquez et Aleman, 2016).

A l'HTM, soit entre 11000 et 3000 ans AA suivant les zones géographiques du Québec (Renssen et al., 2012), les températures estivales sont globalement estimées comme étant de 2 à 3°C plus chaudes que les températures actuelles (Kaufman et al., 2004). Cette période a été interrompue brièvement par un évènement froid survenu il y a 8200 ans AA (Alley et al., 1997). A partir de 6000 ans AA, la baisse progressive de l'insolation estivale serait à l'origine d'un refroidissement du climat qui va s'accentuer à partir de 3000 ans AA marquant le début de la période dite « néoglaciaire » (Viau et al., 2006 ; Viau et Gajewski, 2009 ; Gajewski, 2015 ; Fréchette et al., 2018, 2021). La période néoglaciaire ne semble cependant pas uniforme et plusieurs études suggèrent l'existence d'une variabilité climatique interne caractérisée par une succession d'épisodes chauds (Période Chaude Romaine (RWP) entre 2000-1800 ans AA ; Période Chaude Médiévale (MWP) entre 1000 – 700 ans AA), et froids (Période Froide de l'Age Sombre (DACP) entre 1600-1300 ans AA ; Petit Age Glaciaire (LIA) entre 400 – 100 ans AA) observés à l'échelle de l'Amérique du nord (Ladd et al., 2017).

Au Québec, sur la base des données dendrochronologiques récentes, Delwaide et al. (2021) situent la Période Chaude Romaine entre 1850 et 1550 ans AA, la Période Froide de l'Age Sombre entre 1550 et 1120 ans AA, la Période Chaude Médiévale entre 1120 et 840 ans AA et le Petit Age Glaciaire entre 134 et 50 ans AA. D'après des enregistrements paléohydrologiques basés sur les thécamoebiens (Magnan et Garneau, 2014), le Petit Age Glaciaire survient entre 600 et 100 ans AA. Ainsi, l'interglaciaire holocène sera marqué par ces périodes (HTM, Néoglaciaire) et événements (froid de 8200 ans AA, RWP, DACP, MWP, LIA) climatiques majeurs.

L'asynchronisme aux échelles régionale (Mann et Jones, 2003 ; Viau et al., 2006 ; Renssen et al., 2009 ; Naulier et al., 2015) et mondiale (Mayewski et al., 2004 ; Matthews et Briffa, 2005 ; Renssen et al., 2012) de ces périodes et évènements climatiques remarquables de l'Holocène, auquel s'ajoutent certaines discordances (chronologie, amplitude, durée) des études récentes (Renssen et al., 2009 ; Bajolle, 2018 ; Delwaide et al., 2021), exigent que l'on s'intéresse à la singularité de chaque région (Mayewski et al., 2004). A cet égard, il serait nécessaire de savoir comment les périodes et évènements climatiques majeurs de l'Holocène se sont exprimés dans différentes régions du Québec. Est-ce que leurs amplitudes et durées ont été plus importantes dans certaines régions du Québec ?

Pouvoir retracer l'historique à long terme du climat est essentiel à la compréhension de la dynamique pluriséculaire à plurimillénaire des incendies et subséquemment de la végétation en forêt boréale. En effet, à l'échelle de la planète, le climat influence directement la répartition des plantes (Woodward, 1987). Au Québéc, la diversité de gradients environnementaux favorise une grande diversité écosystémique (Saucier et al., 2009 ; Couillard et al., 2019). En forêt boréale québécoise, le gradient latitudinal sud-nord de refroidissement des températures influence directement la composition et la répartition des formations végétales (Saucier et al., 2009 ; Grondin et al., 2023). Les conditions climatiques relativement sèches (Baie James) à très humides (Côte-Nord) (Jobidon et al., 2015) contribuent à l'allongement des cycles de feux le long du gradient longitudinal ouest-est (Gauthier et al., 2001 ; Couillard et al., 2019). Le climat va donc, par son effet sur les régimes de perturbations par les feux (Johnson, 1992), influencer indirectement la répartition et l'abondance de certaines espèces végétales, notamment *Pinus banksiana* est plus abondant à l'ouest (Asselin et al., 2003) et *Abies balsamea* à l'est (Saucier et al., 2009 ; Couillard et al., 2019 ; Grondin et al., 2023).

1.2.2 Histoire postglaciaire des feux et de la végétation

Les reconstitutions paléoécologiques de l'histoire postglaciaire des feux au Québec (Ali et al., 2012 ; El-Guellab et al., 2015 ; Remy et al., 2017a, b) révèlent que les conditions climatiques chaudes et sèches, avant 3500 ans AA, semblaient plus propices aux feux de forêt. Cependant, contre-intuitivement, certains sites d'étude situés au nord, centre, sud (Carcaillet et Richard, 2000 ; Asselin et Payette, 2005) et sur la Côte-Nord (Bastianelli, 2018) du Québec enregistreront plus de feux durant la période fraîche et humide du néoglaciaire (après 3500 ans AA), dus en partie à des facteurs locaux à l'instar des conditions climatiques estivales sèches

(Carcaillet et Richard, 2000). Entre 3000 et 1000 ans AA, les feux seront très souvent plus étendus ou plus sévères à l'ouest, au centre et à l'est du Québec (Ali et al., 2012 ; Remy et al., 2017a).

L'histoire de la végétation postglaciaire du Québec, différente d'un site à l'autre (Fréchette et al., 2018, 2021), est difficile à présenter de manière détaillée en quelques lignes. Malgré les contrastes et disparités à l'échelle spatiale et temporelle, la dynamique postglaciaire de la végétation peut être résumée en trois grandes phases, principalement liées au climat, aussi bien à l'ouest (Fréchette et al., 2018) qu'à l'est (Fréchette et al., 2021) du Québec.

(1) Une phase non arboréenne à l'est (avant 11000 ans AA) ou une phase d'immigration des espèces végétales à l'ouest (avant 9500 ans AA)
(2) Une phase d'afforestation (de 11000 à 9000 ans AA à l'est ; de 9500 à 7500 ans AA à l'ouest)
(3) Une phase forestière (de 9000 ans AA à aujourd'hui à l'est ; de 7500 ans AA à aujourd'hui à l'ouest)

La végétation actuelle du Québec s'est mise en place il y a environ 4000 ans AA à l'est et 3500 ans AA à l'ouest (Fréchette et al., 2021). Au cours des derniers millénaires, sous l'effet des changements climatiques, la recrudescence des perturbations (p.ex., incendies, épidémies d'insectes) pourrait expliquer l'ouverture du couvert forestier, principalement dans les pessières, avec la transformation de certaines pessières à mousses en pessières à lichens (Carcaillet et Richard, 2000 ; Girard et al., 2009 ; Remy et al., 2017a, b ; Bastianelli, 2018 ; Payette et Delwaide, 2018 ; Couillard et al., 2021).

La complexité des relations climat-feu-végétation pose de nombreuses questions encore en suspens. Il s'agit notamment de déterminer comment les grandes variations du climat holocène exprimées le long d'un transect est-ouest influencent la dynamique des incendies et des végétations. Puis de savoir :

- Quel sera le sort de la forêt boréale du Québec dans la perspective des changements climatiques ;
- Si la pessière à mousses sera-t-elle toujours résiliente aux perturbations induites par les changements climatiques ;
- Si la pessière à mousses sera-t-elle envahie par la pessière à lichens ;
- Si des conditions climatiques similaires entrainent obligatoirement des régimes de feu similaires ;
- Si des feux récurrents à intervalles rapprochés peuvent modifier la trajectoire de la succession végétale.

1.3 Objectifs de la thèse et mise en œuvre

1.3.1 Objectifs de la thèse

Ce travail de recherche a pour objectif général de compléter les reconstitutions holocènes du climat, des régimes de feux, et de la végétation à l'est du Canada. Ceci, en mettant en relation la variabilité naturelle du climat et celle du régime de feux, puis déterminer leurs effets sur la dynamique de la végétation le long d'un transect est-ouest en forêt boréale coniférienne. Il s'agira spécifiquement dans le chapitre 2 d'évaluer la relation entre la dynamique de la végétation et les changements temporels du climat et de l'activité des incendies dans une région peu étudiée où les cycles de feux sont particulièrement longs, résultant d'une faible occurrence de grands incendies ; dans le chapitre 3 de présenter de nouvelles données de températures estivales postglaciaires, puis documenter les changements spatio-temporels des températures estivales postglaciaires le long d'un transect est-ouest du Québec ; dans le chapitre 4 de comprendre les mécanismes susceptibles de provoquer la transformation de la pessière à mousses en pessière à lichens, à partir de deux sites présentant une tendance similaire de la température estivale postglaciaire, mais avec des historiques de feu différents et une végétation moderne contrastée.

1.3.2 Région d'étude

L'aire d'étude appartient au domaine bioclimatique de la pessière à mousses (49° à 52°N). Trois lacs sont échantillonnés, un situé dans le sous-domaine de la pessière à mousses de l'ouest, et deux autres dans le sous-domaine de la pessière à mousses de l'est (Fig.1.2, Saucier et al., 2009 ; Girona et al., 2023c). Comme son nom l'indique, ce domaine est constitué majoritairement d'épinette noire (*Picea mariana* (Mill.) B.S.P.). D'ouest en est, les conditions climatiques et la fréquence des perturbations permettent la cohabitation d'autres espèces. Ainsi, du continent vers la côte atlantique, on observe une baisse de présence des taxons tels le pin gris (*Pinus banksiana* Lamb) (Asselin et al., 2003) et une hausse du sapin baumier (*Abies balsamea* (L.) Mill.) (Saucier et al., 2009 ; Couillard et al., 2019 ; Grondin et al., 2023). Le climat est relativement frais et pluvieux, avec d'ouest en est, des précipitations moyennes annuelles variant entre 650-1150 mm (Jobidon et al., 2015), et le nombre de degrés-jour de croissance qui passe de 1380 à 620 (Jobidon et al., 2015). Les feux (Johnson, 1992 ; Payette, 1992 ; Bergeron et al., 2004b), les épidémies de tordeuse de bourgeons de l'épinette (Navarro et al., 2018 ; Lavoie et al., 2021 ; Subedi et al., 2023) et de l'arpenteuse de la pruche (De Grandpré et al., 2008), les chablis et les trouées (Kneeshaw et Bergeron, 1998 ; Pham et al., 2004 ; Girona et al., 2019), les barrages de castors (Labrecque-Foy et al., 2020) constituent les types de perturbations naturelles qui ont cours dans le domaine de la pessière à mousses. Les incendies étant la principale perturbation naturelle (Payette, 1992 ; Gauthier et al., 2001).

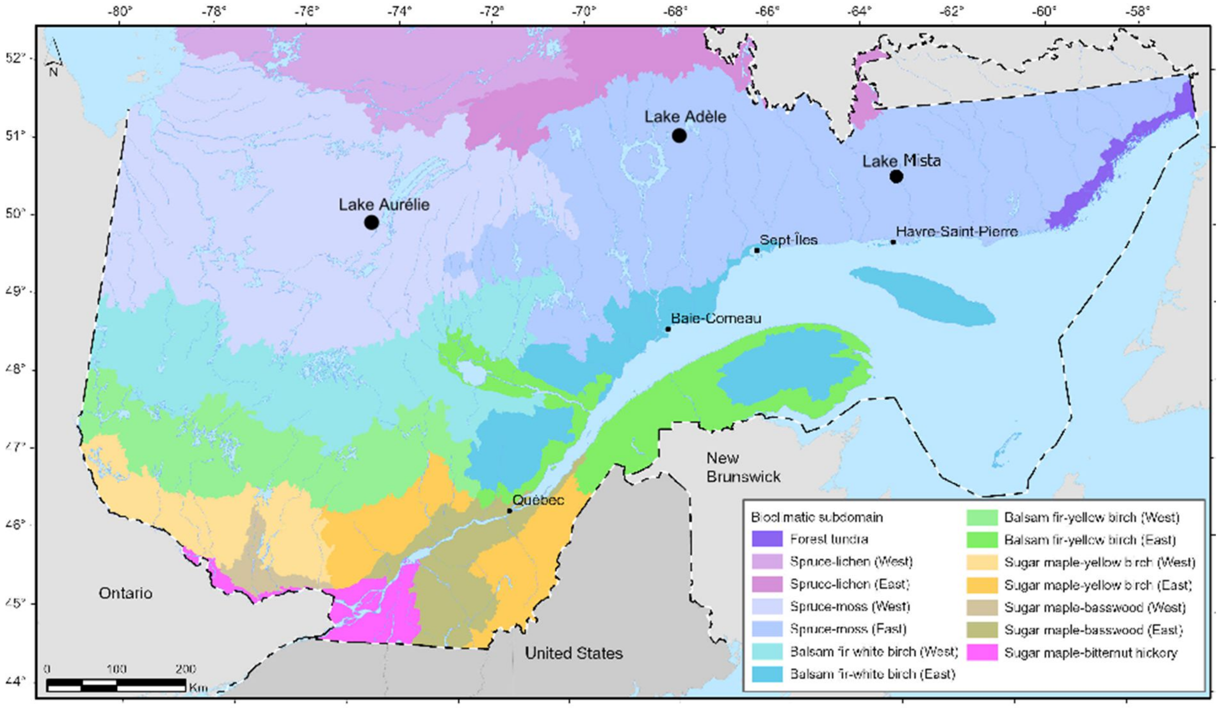

Figure 1.2 Localisation des sites d'étude dans le domaine de la pessière à mousses.

1.3.3 Mise en œuvre d'une approche paléoécologique dans les archives sédimentaires lacustres

1.3.3a Archives sédimentaires lacustres

Le Québec compte de nombreux lacs avec un fort taux de sédimentation et moins de chance de hiatus. L'accumulation de séquences sédimentaires non perturbées au fond des lacs permet d'étudier les changements environnementaux passés à une résolution annuelle, décennale, séculaire ou millénaire. Les sédiments sont récupérés par carottage et les datations au ^{210}Pb et au ^{14}C fournissent la chronologie. Les grains de pollen, charbons et capsules céphaliques des chironomes déposés au fil du temps se conservent parfaitement dans les sédiments lacustres. L'approche multiproxies (chironomes, charbon de bois, pollen) permet de comprendre les interactions climat-feu-végétation pour un bassin versant donné. Les reconstitutions paléo-environnementales à partir des bioindicateurs fossiles tels les grains de pollen, charbons et les chironomides archivés dans des sédiments lacustres (Fig.1.3 ; Fig.1.4), reposent sur l'un des principes fondamentaux de la paléoécologie, le principe de l'actualisme. Ce principe voudrait que la forme et le fonctionnement biologique des organismes vivants se soient maintenus au fil des années, et que les évènements actuels puissent être expliqués à la lumière des évènements passés (Birks et Birks, 1980 ; Rull, 2010).

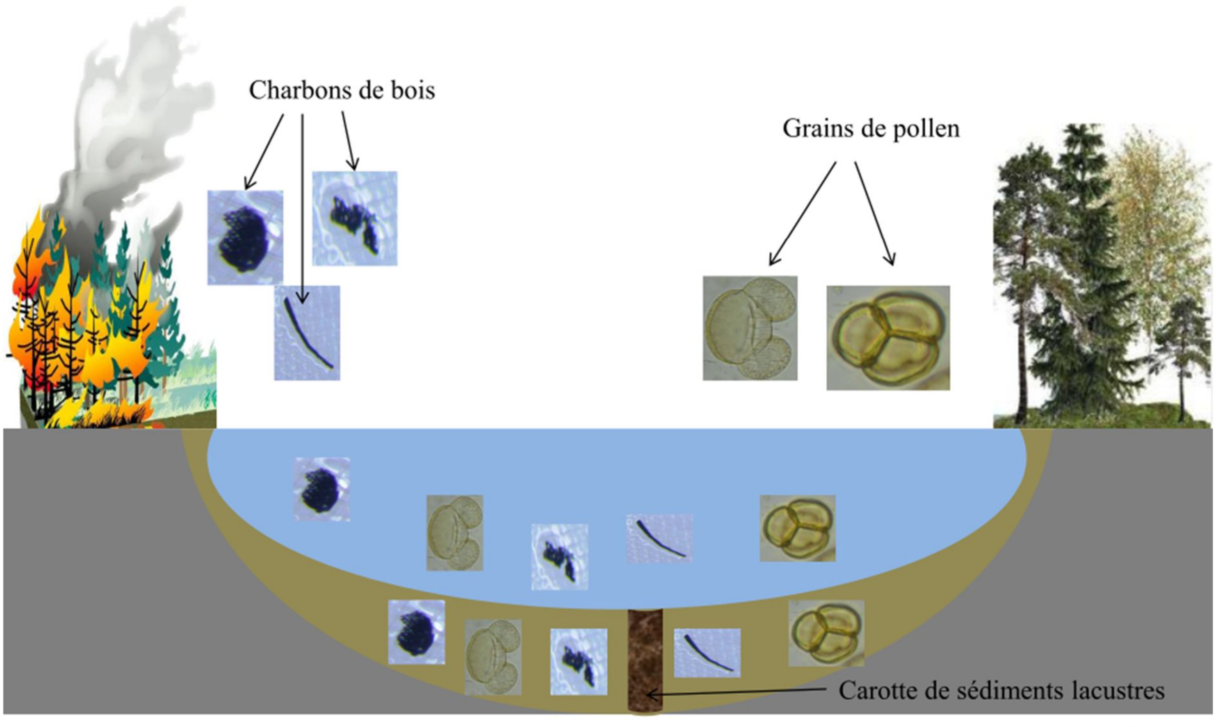

Figure 1.3 Bio-indicateurs (charbons de bois, grains de pollen) et milieu de dépôt.

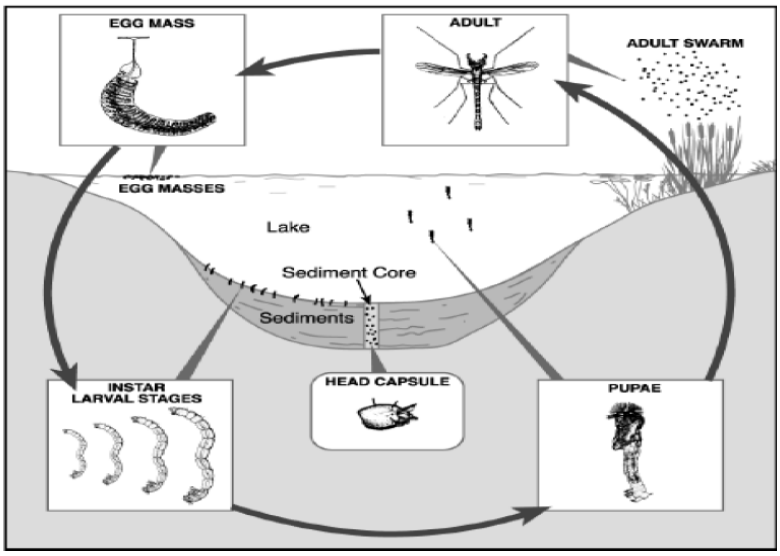

Figure 1.4 Cycle de développement des Chironomidae (d'après Porinchu et MacDonald (2003)).

1.3.3b Datations radiochronologiques et modèles d'âge

Une chronologie précise est un préalable nécessaire à toute étude paléoécologique. Les datations radiochronologiques reposent sur le principe de stratigraphie qui voudrait que les couches les plus anciennes se trouvent sous les couches les plus récentes. Elles permettent de reconstituer des modèles âge-profondeur qui seront plus particulièrement utilisés pour calculer les influx pour les paléobioindicateurs sédimentaires (p.ex., CHAR en mm^2 cm^{-2} an^{-1} ; Influx pollinique en nombre de grains de pollen par cm^2 par an), et comparer temporellement des reconstitutions issues des sites différents. Pour cela, des macrorestes végétaux et des sédiments lacustres seront prélevés pour différents niveaux des profils sédimentaires, puis datés au ^{14}C (à partir de la méthode de spectrométrie de masse par l'accélérateur de particules) et au ^{210}Pb (spectrométrie gamma), respectivement (voir chapitre 2). Les dates radiocarbones seront calibrées en âges calendaires à l'aide de IntCal20 (Reimer et al., 2020). A l'issue des datations, le modèle âge-profondeur sera produit, en combinant les dates au ^{210}Pb et celles au ^{14}C à l'aide du logiciel CLAM (Blaauw, 2010).

1.3.3c Reconstitution des paléotempératures estivales à partir des chironomes

La reconstitution quantitative des températures estivales s'appuie sur l'étude des assemblages de chironomes fossiles et l'utilisation d'une fonction de transfert qui permet de générer les paléotempératures associées aux assemblages fossiles (voir chapitres 2 et 3). Les chironomides sont utilisés en paléoécologie à cause de leur abondance et leur diversité taxonomique, leur identification possible au niveau générique voire spécifique, la bonne préservation de leur capsule céphalique chitinisée dans les sédiments lacustres, leur sensibilité et leurs réponses rapides aux changements environnementaux (Walker, 1987 ; Brooks et al., 2007).

Les chironomides représentent l'une des familles d'insectes appartenant aux diptères nématocères. Leur cycle de vie comporte quatre stades de développement (œufs, larves, nymphe, adulte), tous sensibles aux variations des conditions environnementales (Brooks et al., 2007). Les trois premiers stades de développement sont aquatiques, et le dernier stade est terrestre (Fig.1.4 ; Porinchu et MacDonald, 2003 ; Larocque, 2008). Le développement larvaire passe par 4 phases ou instars. Le passage d'un stade à l'autre est ponctué par la production de mues (exuvies) dont la capsule céphalique (la tête de la larve) chitinisée se conserve dans les sédiments. Apres l'élimination des carbonates éventuellement présents dans l'échantillon de sédiments par HCl (10%) et élimination de la matière organique fine et défloculation par passage dans une solution de de KOH (10%), les sédiments sont passés au tamis de 100µm de maille. Les capsules céphaliques sont triées manuellement du refus de tamis à l'aide d'une pince fine sous loupe binoculaire (X10 à X50). Chaque spécimen est ensuite monté entre lame et lamelle puis identifié à l'aide d'un microscope.

Les clés d'identification dichotomiques existantes (p.ex., Wiederholm, 1983 ; Larocque et Rolland, 2006 ; Brooks et al., 2007 ; Andersen et al., 2013 ; Larocque, 2014) sont basées sur des caractéristiques morphologiques des capsules (forme du mentum, prémandibules, soies céphaliques, mandibules, etc. ; Fig.1.5). La reconstitution de la composition des assemblages passés de Chironomidae nécessite à minima le tri et l'identification de 50 spécimens par échantillon (Larocque et al., 2001 ; Heiri et Lotter, 2010). Un assemblage est défini par les abondances relatives (pourcentages) de chaque taxon dans l'échantillon.

Les facteurs qui contrôlent la composition des communautés larvaires de chironomes dans un lac peuvent être multivariés. La composition taxonomique des assemblages de chironomes peut changer sous l'effet direct ou indirect des facteurs biotiques et abiotiques difficiles à dissocier. En effet, des facteurs internes au lac, tels que la nature du substrat, les conditions physico-chimiques de l'eau (pH, oxygénation, salinité) ou la nature et la quantité de la ressource alimentaire dont se nourrissent les larves de chironomes, peuvent influencer les changements à court terme des assemblages de chironomes (Velle et al., 2005 ; Brodersen et Quinlan, 2006).

Néanmoins, ces facteurs sont plus ou moins liés directement ou indirectement à la température de l'air et de l'eau (Fig.1.6 ; Eggermont et Heiri, 2012). Les travaux pionniers de Walker et al. (1991) ont démontré que la température de l'eau est l'un des facteurs principaux expliquant la répartition des chironomes à large échelle géographique.

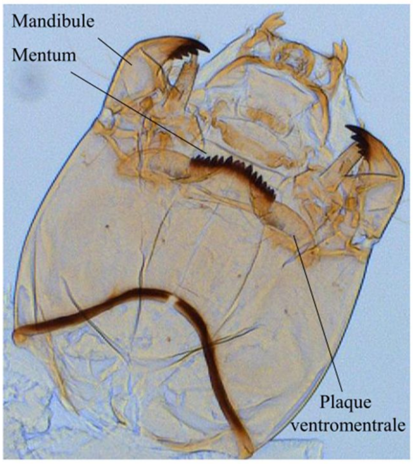

Figure 1.5 Exemple de capsule céphalique de Chironomidae (spécimen du genre *Sergentia*).

Les relations directes et indirectes entre la température de l'air, la température de l'eau et la répartition des communautés de chironomes permettent de développer des fonctions de transfert basées sur les chironomes et des reconstitutions quantitatives de la température (Larocque et al., 2001 ; Eggermont et Heiri, 2012).

Au Canada, il existe cinq fonctions de transfert (Tableau 1.1 ; Walker et al., 1997 ; Larocque, 2008 ; Fortin et al., 2015 ; Medeiros et al., 2022 ; Suranyi et al., *in press*) qui permettent de reconstituer les températures au Canada. Chacune de ces fonctions de transfert est développée à partir de l'étude de la répartition actuelle des taxons de Chironomidae dans les sédiments de surface (premier centimètre) de lacs répartis selon un large gradient de température (matériel supplémentaire S1c ; chapitre 2). Pour chaque lac, les paramètres physiques (p.ex., profondeur, superficie), chimiques (p.ex., pH de l'eau, conductivité, carbone organique) et climatiques (p.ex., température de l'eau) sont mesurés, le sédiment de surface est prélevé, et les capsules céphaliques de Chironomidae sont extraites puis identifiées. La température de l'air est extrapolée à partir des données météorologiques des stations les plus proches (Larocque et al., 2006). Une analyse multidimensionnelle (p.ex., CCA) permettra de déterminer lequel des paramètres physiques, chimiques ou climatiques explique le mieux la répartition des assemblages de Chironomidae des lacs associés à la base de données. Si ces analyses montrent que la température estivale de l'air explique le mieux cette répartition, la fonction de transfert basée sur la température optimale de chaque taxon pourra être établie et appliquée ensuite aux assemblages de Chironomidae fossiles extraits des carottes sédimentaires des lacs étudiés afin d'inférer les températures passées (Bajolle, 2018). Les températures moyennes de l'air du mois d'août seront calculées à partir d'un modèle de régression de type WAPLS (Weighted Averaging-Partial Least-Squares, ter Braak et Juggins, 1993). Une comparaison des performances statistiques (p.ex., coefficient de corrélation (r^2), l'erreur de prédiction du modèle (RMSEP)) des cinq fonctions de transfert dont nous disposons, permettra de retenir la plus fiable selon les forces et faiblesses de chacune.

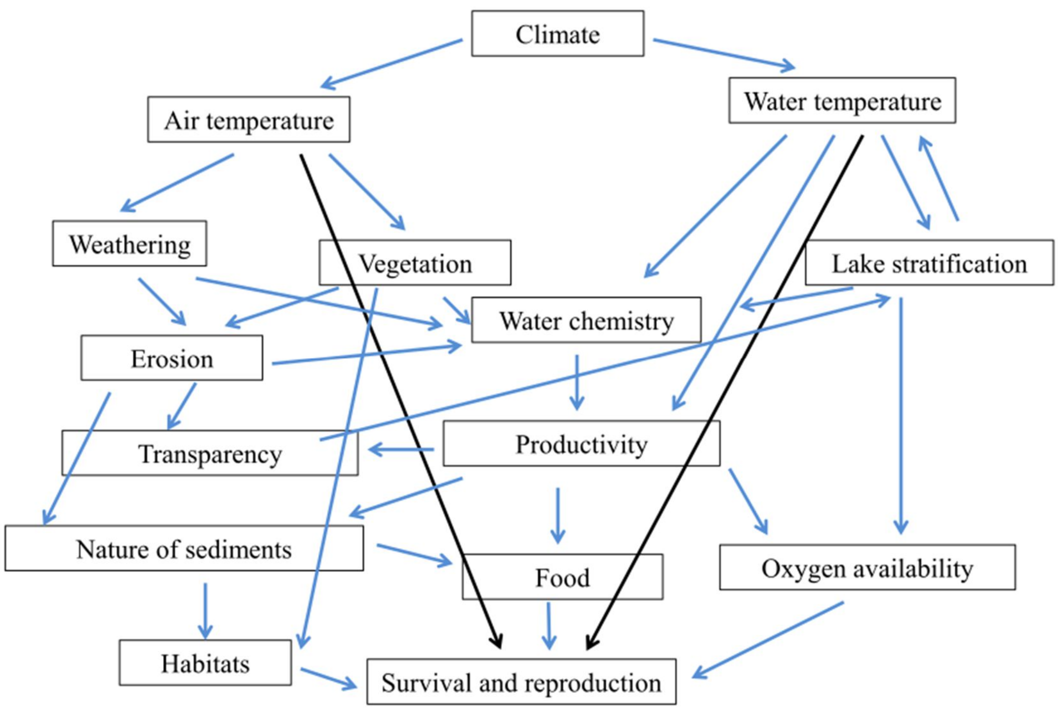

Figure 1.6 Représentation schématique des relations directes (flèches bleues) et indirectes (flèches noires) entre le climat et les communautés de Chironomidae (d'après Eggermont et Heiri (2012)).

Tableau 1.1 : Caractéristiques des fonctions de transfert disponibles

Auteur de la fonction de transfert	**Localisation des lacs de la base de données modernes**	**Nombre de lacs de la base de données modernes**	**Nombre de taxon de la base de données modernes**
Walker et al.1997	Île Devon, Île de Baffin, Nord-est du Québec, Labrador, Nouveau Brunswick, Nouvelle-Écosse, et les Territoires du nord-ouest	39	34
Larocque 2008	Nord-ouest du Québec	75	79
Fortin et al.2015	Canada	435	78
Medeiros et al.2022	Canada, Groenland, Islande, Svalbard	402	172
Suranyi et al.*in press*	Est du Canada et Terre-Neuve	130	130

1.3.3d Reconstitution de l'historique des paléoincendies à partir des charbons de bois

Les charbons de bois extraits des sédiments lacustres ont permis de reconstituer l'histoire postglaciaire des feux (voir chapitres 2 et 4). Pour chaque centimètre d'intervalle de carotte, un volume de 1 cm^3 de sédiment sera prélevé, trempé dans l'eau de javel pendant 24 heures, puis tamisé à 150 µm à l'eau. Les macrocharbons devraient provenir majoritairement d'incendies situés à moins d'une dizaine de kilomètre du lac (Carcaillet et al., 2001 ; Higuera et al., 2007) bien qu'exceptionnellement ceux-ci soient transportés à plus grande distance (Oris, et al., 2014 ; Hennebelle et al., 2020). La quantification (nombre et surface) des charbons s'est faite sous une loupe binoculaire, équipée d'une caméra rattachée au logiciel de traitement d'images WINSEEDLE 2016 (Regent Instruments Canada Inc.). Le taux de sédimentation (en cm^2 an^{-1}), obtenu grâce au modèle âge profondeur, permet de calculer taux d'accumulation des charbons (CHAR ; en mm^2 cm^{-2} an^{-1}), à partir de la surface mesurée des charbons (en mm^2) (Whitlock and Anderson, 2003). Les évènements de feux sont reconstruits à l'aide du logiciel CharAnalysis (Higuera et al., 2009). Les méthodes de Ali et al. (2009), Blarquez et al. (2013), permettront par la suite de séparer les évènements de feu (CHAR series), en feux locaux et régionaux (CHAR fire) et bruit de fond (CHAR background) ou charbons lointains ou remaniés, puis de calculer les intervalles de retour des feux qui est le nombre d'années entre deux évènements successifs de feux.

1.3.3e Reconstitution de l'histoire de la végétation à partir des grains de pollen

En 1916, pour la première fois, Von Post se servira de l'analyse pollinique des sédiments pour reconstituer la végétation passée (Von Post, 1916). La reconstitution des communautés végétales à partir des grains de pollen est régie par des hypothèses de base de la palynologie. D'après Reille (2013), « Les études palynologiques reposent sur un principe : le contenu en grains de pollen du sédiment indique la population de plantes vivant à l'époque du dépôt ». Ce principe dépend de trois autres hypothèses à savoir :

- *la pluie pollinique représente fidèlement la végétation et se dépose uniformément ;*
- *le dépôt, la conservation et l'extraction du pollen ne modifient pas la pluie pollinique ;*
- *la reconnaissance des grains de pollen sous microscope et leur comptage restituent fidèlement la pluie pollinique*

L'analyse pollinique est réalisée sur des échantillons de 1 cm^3 de sédiments prélevés tous les 4 ou 5 cm le long de la carotte. Ce qui correspondrait à une résolution temporelle allant de 100 à 120 ans, selon le taux d'accumulation des sédiments du niveau concerné. Avant l'extraction, un comprimé de Lycopode sera ajouté à chaque échantillon afin de permettre le calcul des concentrations par taxon pollinique. L'extraction pollinique se fera suivant la méthode de Fægri et Iversen (1989). Les grains de pollen seront identifiés au microscope, à l'aide des atlas de Richard (1970), McAndrews et al. (1973) et de la collection de référence du laboratoire de paléoécologie de l'Université de Montréal. L'analyse pollinique a pour finalité l'identification botanique des grains de pollen. Après l'identification et le comptage des taxons présents, nous construirons des diagrammes polliniques caractérisant la végétation (voir chapitres 2 et 4).

1.4 Organisation du manuscrit

Le format de cette thèse est le suivant :

- **Le chapitre 1** décrit le contexte et la problématique, rappelle l'histoire postglaciaire du climat, des régimes de feux et de la dynamique de la végétation au Québec, précise les objectifs de cette thèse et sa mise en œuvre.
- **Le chapitre 2** documente *8500 ans d'histoire des interactions climat-feu-végétation dans le domaine bioclimatique de la pessière à mousses de l'est du Québec, Canada*. Il s'agit spécifiquement de (1) acquérir des données nouvelles de températures, incendies et végétation postglaciaires au lac Mista ; (2) reconstituer l'histoire postglaciaire du climat, des incendies et de la végétation régionale sur la Côte-Nord ; (3) explorer les interactions climat-feu-végétation au cours des 8500 dernières années ; (4) déterminer les facteurs explicatifs de la modification de la végétation régionale au cours des 8500 dernières années. A ce jour, aucune étude paléoécologique multiproxies (chironomes, charbon de bois, pollen), alliant l'histoire postglaciaire du climat, des incendies et de la végétation, n'a été menée dans cette partie de la Côte-Nord. Beaucoup reste donc à apprendre en ce qui concerne les conditions de mise en place et la dynamique de développement préindustrielle voire holocène des forêts de la Côte-Nord. La question à laquelle nous essayons de répondre à travers ce chapitre est de savoir comment les variations de températures postglaciaires influencent la dynamique temporelle de la végétation dans une région de la Romaine (lac Mista ; Fig.1.2) où le climat maritime rend les feux peu récurrents.
- **Le chapitre 3** documente les *changements climatiques postglaciaires inférés par les Chironomidae le long d'un transect est-ouest dans la forêt boréale de coniférienne du Québec, à l'est du Canada*. Il s'agit spécifiquement de (1) acquérir des données nouvelles de températures postglaciaires au lac Adèle ; (2) savoir comment les grandes variations du climat postglaciaire se sont exprimées le long de notre transect ; (3)

vérifier si les principales périodes (HTM, Néoglaciaire) et phases (RWP, DACP, MWP, LIA) climatiques de l'Holocène sont apparents à l'est (lacs Mista et Adèle) et à l'ouest (lac Aurélie) du Québec ; (4) savoir si leurs amplitudes et durées sont plus important à l'est ou à l'ouest du Québec. Trois sites ont été retenus pour ce chapitre (les lacs Aurélie, Adèle et Mista ; Fig.1.2). Pour chacun des trois sites, nous avons reconstituer les paléotempératures à partir de l'approche des Chironomidae (fonction de transfert). Le site se trouvant dans la pessière à mousses de l'ouest (lac Aurélie) a déjà été étudié par Bajolle (2018), ses données Chironomidae sont utilisées dans le cadre de ce chapitre. Etant donné que nous disposerons déjà des données Chironomidae du lac Mista (cf. Chapitre 2), il nous reste donc à reconstituer les paléotempératures du lac Adèle.

- **Le chapitre 4** montre comment *une longue période (multimillénaire) d'incendies récurrents à intervalles rapprochés altère la résilience de la pessière à mousses dans l'est du Canada*. Il s'agit spécifiquement de (1) acquérir des données nouvelles de la végétation postglaciaire au lac Adèle ; (2) savoir si des sites (p.ex., lacs Mista et Adèle ; Fig.1.2) présentant une tendance similaire de la température estivale postglaciaire (cf. Chapitre 3), peuvent avoir des historiques de feu différents ; (3) identifier les facteurs de causalité susceptibles de compromettre la régénération de la pessière à mousses et modifier la trajectoire de la succession végétale ; (4) évaluer la résilience de la pessière à mousses aux incendies. Au cours des derniers millénaires, sous l'effet des changements climatiques, le régime des feux a conduit à l'ouverture du paysage, avec la transformation des pessières à mousses en pessières à lichens (Payette et Delwaide, 2018). Cependant, les mécanismes responsables de cette transformation à l'est du Québec (Couillard et al., 2021 ; Fréchette et al., 2021), particulièrement autour du lac Adèle (Bastianelli, 2018), restent peu connus. Ce chapitre portera sur 2 sites dont les données pollen, charbon et de Chironomidae sont déjà disponibles (Cf. chapitres 2 et 3 ;

Bastianelli, 2018 ; Hennebelle et al., 2018) ou en voie de l'être (nouvelles donnés polliniques du lac Adèle à acquérir, chapitre 4).

- **Le chapitre 5** présente les principaux résultats et contributions de cette thèse, puis suggère des perspectives de recherches futures.

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Chapitre 2

An 8500-year history of climate-fire-vegetation interactions in the eastern maritime black spruce–moss bioclimatic domain, Québec, Canada

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2.1 Abstract

The eastern, maritime portion of the black spruce–moss bioclimatic domain in Québec (Canada) is characterized by large wildfires with low occurrence. However, it is still poorly understood how climate–fire interactions influenced long-term vegetation dynamics in the boreal forest of eastern Québec. The long-term historical climate–fire–vegetation interactions in this region were investigated using a multiproxy (chironomids, charcoal, and pollen) paleoecological analysis of an 8500-year sediment core. Chironomid-inferred August air temperatures suggest that the warm Holocene Thermal Maximum (HTM; between ca. 7000-4000 cal yr BP) shifted to the cooler Neoglacial period (4000 cal yr BP to present), consistent with other temperature reconstructions across Québec. The shift to spruce-moss forest dominance around 4800 cal yr BP occurred nearly a thousand years before the climatic shift to the Neoglacial period and rather coincided with a shift from frequent low-severity small fires to infrequent but large and severe fire events. Our results suggest that long-term changes in the summer temperature are probably not the main factor controlling fire and vegetation dynamics in eastern Québec. It seems that, throughout the postglacial period, summer temperatures never fell below a threshold that could have induced a significant vegetation response.

2.2 Résumé

La partie orientale et maritime du domaine bioclimatique de la pessière à mousse au Québec (Canada), est caractérisée par des grands incendies à très faible occurrence. Cependant, l'effet des interactions climat-feu sur la dynamique à long terme de la végétation dans la forêt boréale de l'est du Québec est peu connu. A l'aide d'une analyse paléoécologique multiproxies (chironomes, charbon de bois, pollen) d'une carotte sédimentaire de 8500 ans, nous avons documenté les interactions à long terme entre le climat, le feu et la végétation à l'est du Québec. Les températures de l'air du mois d'août reconstituées par les chironomes suggèrent que la période chaude de l'Optimum climatique Holocène (7000-4000 ans avant aujourd'hui (AA)) a

cédé place à la période froide du Néoglaciaire (4000 ans AA à l'actuel) en cohérence avec les reconstitutions climatiques réalisées ailleurs au Québec. L'établissement de la pessière à mousses il y a environ 4800 ans s'est produit près d'un millier d'années avant la transition vers le Néoglaciaire et a plutôt coïncidé avec le changement de petits incendies peu sévères fréquents, à de grands incendies sévères peu fréquents. D'après nos résultats, les changements de températures estivales ne semblent pas jouer un rôle prépondérant dans la dynamique de la végétation et des feux dans l'est du Québec. Il semble que, tout au long de la période postglaciaire, les températures estivales n'aient jamais diminué sous un seuil qui aurait induit une réponse significative de la végétation.

2.3 Introduction

In eastern Canada, modern boreal vegetation composition is driven mostly by climatic conditions (Saucier et al., 2009; D'Orangeville et al., 2018; Couillard et al., 2019a) and fire regimes (Gauthier et al., 2001; Baltzer et al., 2021; Couillard et al., 2022). The eastern portion of the black spruce–moss bioclimatic domain (Saucier et al., 2009) is a unique ecosystem at the circumboreal scale (Saucier et al., 2015). This ecosystem is characterized by low fire occurrence and a fire cycle of more than 300 years (Bouchard et al., 2008; Portier et al., 2016; Couillard et al., 2022). As a result, the region's forests consist mainly of old-growth stands (De Grandpré et al., 2009).

A recent synthesis of the postglacial vegetation and climate history of eastern Québec and Labrador (Fréchette et al., 2021) suggests that the initial forests were slow to close due to the persistence of a cold climate until ca. 7500 cal yr BP (calibrated years before present). The current regional vegetation was established about 4000 years ago (Fréchette et al., 2021). However, little is known about the postglacial vegetation history of some parts of eastern Quebec as data are missing across the territory. For example, it is still unclear whether the vegetation composition remained unchanged throughout the postglacial period and across the territory.

Long-term paleoecological and paleoclimate records are important for investigating long-term fire–vegetation interactions since direct measurements of climate and environmental changes are missing for the pre-instrumental period. However, previous studies (Bouchard et al., 2008; Gauthier et al., 2010; Cyr et al., 2012; Portier et al., 2018) looking at the structural and compositional characteristics of old-growth forests over time covered only the last three centuries. In addition, Couillard et al. (2021) used mineral soil charcoal to study past vegetation and fire dynamics, but no link was made to Holocene climate change. Much remains to be learned regarding the drivers of vegetation dynamics during the preindustrial period in the eastern portion of the black spruce–moss bioclimatic domain.

Available paleoecological studies in the eastern portion of the black spruce–moss bioclimatic domain, provide fragmentary knowledge of vegetation, climate, and fire in the Baie-Comeau region (Magnan and Garneau, 2014; Remy et al., 2017a), Sept-Îles region (Mott, 1976; King, 1986), Havre-Saint-Pierre region (Payette et al., 2013; Magnan and Garneau 2014; Sauvé 2016), and Blanc-Sablon region (Lamb, 1980; Engstrom and Hansen, 1985). Portier et al. (2016, 2018) and Couillard et al. (2022) documented regional fire regimes, while Fréchette et al. (2021) presented the postglacial vegetation and climate history in eastern Québec and southern Labrador. However, to date, no paleoecological study, using a multiproxy approach, has been done to understand the postglacial history of climate, fire, and vegetation in the eastern portion of the black spruce–moss bioclimatic domain.

The aim of this study was to examine the relationship between vegetation dynamics and temporal changes in climate and fire activity in eastern Québec, where the current fire regime is currently characterized by a low occurrence of large severe fires (Portier et al., 2018). The climate-fire-vegetation interactions were investigated using a multiproxy (chironomids, charcoal, pollen) paleoecological analysis of an 8500 years core.

2.4 Material and methods

2.4.1 Study site

Lake Mista (51.10279 N -63.44291 W, ~500 m.a.s.l.; Fig. 2.1) is a small (ca. 0.27 ha surface area) and shallow lake (5 m maximum depth) with no major inlet. Most of the water drains to the lake from a small forested watershed (ca. 8 ha). It is located in the eastern Canadian boreal forest, within the eastern portion of the black spruce–moss bioclimatic domain (Saucier et al., 2009). According to Dalton et al (2020), the deglaciation of the study area occurred at approximately 10300 cal yr BP. The landscape is hilly, dominated by undifferentiated till between numerous rock outcrops. The climate is relatively cold and rainy, with a mean annual temperature of -1°C, a mean August temperature of 13.5°C and mean total annual precipitation of 976 mm (reference period: 1981-2010; Régnière et al., 2017). The current vegetation surrounding lake Mista is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.) with balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch) and white birch (*Betula papyrifera* Marsh.) as companion tree species. Groundcover vegetation is mostly composed of feather mosses (*Pleurozium schreberi*) with occasional patches of *Sphagnum* spp. Fire is a major natural disturbance (Gauthier et al., 2001), but windthrow (Pham et al., 2004), spruce budworm (*Choristoneura fumiferana* Clemens) and hemlock looper (*Lambdina fiscellaria* Guenée) outbreaks (De Grandpré et al., 2009; Morin et al., 2009) are also important disturbances.

2.4.2 Coring and chronology

In May 2017, a sediment core (373 cm total length) was retrieved from the deepest part of lake Mista using a Kajak-Brinkhurst gravity corer for the top 20 cm, and a 5 cm diameter modified

Livingstone-type square-rod corer for the subsequent 353 cm. Sampling of the top 20 cm at 0.5 cm resolution was performed in the field using an extruder device. The 353 cm long core was retrieved in 4 successive and partly overlapping sections of 1 meter each.

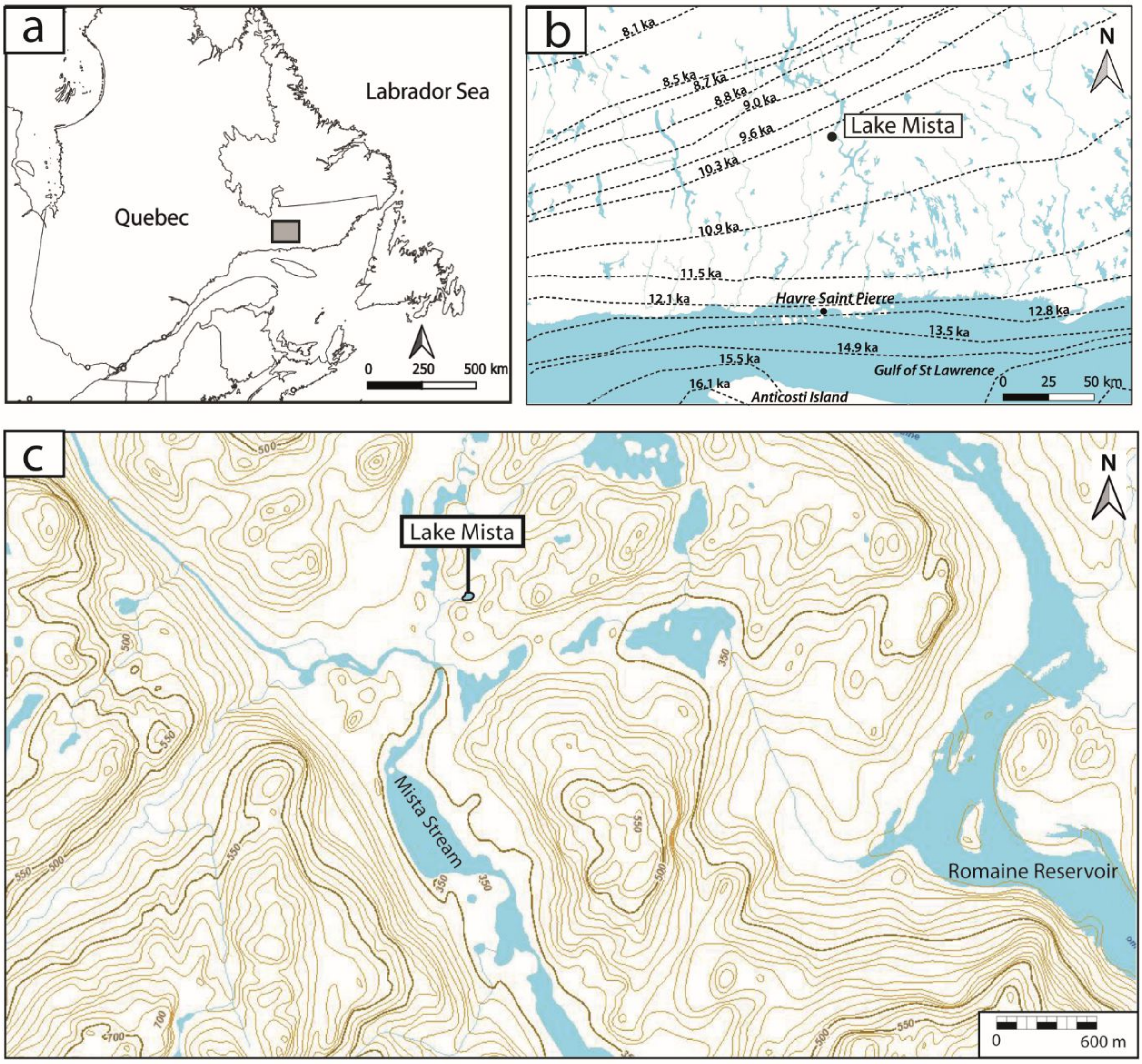

Figure 2.1 Location map of the study site (Lake Mista). (a) Location of the study area (grey square) in Québec-Labrador; (b) location of the study site (Lake Mista) and deglaciation isochrones of the Laurentide ice sheet with ages in ka BP according to Dalton et al. (2020); and (c) location of the study site showing topography (https://vgo.portailcartographique.gouv.qc.ca/).

The chronology of Lake Mista is based on accelerated mass spectrometry (AMS) radiocarbon (^{14}C) dating of five samples (Table 2.1). The five radiocarbon dates were calibrated to calendar ages (cal yr BP) using the IntCal20 software (Reimer et al., 2020). In addition, to obtain an age-depth model for the top sediment core, short-lived radionuclides (^{210}Pb, ^{226}Ra, ^{137}Cs, and ^{241}Am) were measured in the top 20 cm surface sediment using a gamma spectrometer. Measurements were made in a very low background environment in the underground laboratory of Modane (LSM/Chrono-Environment Radionuclide Unit). Supported ^{210}Pb was determined from raw ^{226}Ra. The activity of excess ^{210}Pb in each sediment layer was determined from subtraction of total ^{210}Pb and supported ^{210}Pb (Supplemental Material S2.1). The equilibrium depth was reached at 10cm based on the Constant Rate Supply (CRS; Appleby and Oldfield, 1978) model. A composite age-depth model was built from the combination of ^{210}Pb and ^{14}C dates using the clam 2.2 (Blaauw, 2010) and R 3.3.2 (R Core Team, 2016) softwares.

2.4.3 Pollen analysis

Seventy-nine subsamples of 1cm^3 each were taken at 4-5 cm intervals (i.e.100-120 years temporal resolution depending on sedimentation rate). Before extraction, a *Lycopodium* tablet was added to each subsample in order to calculate pollen concentration (grains cm^{-3}) and pollen accumulation rate (PAR; grains cm^{-2} year^{-1}). Pollen extraction followed standard methods described in Fægri and Iversen (1989).

Three hundred pollen grains were counted in each of the 79 subsamples. Counting was performed under a light microscope at 400x magnification. Pollen grains were identified for family, genus, and species levels following Richard (1970), McAndrews et al. (1973) and the reference collection of the University of Montréal paleoecology lab. Differentiation of *Picea mariana* and *Picea glauca* pollen grains was based on their morphological characteristics (i.e., saccus shape, position of attachment of saccus to corpus, density and arrangement of internal reticulate structure of saccus, corpus area differences; Richard, 1970; Hansen and Engstrom, 1985). The *Betula* pollen grains were identified at genus level as we did not differentiate birch tree species (e.g., *Betula alleghaniensis* Britton, *Betula papyrifera* Marshall) and shrubby birch species (e.g., *Betula glandulosa* Michaux) by measuring their pollen diameter size (Richard, 1970).

Table 2.1 ^{210}Pb and ^{14}C ages used for age-depth model of Lake Mista sediment stratigraphy.

Laboratory code	Dated material	Depth (cm)	Radiocarbon age (^{14}C years BP, 1σ error)	Age cal BP (2σ error)
Pb-01	Sediment	0-1.5		-67
Pb-02	Sediment	1.5-2.5		-54±1
Pb-03	Sediment	2.5-3.5		-48±1
Pb-04	Sediment	3.5-4.5		-27±4
Pb-05	Sediment	4.5-5.5		-12±7
Pb-06	Sediment	5.5-6.5		8±11
Pb-07	Sediment	6.5-7.5		11±9
Pb-08	Sediment	7.5-8.5		16±8
Pb-09	Sediment	8.5-9.5		33±11
Pb-010	Sediment	9.5-10.5		71±18
D-AMS 025608	Herbaceous stems	69-74	2103±21	2064 (1997-2123)
D-AMS 025609	Herbaceous stems	151-156	3694±27	4036 (3928-4145)
D-AMS 025610	Herbaceous stems	229-234	5109±27	5812 (5751-5923)
D-AMS 025611	*Picea glauca* cone	342-343	7472±33	8283 (8193-8367)
D-AMS 025612	*Picea glauca* cone	359-360	7741±32	8511 (8430-8590)

2.4.4 Charcoal analysis and fire regime reconstruction

Macroscopic charcoal extraction and counting

Contiguous subsamples of 1 cm^3 taken at 1 cm intervals were soaked in aqueous 8% sodium hypochlorite (NaClO) during 24 h in order to bleach non-charcoal organic matter. The subsamples were wet, sieved through a 150 µm mesh then transferred to a Petri dish for counting (charcoal abundance) and measuring (charcoal area) macroscopic charcoal particles under a stereomicroscope coupled with the WINSEEDLE 2016 software (Regent Instruments Canada Inc.). The macroscopic charcoal particles (≥ 150 µm) were expected to come from a mix of local and regional fire events having occurred less than 10 km from the lakeshore (Oris et al., 2014; Hennebelle et al., 2020).

Reconstruction of paleofire history

Statistical analyses of charcoal data were performed using the CharAnalysis 1.1 program (Higuera et al., 2009). The sedimentation rate ($cm^2.year^{-1}$) obtained from the age-depth model, was used to calculate charcoal accumulation rates (CHAR; mm^2 cm^{-2} $year^{-1}$), from the measured area (mm^2) of charcoal pieces (Whitlock and Anderson, 2003). The CHAR series were interpolated to a median sample resolution of 23 years in order to remove bias induced by variable sedimentation rates (Higuera et al., 2010), then separated into local fires (CHAR peak) and nonlocal or redeposited charcoal (CHAR background). CHAR background was estimated using a 500-year moving window with LOWESS smoother robust to outliers (Higuera et al., 2008). This window width captured centennial-scale variation in CHAR series. It was least affected by the high-frequency CHAR peaks (Gavin et al., 2006) and provided the best signal-to-noise index (SNI > 3; Kelly et al., 2011; Brossier et al., 2014). The locally defined CHAR peak was calculated by subtracting the CHAR background from the interpolated CHAR series. The CHAR peak component was split into two subcomponents (CHAR peak noise (non-fire event) and CHAR peak signal (fire event) using a Gaussian mixture model (Higuera et al., 2007). A 99th percentile cutoff of the noise distribution was considered as the threshold value for fire event identification. Fire occurrence (number of fire events per 1000 years) was estimated by smoothing the CHAR peak signal, with a 1000-yr moving window. The cutoff probability for the minimum count analysis value was set to 1. The fire return intervals (FRIs) were calculated from the CHAR series. CHAR peak magnitude was used as an indicator of fire size and/or severity (Higuera et al., 2005; Ali et al., 2012).

2.4.5 Chironomid analysis and temperature reconstruction

Paleotemperatures were reconstructed from chironomids, a climate proxy independent of pollen. Chironomids are a useful paleoecological proxy because of their abundance and taxonomic diversity, their possible identification to subfamily, tribe, genus, or even species group levels, the good preservation of their head capsules in lake sediments, their sensitivity, and their rapid response to environmental changes (Walker, 1987). Direct and indirect relationships between air temperature, water temperature, and distribution of chironomid communities enable the development of chironomid-based transfer functions and quantitative temperature reconstructions (Eggermont and Heiri, 2012).

Chironomid extraction, identification and counting

Seventy-nine subsamples of wet sediments were taken at 4-5 cm intervals, at the same depths as for pollen analysis. The size of each analyzed subsample was adjusted to have a minimum count of 50 head capsules. Chironomid head capsule extraction and mounting followed standard preparation technique described in Brooks et al. (2007). Specimen identification was performed under a light microscope at 400x magnification. The identification of chironomid specimens to genus and species-group relied on several keys (e.g., Larocque and Rolland, 2006; Brooks et al., 2007; Andersen et al., 2013; Larocque, 2014).

Temperature reconstruction

For Canada, several transfer functions are now available to infer summer air temperatures from subfossil assemblages of Chironomidae (i.e. Larocque, 2008; Fortin et al., 2015; Medeiros et al., 2022). These inference models are built on the study of the modern distribution of subfossil Chironomidae assemblages in lake surface sediments distributed along latitudinal climate gradients. They differ in the number of modern sites, their geographical distribution, the climatic gradient covered, and the taxonomic resolution of chironomid taxa identification (Supplemental Material S2.2a, b). For this study, we chose to use the transfer function of Larocque (2008). Indeed, based on their performance statistics (Supplemental Material S2.2a), the transfer function (TF) of Larocque (2008) was more likely to yield accurate reconstructions. The temperature reconstruction patterns obtained with other TFs were similar (Supplemental

Material S2.2c), but the ones obtained using the Larocque (2008) TF yielded values closer to the monitored values for the current period (13.5°C; Régnière et al., 2017).

The eastern Canadian modern calibration dataset of Larocque (2008) comprises 75 lakes and 79 taxa. This calibration dataset covered August air temperature ranging from 3°C to 21°C i.e. an 18°C gradient. Two components Weighted Averaging Partial Least-Squares regression (WAPLS) served as inference model and bootstrapping was used to estimate the sample-specific errors for the fossil samples. Taxa absent from the modern calibration dataset were removed from the fossil dataset (Birks et al., 1990). The robustness of the inferred August air temperature was assessed by calculating (1) the chi-square distance to the closest modern assemblage; (2) the goodness-of-fit with temperature (Birks et al., 1990); (3) the percentage of chironomid taxa considered to be rare in the modern calibration dataset (i.e., with a Hill's N2 (Hill, 1973) less than 5; Heiri et al., 2003); (4) the statistical significance of the reconstructions (Telford and Birks, 2011). Based on their chi-square distance to the closest modern assemblage, fossil chironomid assemblages were identified to be "good analogs" (if the chi-square distance was within the 1st-5th percentiles), "poor analogs" (>10th percentile and <20th percentile) or "no analog" (>20th percentile). Goodness-of-fit to temperature was assessed by passively fitting fossil samples to the canonical correspondence analysis (CCA) of the modern calibration dataset with August temperature as the only constraining parameter. Fossil samples with a squared residual length to CCA axis 1 above the 90th and 95th percentiles of the residual distances of all modern samples were considered as having a "poor fit" and "very poor fit" with temperature respectively (Birks et al., 1990). The percentage of chironomid taxa considered to be rare in the modern calibration dataset was estimated with the "compare" function in analogue R package (Simpson, 2007). The chironomid effective diversity (Hill's N2 index) was measured using the utility function in rioja R package (Juggins, 2014).

2.4.6 Numerical and statistical analysis

Both the pollen percentage diagram as well as the chironomid abundance diagram were plotted using the strat.plot function in the rioja R package (Juggins, 2014). Zonation of the pollen and chironomid percentage diagrams were defined using stratigraphically constrained cluster analysis (CONISS; Grimm, 1987). For both proxies, the number of statistically significant assemblage zones was determined by applying the broken-stick model (Bennett, 1996).

A detrended correspondence analysis (DCA) was performed separately on the chironomid and pollen percentage matrix using the decorana command in the vegan R package (Oksanen et al., 2018). Only chironomid taxa and pollen taxa present in at least two samples and with a relative abundance higher than 2% in at least one sample were included in the analysis. The length of each first axis of the DCA determined whether the distribution pattern of each proxy along the DCA axis 1 was linear or unimodal (Borcard et al., 2011). Following the gradient length of the DCA axis 1 (chironomid: 1.44 standard deviation (SD) units; pollen: 1.15 SD), a principal component analysis (PCA) was performed on the pollen and chironomids square-root-transformed percentage matrix in order to highlight main changes in assemblage composition during the postglacial period.

2.5 Results

2.5.1 Chronology

Radiocarbon (^{14}C) and ^{210}Pb dating were used to generate the age-depth model showing a mean sedimentation rate of ~0.045 cm per year. The extrapolation of the age-depth model to the bottom of the core (373 cm) suggests that the accumulation of organic sediment began at ca. 8500 cal yr BP (Fig. 2.2). The top 10 cm represents ca 150 years (from 1880 to 2017 AD).

2.5.2 Pollen record

The stratigraphically constrained cluster analysis of the Lake Mista pollen record indicated eight significant pollen assemblage zones (PAZ-1 to PAZ-8; Fig. 2.3).

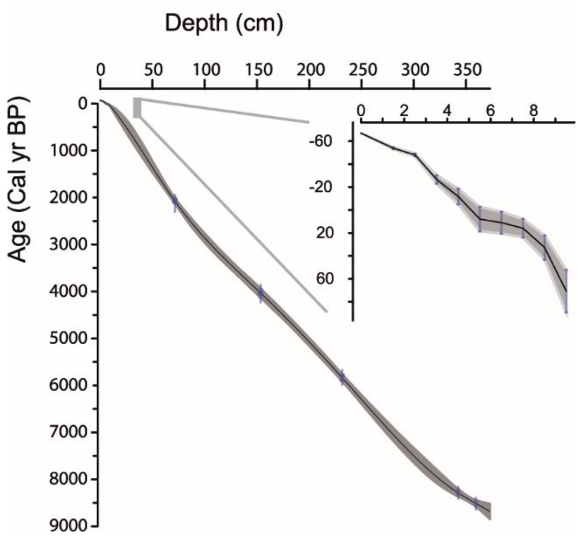

Figure 2.2 Age-depth model of Lake Mista based on ^{14}C and ^{210}Pb dates. The black line represents the inferred chronology modeled using a smoothing spline function (spar=0.3). The 95% confidence intervals for the model are shown in grey.

PAZ-1 (ca. 8500-8100 cal yr BP)

PAZ-1 corresponds to progressive afforestation of the vicinity of the lake, with high values of *Picea mariana* (37-73%), *Betula* spp. (9-22%) and *Alnus crispa* (Aiton) Raus (6-15%). Cones of *Picea glauca* found at 359.5 and 342.5 cm (Table 2.1) confirm that more than 8500 years ago, the vegetation surrounding Lake Mista already hosted *Picea glauca* populations mature enough to reproduce.

PAZ-2 (ca. 8100-7800 cal yr BP)

Abies balsamea (25-46%) settled in the vicinity of the lake during PAZ-2. They dominated with *Betula* spp. (22-32%), perhaps with *Alnus crispa* (5-12%). *Picea glauca* (5-9%) was probably still present and *Picea mariana* (8-13%) decreased in abundance (Fig. 2.3; Supplemental Material S2.3).

PAZ-3 (ca. 7800-6700 cal yr BP)

Abies balsamea (7-19%) remained present, although less abundant during PAZ-3. Despite the

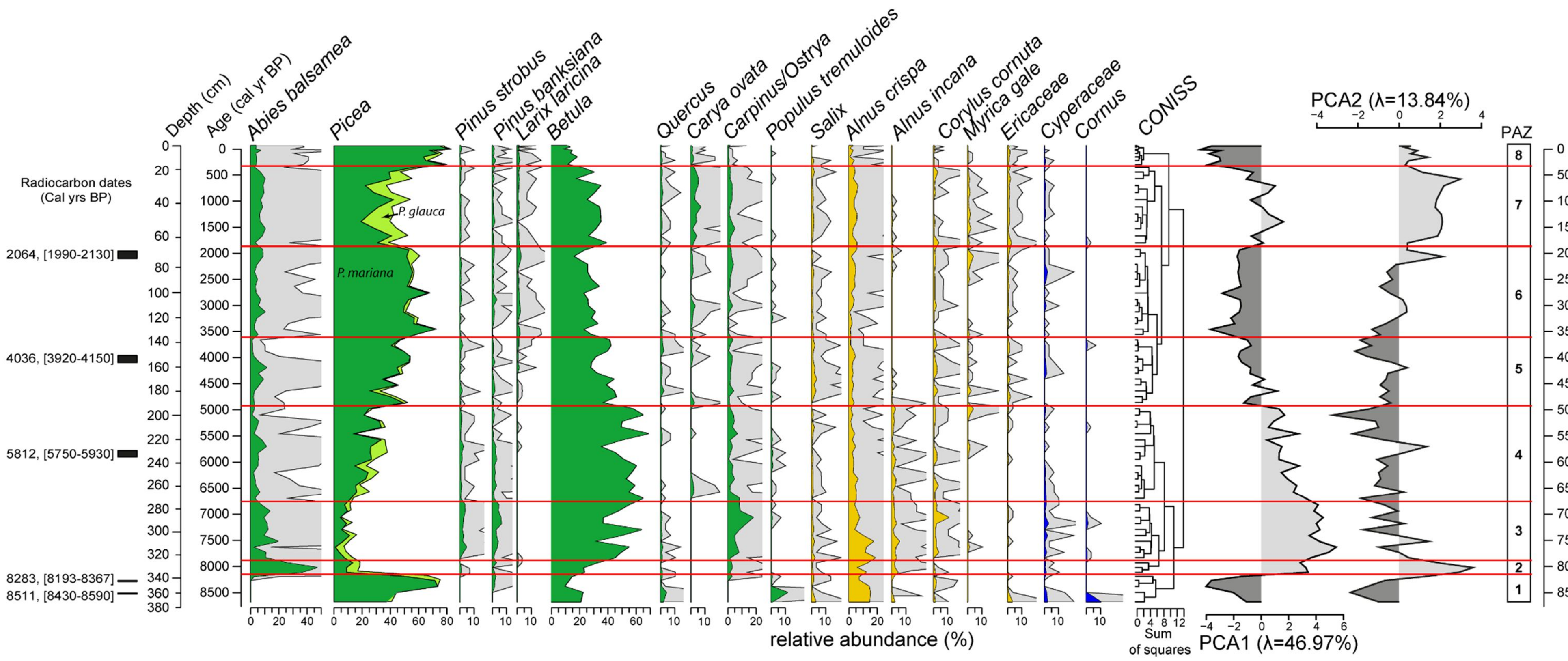

Figure 2.3 Simplified pollen percentage diagram, with trees (green), shrubs (yellow), and herbs (blue). The CONISS cluster dendrogram is also shown. Pollen PC axis 1 and axis 2 sample scores (λ indicates the proportion of variance explained by the PC axis of the fossil data), and pollen assemblage zones (PAZ; horizontal solid red lines) are also displayed

rising percentage of *Betula* spp. (30-63%), the influxes (Supplemental Material S2.3) show that their populations have not increased around the lake. *Carpinus/Ostrya* grains likely represent increased pollen inputs from the south, perhaps due to an opening of the regional forest, also indicated by low values of total pollen influx (Supplemental Material S2.3). The boundary between PAZ-3 and PAZ-4 marks the end of afforestation.

PAZ-4 (ca. 6700-4800 cal yr BP)

PAZ-4 is a transitional zone marked by a regional increase in *Picea mariana* tree populations as supported by the pollen percentages (12-33%; Fig. 2.3) and influxes (Supplemental Material S2.3). *Betula* spp. (34-68%) reached its maximum postglacial abundance according to pollen percentages and influxes (Fig. 2.3; Supplemental Material S2.3). *Picea glauca* (1-12%) was probably still present according to the influxes. From PAZ-4 to PAZ-8, the pollen influx trends of major taxa (Supplemental Material S2.3) show the same pattern as their pollen percentages (Fig. 2.3).

PAZ-5 (ca. 4800-3600 cal yr BP)

Picea mariana tree populations continued to increase in PAZ-5. Subsequently, *Picea mariana* (25-54%) became the dominant taxon with *Betula* spp. (27-45%) and *Abies balsamea* (1-11%) as companion tree species.

PAZ-6 (ca. 3600-1800 cal yr BP)

Picea mariana (49-72%) dominated the forest canopy in PAZ-6. *Abies balsamea* (2-10%) was still a companion species, whereas *Betula* spp. (15-33%) slightly decreased. *Picea glauca* (1-9%) was scarcer than before and thereafter. *Alnus crispa* (1-5%) experienced a modest revival, without abounding.

PAZ-7 (ca. 1800-300 cal yr BP)

Picea mariana (19-57%) regressed in PAZ-7 and was likely replaced by *Picea glauca* (5-20%) (see percentage and influx; Fig. 2.3 and Supplemental Material S2.3). *Carya ovata* (Miller) K. Koch. (1-6%) showed surprisingly high percentages and its influxes increased (Fig. 2.3; Supplemental Material S2.3).

PAZ-8 (ca. 300 cal yr BP to present)

PAZ-8 marks the closure of the forest cover. *Picea mariana* (63-81%) increased (see influx; Supplemental Material S2.3). *Betula* spp. (7-18%) regressed but *Abies balsamea* (3-7%) remained a companion tree in the spruce moss forest.

2.5.3 Charcoal record

During the past 8500 years, there were 49 fire events with a mean FRI of 181 years (95% confidence interval 149-215 years) and a range of 111 to 331 years (Fig. 2.4). The signal-to-noise index at 163 cal yr BP (SNI=2.85) and from ca. 140 cal BP to present (SNI=0) were unreliable due to difficulties in separating CHAR peak noise (non-fire event) and CHAR peak signal (fire event). Excluding these periods, the SNI values were above 3, with a median value of 8.49 for the entire sequence, supporting therefore their reliability for the reconstruction of local fire activity (Courtney-Mustaphi et al., 2015).

Four periods with distinct fire occurrence can be distinguished in the record (Fig. 2.4). From 8500 to 5000 cal yr BP, fire occurrence dropped from its highest level of 9, to 4 fires kyr^{-1}. Between 5000 and 3600 cal yr BP, fire occurrence reached its lowest values and varied between 2 and 4 fires kyr^{-1}. Peak magnitudes were larger than before 5000 cal yr BP. From 3600 to 1300 cal yr BP, fire occurrence increased slightly from 4 to 6 fires kyr^{-1}. The largest peak magnitude was recorded during this period. After 1300 cal yr BP, fire occurrence dropped to present day 3 fires kyr^{-1}. A notable peak magnitude was recorded around 1000 cal yr BP. The lowest and highest FRI values were reached at ca. 8500 cal yr BP (111 yr/fire) and ca. 4000 cal yr BP (331 yr/fire), respectively.

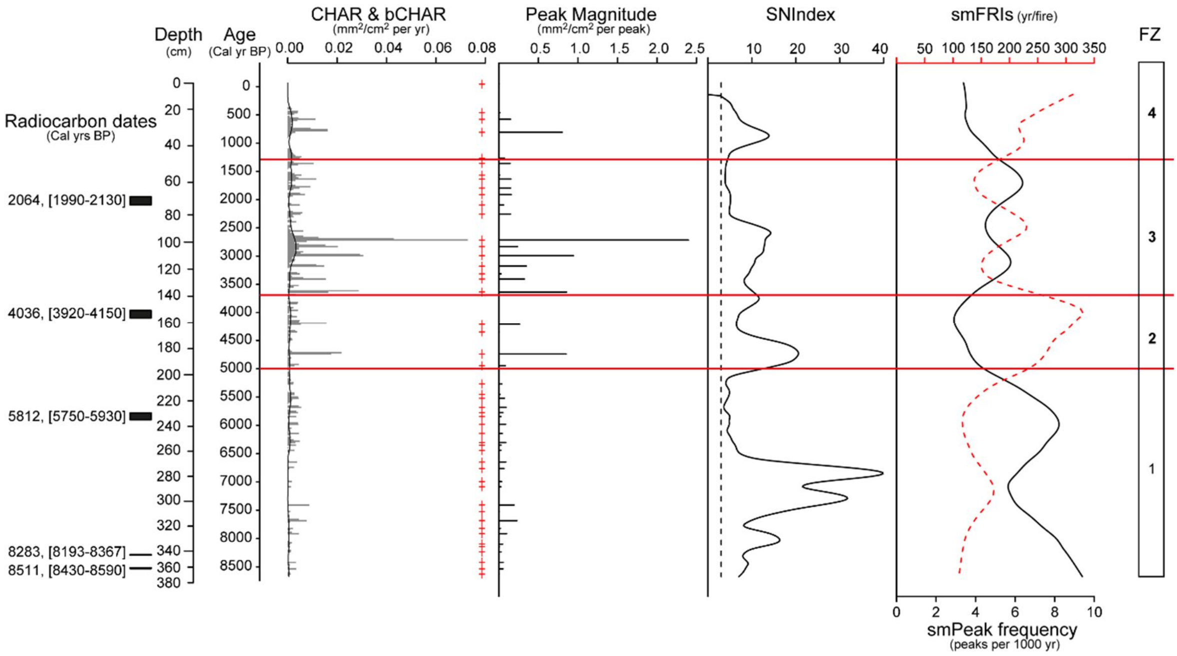

Figure 2.4 Charcoal accumulation rates (CHAR), CHAR background (bCHAR), fire events, peak magnitude of fire events, signal-to-noise index (threshold value of 3: vertical dashed black line), fire occurrence (smPeak frequency) and return interval (smFRIs). Fire zones (FZ; horizontal solid red lines) are also shown.

2.5.4 Chironomid stratigraphy and inferred August temperature

The chironomid record was split into two significant chironomid assemblage zones (CAZ-1 and CAZ-2; Fig. 2.5) due mainly to changes in *Micropsectra insignilobus*-type relative abundance. This biozonation suggested by the stratigraphically constrained cluster analysis is further supported by the sharp increase in chironomid PC axis 1 sample scores (Supplemental Material S2.4a).

CAZ-1 (ca. 8500-1200 cal yr BP)

Micropsectra insignilobus-type abundance was less than 15% throughout CAZ-1, which was further divided into three sub-biozones (CAZ-1a to CAZ-1c) according to minor changes in some chironomid taxa.

CAZ-1a (ca. 8500-8100 cal yr BP) was characterized by the dominance of cold stenotherm taxa such as *Heterotrissocladius marcidus*-type, *Chironomus anthracinus*-type, *Corynocera oliveri*-type, *Tanytarsus lugens*-type, and *Sergentia coracina*-type (Brooks et al., 2007). A notable and characteristic presence (at less than 2%) of chironomids with colder optima (e.g., *Heterotrissocladius subpilosus*-type, *Paracladopelma*, *Pseudodiamesa*, *Protanypus*, *Diplocladius*; Supplemental Material S2.4b; Brooks et al., 2007) suggests that a particularly cold phase occurred over a short period centered on 8200 cal yr BP.

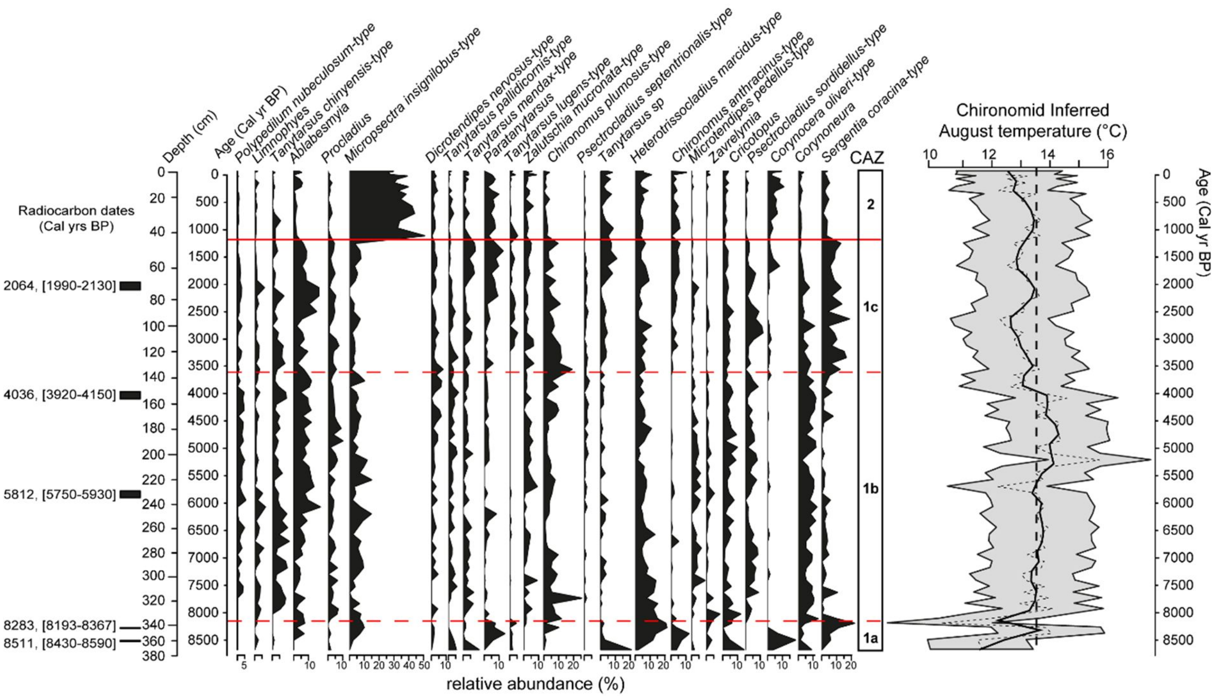

Figure 2.5 Simplified chironomid percentage diagram, chironomid assemblage zone (CAZ; in horizontal solid red line, sub-biozones in horizontal dashed red lines), chironomid inferred August temperature (dashed black line; with a LOWESS smoother in solid black line (span=0.073), with the grey area delimiting the minimum and maximum sample-specific estimated standard error of prediction (eSEP)). Present day August temperature (13.5°C; Régnière et al. (2017)) is also shown (vertical dashed black line).

CAZ-1b (ca. 8100-3600 cal yr BP) was characterized by the high abundance of *Ablabesmyia*, *Heterotrissocladius marcidus*-type, *Micropsectra insignilobus*-type, *Corynoneura*, and *Tanytarsus chinyensis*-type. There was a notable development of taxa associated to aquatic macrophytes like *Limnophyes*, *Polypedilum nubeculosum*-type, *Chironomus plumosus*-type, *Psectrocladius sordidellus*-type, and *Microtendipes pedellus*-type (Brooks et al., 2007; Millet et al., 2007, 2012). The abundance of *Polypedilum nubeculosum*-type between ca. 7500-4000 cal yr BP, a taxon with warm optima in European and Canadian modern data sets (e.g., Larocque, 2008; Heiri et al., 2011), suggests warm conditions.

CAZ-1c (ca. 3600-1200 cal yr BP) was characterized by an increase in *Sergentia coracina*-type. From ca. 3600 cal yr BP, there was a decrease in *Polypedilum nubeculosum*-type, a taxon characteristic of warm eutrophic lakes, in favor of taxa indicative of cold and well-oxygenated oligotrophic lakes such as *Sergentia coracina*-type, *Chironomus anthracinus*-type, *Tanytarsus lugens*-type, *Heterotrissocladius marcidus*-type, and *Corynocera oliveri*-type (Brooks et al., 2007).

CAZ-2 (ca. 1200 cal yr BP to present)

CAZ-2 was characterized by the dominance of *Micropsectra insignilobus*-type, a cold stenotherm chironomid characteristic of well-oxygenated oligotrophic lake environments (Brooks et al., 2007). The presence of *Corynocera oliveri*-type and *Sergentia coracina*-type likely supports the assumption of cold conditions (Brooks et al., 2007). On the other hand, around ca. 1200 cal yr BP the drop in the relative abundance of cold indicating taxa (e.g., *Sergentia coracina*-type) before rising again at ca. 500 cal yr BP probably marked a warmer phase between 1200 and 500 cal yr BP. The reappearance of *Heterotrissocladius subpilosus*-type, *Protanypus*, and *Diplocladius* at ca. 300 cal yr BP (Supplemental Material S2.4b) implies a very cold and ultraoligotrophic lake environment at the time (Brooks et al., 2007).

Out of the 79 fossil samples, 51 samples had “poor” analogs, while 12 others had “no” analog with the calibration dataset. The bottom sample had a very poor fit to temperature, while eight other samples within the sequence had a poor fit with temperature (Supplemental Material S3c).

All fossil samples contained less than 20% (range 4.3-17.48%) of rare taxa in the training set (Supplemental Material S2.4c) as needed to obtain reliable estimation of temperature from a fossil sample (Brooks and Birks, 2001; Larocque-Tobler, 2010). The sample-specific estimated standard error of prediction (eSEP) for inferred temperature varied between 1.67 and 1.92°C. Inferred temperatures were statistically significant (p=0.041) when compared to 999 random reconstructions as recommended by Telford and Birks (2011).

Chironomid inferred August temperature (Fig. 2.5) suggests a warming climate from ca. 8500 to 4000 cal yr BP (average temperature 13.5°C; range 10.2-15.7°C) followed by a cooling trend from ca. 4000 cal yr BP to present (average temperature 13°C; range 12.2-13.7°C).

2.6 Discussion

2.6.1 Temperature reconstruction

Reliability of the chironomid-inferred mean August air temperature

The chironomid stratigraphy suggests that other environmental and limnological factors than summer temperature may have played a role on assemblage changes. These factors may ultimately be related to the climate, but because of the indirect nature of the relationship between chironomid assemblages and climate, it is necessary in this case to go further in assessing the reliability of the chironomid inferred August temperature by looking at the diagnostic elements (i.e. rare taxa, fit to temperature, modern analogs).

Rare taxa. All fossil samples had at least 82% of their taxa represented in the modern training set (i.e. beyond the 80% objective criterion; Larocque-Tobler, 2010). Inferred temperatures are likely to be less well estimated for 38 fossil samples containing more than 10% of taxa that are considered to be rare taxa in the training set (Brooks and Birks, 2001). This concerned particularly the period before 4000 cal yr BP (Supplemental Material S2.4c) in which all fossil samples had poor or no analog. However, the WAPLS regression performs well even under non-analog situations once the above-mentioned rare taxa objective criterion is met (Birks, 1998).

Fit to temperature. After 6000 cal yr BP, all fossil assemblages were well fitted by temperature. The eight fossil assemblages which are poorly or very poorly fitted by temperature before 6000 cal yr BP suggest that other controlling factors than climate may have punctually influenced chironomid changes between ca. 8500 and 6000 cal yr BP (Velle et al., 2005, 2010). Therefore, the inferred temperatures for this period should be interpreted with caution. Indeed, in-lake variables can influence chironomid assemblages over shorter timescales (Brodersen and Quinlan 2006). Multiple factors likely controlled chironomid distributions. Nevertheless, the period before 6000 cal yr BP was documented by a total of 24 samples, with two-thirds (i.e.16) having their assemblages well fitted by temperature.

Modern analog. Although the present-day temperature was within the error margin of our reconstructions, the accuracy of the chironomid inferences, especially for the period before 4000 cal yr BP that had the highest number of rare taxa and also poor or no analog, could be improved by sampling and adding more lakes with temperatures between 16 and 19°C to the calibration set as earlier suggested by Bajolle et al. (2018). The majority of fossil samples having a high number of rare taxa and also poor or no analog were found during the warmest period suggesting that the lake environment was probably different from the current situation. Therefore, the best analogs for early and mid-Holocene assemblages are likely to be found in present-day southern lakes. The reconstructed modern temperature differed from present day mean August temperature of 13.5°C likely because surface sample had poor analogs in the training set or because the top surface sample was missing.

Thus, interpretations of August-temperatures reconstructed from Chironomidae assemblages will be restricted to major changes that have occurred at millennial to multi-millennial time scales.

Chironomid-inferred major climatic periods

Holocene Thermal Maximum (HTM): ca. 7000-4000 cal yr BP. The chironomid inferred reconstructions (Fig. 2.5, 2.6) suggest that warm temperatures were recorded in the Lake Mista region between ca. 7000 and 4000 cal yr BP. This corresponds to the HTM, which mostly occurred between 7000 and 5000 in northeastern North America (Renssen et al., 2012). For instance, in eastern Québec and Labrador (Eastern Canada), pollen-based reconstructions indicated maximum temperatures between ca. 7500 and 3500 cal yr BP (Fréchette et al., 2021). The timing and duration of the HTM depends on various forcings including orbitally forced insolation, the deglaciation of the Laurentide Ice Sheet (LIS) and the atmospheric greenhouse gases (Renssen et al., 2012). For Québec, the presence of the LIS and its decay may partly explain the differences observed between the sites depending on their proximity to LIS remnants (Fréchette et al., 2021).

In western Québec, chironomid inferred August temperatures were warmer with high magnitude values during the HTM (Bajolle et al., 2018). The low magnitude values at lake Mista may partly be due to the increasing east-to-west temperature gradient of continentality in the black spruce-moss bioclimatic domain (Saucier et al., 2009; Couillard et al., 2019a).

Neoglacial period: ca. 4000 cal yr BP to present. The chironomid-based temperature reconstructions from Mista suggest that after 4000 cal yr BP, temperature decreased and were about 1°C cooler than those recorded before this turning point (Fig 2.6). This cooler period corresponds to the so-called Neoglacial period. Indeed, at mid and high latitudes of the Northern Hemisphere, climate gradually shifted from a warm HTM to a cool Neoglacial with steadily decreasing summer insolation (Ali et al., 2012). Compared to other inferred temperature records across Canada (Gajewski, 2015; Bajolle et al., 2018; Fréchette et al., 2018, 2021), the onset of the Neoglacial period was delayed in some areas of Quebec and Labrador until after 3200 cal yr BP (Gajewski, 2015). Close to our study site, in Havre Saint Pierre, the peat-based paleohydrological records indicated that the Neoglacial cooling characterized by major changes in peat accumulation rate and bog surface moisture began around 3000 cal yr BP (Magnan and Garneau, 2014).

The Neoglacial period was probably characterized by a series of higher frequency climate variability that should be interpreted cautiously because the variations remain within the error margin of the inferred temperatures (Supplemental Material S2.4c).

2.6.2 Climate-fire-vegetation interactions

The vegetation history was marked by two major phases (Fig. 2.6), afforestation (8500-6700 cal yr BP) and forest phases (6700 cal yr BP to present).

Afforestation phase 8500-6700 cal yr BP

Spruce-moss forest 8500-8100 cal yr BP. Pollen assemblages from the bottom of the core suggest that vegetation – a *Picea mariana*-dominated woodland or forest – gradually colonized the ice-free areas following the slow decay of the Laurentide Ice Sheet (Blarquez and Aleman, 2015; Richard et al., 2020; Fréchette et al., 2021).

Balsam fir-birch forest 8100-6700 cal yr BP. Starting from 8100 cal yr BP, the prevailing warm temperatures were suitable (Sims et al., 1990; Bergeron et al., 2014) to the establishment of *Abies balsamea*-*Betula* spp. mixed-woods. Smaller and less severe fires likely due to wet conditions between 7350 and 6560 cal yr BP (Magnan and Garneau, 2014) probably exempted some areas from burning, allowing *Abies balsamea* and *Betula* spp. (mostly *Betula papyrifera*; Fréchette et al., 2021) from remnant stands to reinvade burned areas (Asselin et al., 2001; Bergeron et al., 2004). The very low abundance of *Picea mariana* pollen could question the actual presence of the species in the local vegetation at that time (Payette, 1993). However, based on macro-remains, Couillard et al. (2018) confirmed the local presence of *Picea mariana* and *Abies balsamea* not later than 8300 cal yr BP south of Lake Mista. Furthermore, Couillard

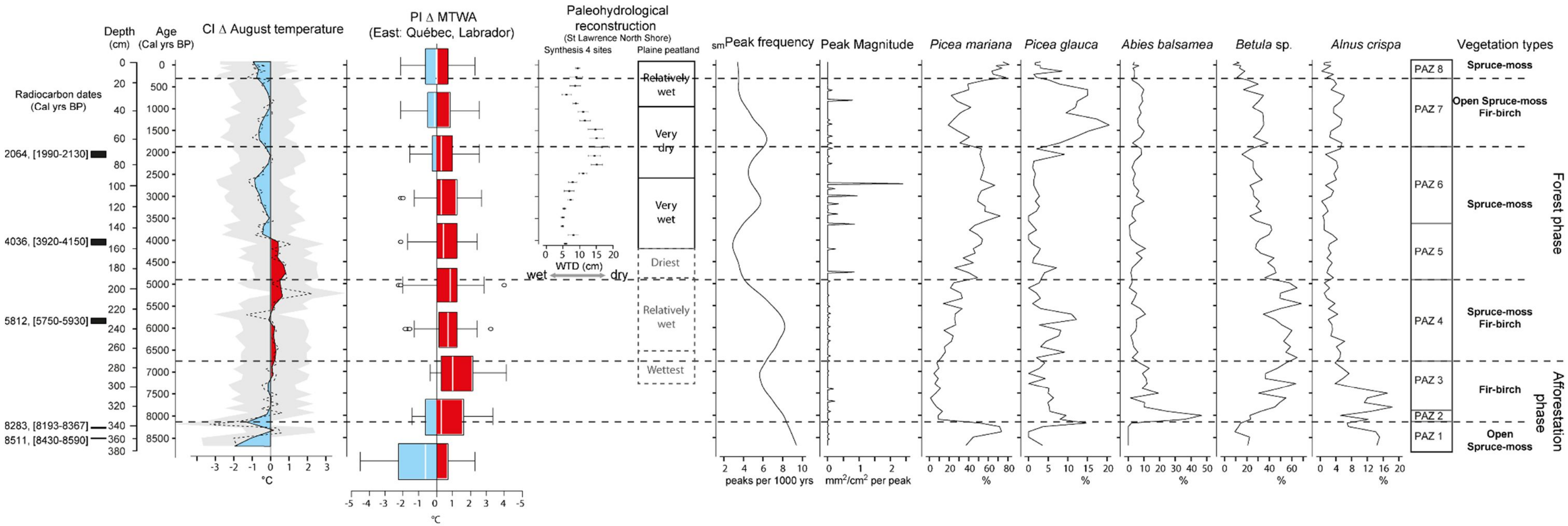

Figure 2.6 Climate-fire-vegetation interactions. From left to right: chironomid inferred August temperature anomaly, mean temperature of the warmest month (MTWA; eastern Quebec and Labrador) presented by box-plot every 1000 years and expressed as an anomaly relative to the current period ((Δ); Fréchette et al., 2021), synthesis of the reconstructed water table depths from four peat records since 4200 cal yr BP (Mean water table depth (WTD) with standard errors calculated for each 200-year period; Magnan and Garneau, 2014). Summary of water table depth changes from the records of Plaine peatland (Havre St-Pierre) for the last 7000 cal yr BP (Magnan and Garneau, 2014), fire occurrence (smPeak frequency), peak magnitude of fire events, pollen abundance of main taxa (*Picea mariana*, *Betula* spp., *Picea glauca*, *Abies balsamea*, *Alnus crispa*), pollen assemblage zone (PAZ; in horizontal solid grey lines) and vegetation types (in horizontal dashed grey lines) from Lake Mista.

et al. (2019b) dated a spruce charcoal aged 8725 cal yr BP. Therefore, the observed decline of *Picea mariana* at the expense of *Abies balsamea* could be the result of a primary succession where *Picea mariana* is being overtaken by the late successional species (*Abies balsamea*) under longer fire cycle (Couillard et al., 2021). Then it was not until ca. 4800 cal yr BP that *Picea mariana* returned, perhaps favored by severe or larger fires (Fig. 2.6).

Abies balsamea dominated boreal forests were also observed in the Sept-Îles region between 8000-6500 cal yr BP (Mott, 1976; King, 1986) and in southeastern Labrador (Lamb, 1980; Engstrom and Hansen, 1985). Maximum abundance of *Abies balsamea* from ca. 8100 to 6700 cal yr BP (Fig. 2.6) is also consistent with Fréchette et al. (2021).

Forest phase 6700 cal yr BP to present

Spruce-moss balsam fir-birch forest 6700-4800 cal yr BP. Warmer climatic conditions coupled with smaller and less severe fires (Fig. 2.6) due partly to wet climatic conditions between 6560 and 4800 cal yr BP (Magnan and Garneau, 2014), created a propitious environment for the recruitment and proliferation of *Betula papyrifera*, *Picea glauca* and *Abies balsamea*. The wet climatic conditions may also have supported the decreasing trend in fire occurrence. Such species assemblage (*Picea mariana*, *Betula papyrifera*, *Picea glauca* and *Abies balsamea*) is observed in modern boreal mixed-wood (Sims et al., 1990; Galipeau et al., 1997). According to Fréchette et al. (2021), the pollen percentage values of *Betula* spp., *Picea mariana* and *Abies balsamea* (Fig. 2.6) suggest the presence of two postfire successional pathways as described by Couillard et al. (2021) at the stand scale. The first pathway, from *Betula* spp. to *Abies balsamea* with presence of *Picea glauca* (*Abies balsamea-Picea glauca-Betula* spp.), and the second pathway from *Picea mariana* to *Abies balsamea*.

Spruce-moss forest 4800-1800 cal yr BP. 4800 cal yr BP marks a notable vegetation shift with the expansion and densification of *Picea mariana* (higher percentage and influx; Fig. 2.3;

Supplemental Material S2.3). It is likely that severe and larger fires promoted the fire-prone *Picea mariana*, as vegetation and soil burning creates suitable conditions for the establishment and regeneration of *Picea mariana* seedlings (Black and Bliss, 1980; Viereck, 1983). Fire occurrences were particularly low between ca. 4800 and 3600 cal yr BP, but the abundance of the highly flammable *Picea mariana* coincided with particularly dry climatic conditions between 4800 and 4200 cal yr BP (Magnan and Garneau, 2014), possibly due to larger fires during this period (Fig. 2.6). Wet climatic conditions between 4200 and 2600 cal yr BP (Magnan and Garneau, 2014) possibly favored *Picea mariana*, thus increasing fuel accumulation, landscape flammability, and biomass burning. Biomass burning was particularly high between ca. 3600 cal yr BP and ca. 2700 cal yr BP. This is in line with the results of other studies in the North American boreal forest indicating that biomass burning peaked between 6000 and 1000 cal yr BP (Ali et al., 2012; Kelly et al., 2013; Remy et al., 2017a, b), perhaps because of warmer and drier spring and summer conditions (Ali et al., 2012; Remy et al., 2017a), and also the increase of landscape flammability following the densification and expansion of *Picea mariana* (Hély et al., 2001; Terrier et al., 2013; Blarquez et al., 2015). In addition, fire occurrences displayed centennial to millennial scale patterns. These changes in wildfire regime could be the result of centennial to millennial scale climatic control on fire activity (Gavin et al., 2006), and to some extent, that of vegetation succession (Blarquez et al., 2015) including other bottom-up controls (e.g., topography, waterbodies; Cyr et al., 2007; Courtney-Mustaphi and Pisaric, 2013; Portier et al., 2019).

Open spruce-moss balsam fir-birch forest 1800-300 cal yr BP. A slight increase in fire occurrence between 2000 and 1500 cal yr BP (Fig. 2.6) coupled with very dry climatic conditions between 2600 and 950 cal yr BP (Magnan and Garneau, 2014) probably limited tree cover, leading to gradual opening of the vegetation cover as suggested by the total influx decrease until ca. 1000 cal yr BP when it started rising again (Supplemental Material S2.3) with wetter conditions between 950 and 0 cal yr BP (Magnan and Garneau, 2014). By contributing to the opening of the forest landscape (Supplemental Material S2.3; sharp drop in total pollen accumulation rate), the increase in fire occurrence thus facilitated the deposition of *Carya ovata* (Miller) K. Koch. Pollen, a species that is absent from most nearby regional pollen spectra (e.g., Fréchette et al., 2021) or sparse and considered exotic (Remy et al., 2017b). It suggests that the opening of the forest was not limited to the lake Mista catchment area. The late-Holocene decline in total pollen influx was also observed to the southwest (e.g., lake Matamek; Fréchette et al., 2021) and northeast (e.g., lake Eagle; Lamb (1980); lake Moraine and lake Hope Simpson (Engstrom and Hansen, 1985)) of our study site. Suitable climatic conditions and smaller or less severe fires enabled *Abies balsamea* and *Picea glauca* to recolonize opened sites by seed rain from survivors in unburned areas (Galipeau et al., 1997; Asselin et al., 2001; Bergeron et al., 2004; Cyr et al., 2012).

Spruce-moss forest 300 cal yr BP to present. Starting ca. 300 cal yr BP, vegetation composition was similar to that of the modern black spruce-moss boreal forest. The relative pollen frequencies of the major taxa are similar to modern pollen spectra percentages obtained from surface sediments of nearby lakes (Lamb, 1984; Engstrom and Hansen, 1985). *Picea mariana* is the dominant tree in modern pollen assemblages throughout eastern Quebec and Labrador (Fréchette et al., 2021). The pollen influx data from lake Mista (Supplemental Material S2.3) suggest that the spruce-moss forest opened around 2000 cal yr BP, but without shifting into a spruce-lichen woodland, as it subsequently became denser during the last 300 years.

Fire occurrence and biomass burning were low during the last 300 years, consistent with the decreasing trend in fire frequency (Drobyshev et al., 2017) and burn rates (Chavardès et al., 2022) across eastern Québec from the Little Ice Age to the present. The colder and wetter climatic conditions in the study area (Magnan and Garneau, 2014) seem to have helped maintain fire occurrence and biomass burning low despite the high abundance of flammable *Picea mariana* (Fig. 2.6).

2.6.3 Drivers of fire and vegetation trajectories

Compared to the HTM period, the cooler climatic conditions that prevailed during the Neoglacial were less conducive to fire events (Fig. 2.6). Notwithstanding the rising and fluctuating trend of fire occurrence, fires remained less frequent than before 4800 cal yr BP, probably because of the Neoglacial cooler climate conditions linked to decreased solar irradiance (Ali et al., 2012). However, despite less suitable climatic conditions to fire activity, the densification and expansion of *Picea mariana* forests overrode the effects of cooler climate conditions, then led to greater biomass burning and/or larger fires (Fig. 2.4).

The transition from the warm HTM to the cooler Neoglacial period around 4000 cal yr BP does not coincide with the long-term changes in fire regime and vegetation dynamics (Fig. 2.6). A marked decrease in fire frequency occurred around 5000 cal yr BP when the climate was still warm, suggesting that fire occurrence was probably not controlled directly by summer temperature. Other climatic variables (e.g., warm springs, intra-seasonal variability in precipitation, fire season length and drought code; Remy et al., 2017a; Portier et al., 2019) could have had a direct control on fire occurrence in eastern Québec at the time.

The shift to spruce-moss forests around 4800 cal yr BP occurred nearly a thousand years before the climatic shift to the Neoglacial period. This is rather fire that came into play, in particular a decrease in fire occurrence and an increase in fire size or severity (higher magnitude fire peaks stating from ca.4800 cal yr BP; Fig. 2.6). Long-term vegetation changes coincided with shifts from frequent small low-severity fires to infrequent, large, high-severity fires. On the other hand, the shift to higher biomass burning coincides with the shift from spruce-moss balsam fir-birch forest to spruce-moss forest. On a millennial timescale, decreasing summer insolation influenced climate, fire occurrence and vegetation changes. The high abundance of *Betula* (likely *Betula papyrifera*; Fréchette et al., 2021), which is less flammable (Sims et al., 1990), and wet climatic conditions mediated the impacts of HTM warming on biomass burning. Subsequently, the high abundance of flammable *Picea mariana* promoted biomass burning during the Neoglacial.

Vegetation changes at lake Mista may also reflect the influence of other ecological factors operating at various spatial and temporal scales such as climate (annual and seasonal temperature and precipitation), types of surface deposits and soils, and disturbances (fires, insect outbreaks, windthrow) (Sims et al., 1990; Saucier et al., 2009; Couillard et al., 2019a).

2.7 Conclusion

The changes in chironomids, pollen, and macroscopic charcoal from the sediment core of Lake Mista disclosed 8500 years of postglacial climate-fire-vegetation interactions. The climate was warmer during the HTM (7000-4000 cal yr BP), then shifted to cooler conditions during the Neoglacial period (4000 cal yr BP to present). However, the long-term changes in summer temperature records are probably not the main factor controlling fire and vegetation dynamics in the Lake Mista area. Throughout the postglacial period, summer temperatures never fell below a threshold that could have induce a significant vegetation response. Other climatic and biophysical variables are probably more important and would need to be studied further.

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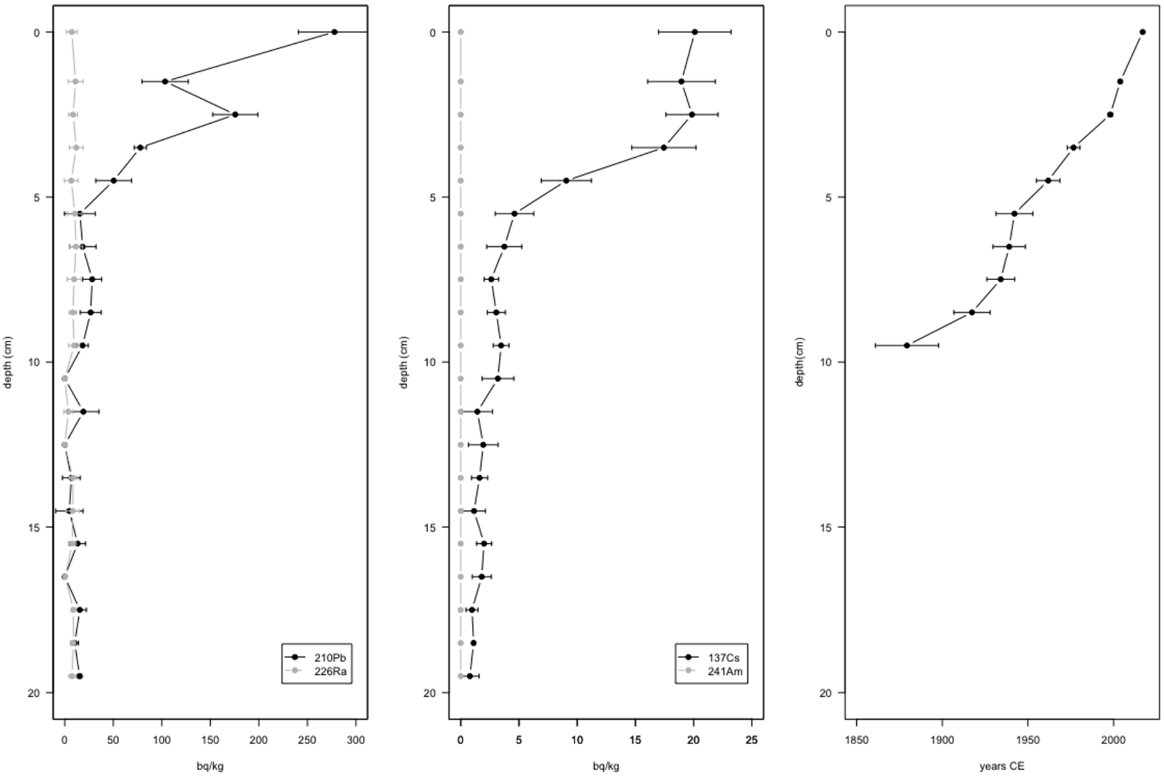
2.10 Supplemental Materials

Supplemental Material S2.1: Details on the activity profile of ^{210}Pb, ^{226}Ra, as well as ^{137}Cs and ^{241}Am.



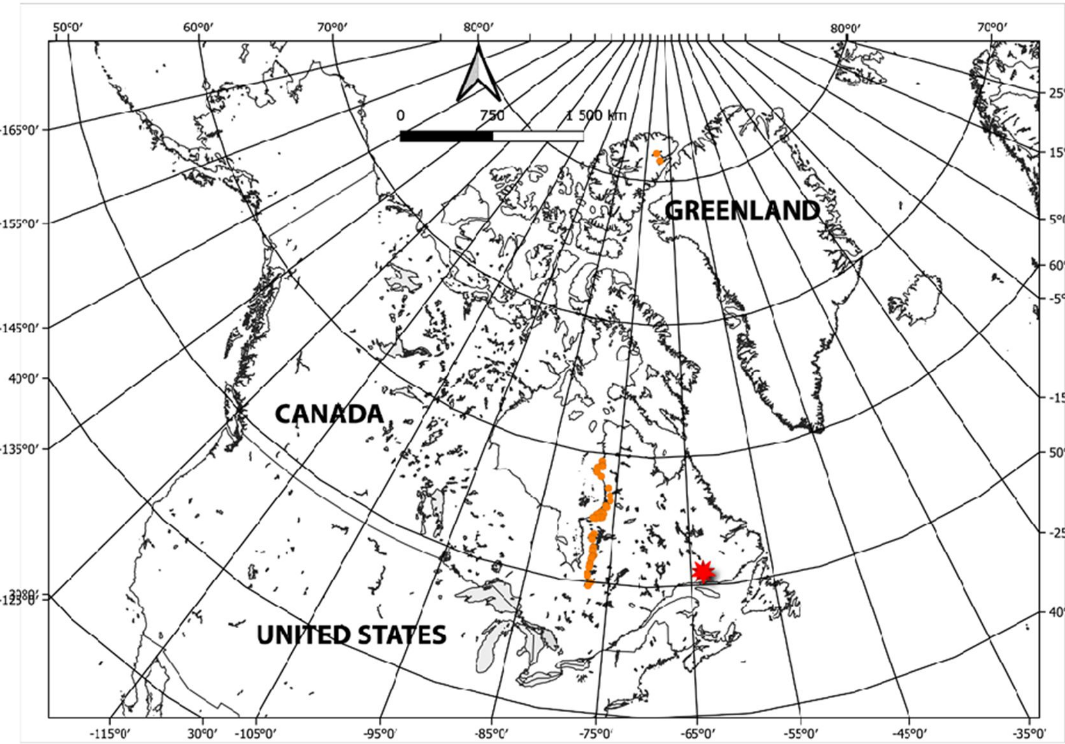
Supplemental Material S2.2 Mean August air temperatures were reconstructed using three transfer functions (i.e. Larocque 2008; Fortin et al. 20215; Medeiros et al. 2022). Following their performance statistics (Supplemental Material S1a), the transfer function (TF) of Larocque (2008) is more likely to yield accurate reconstructions. The temperature reconstruction patterns are similar (Supplemental Material S1c). But, the TF of Larocque et al. (2008) seems to be more adapted to our study site. In particular, it is the TF that provides values closer to the monitored values for the current period (13.5°C; Régnière et al. 2017) than those inferred using TF of Fortin et al. (2015) and Medeiros et al. (2022).

Supplemental Material S2.2a Transfer functions performance statistics;

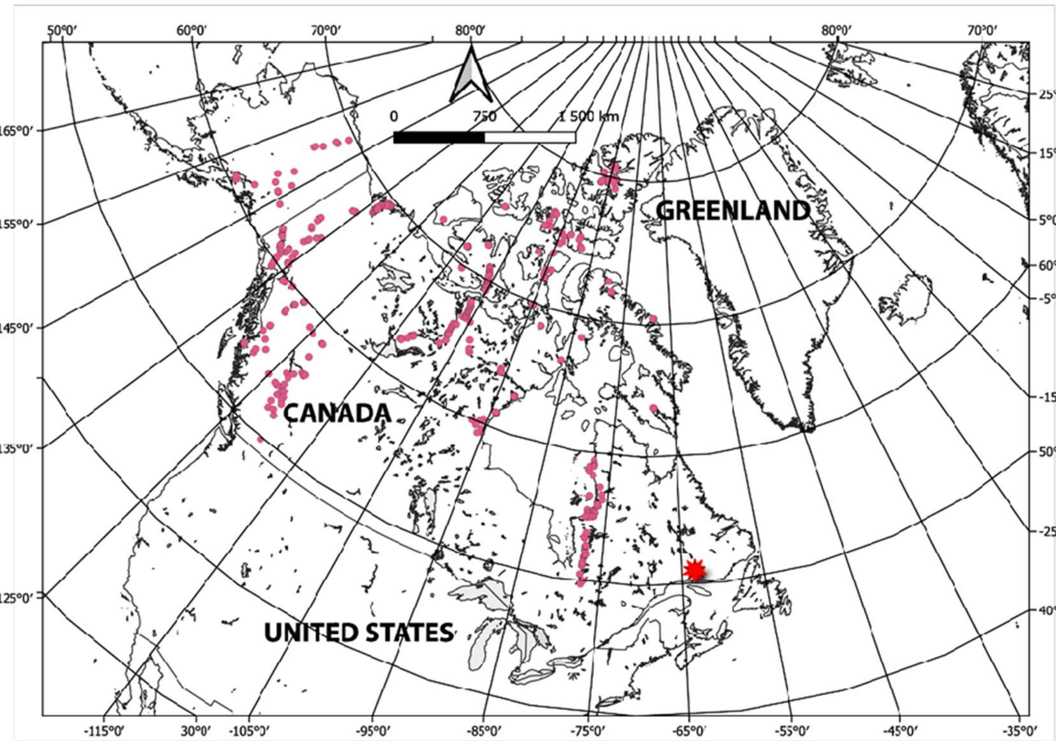
Transfer functions	**Number of lakes**	**Number of taxa**	**Variable**	**Temperature gradient**	**Model type**	**$RMSEP_{boot}$**	**R^2_{boot}**	**Max bias**
Larocque (2008)	75	79	August temperature	18°C (range 3 to 21°C)	WAPLS two components	1.65°C	0.80°C	3.04°C
Fortin et al. (2015)	435	78		16°C (range -0.3 to 15.7°C)		2.39°C	0.59°C	3.93°C
Medeiros et al. (2022)	402	172		13.5°C (range - 0.7 to 12.8°C)		1.70°C	0.64°C	3.94°C

Supplemental Material S2.2b Location of sites in the modern calibration-set of (a) Larocque (2008), (b) Fortin et al. (2015) and (c) Medeiros et al. (2022). Lake Mista in red asterisk.

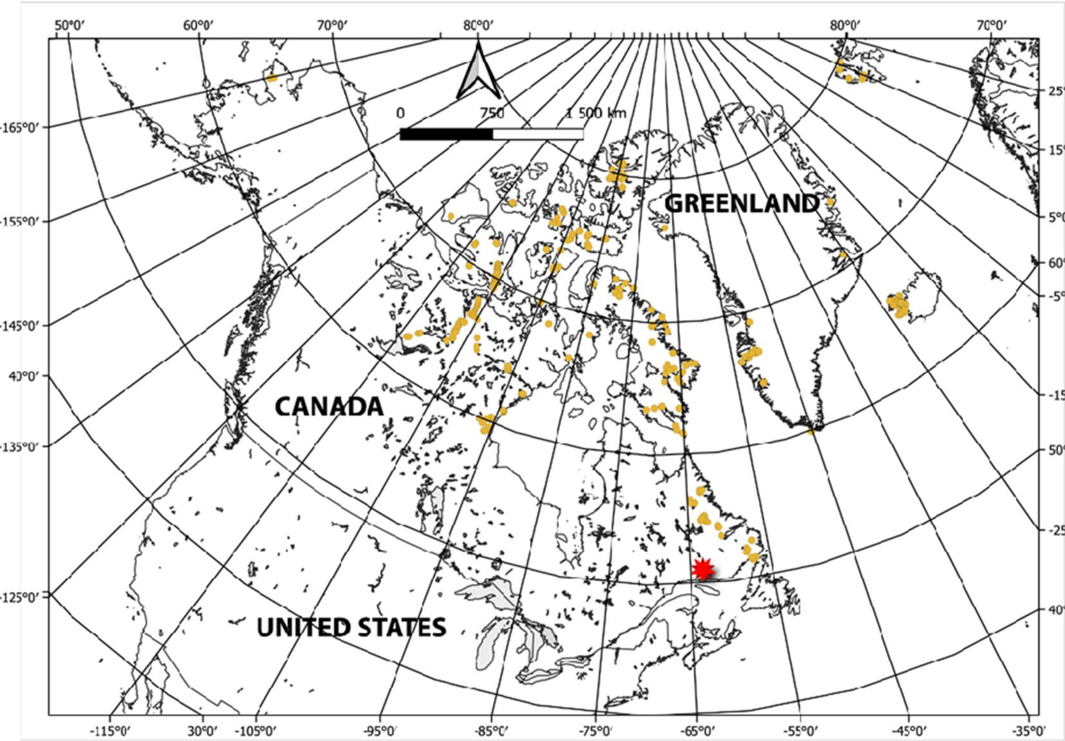
(a) Larocque (2008)



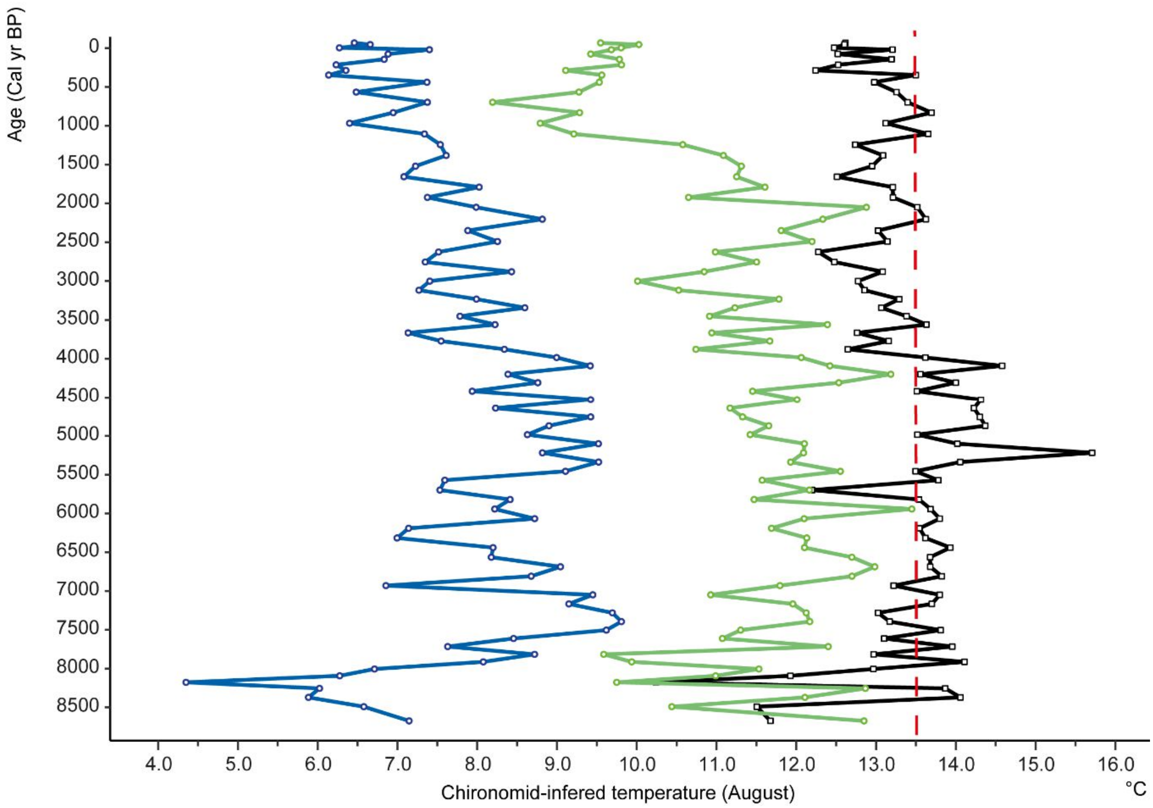
(b) Fortin et al. (2015)



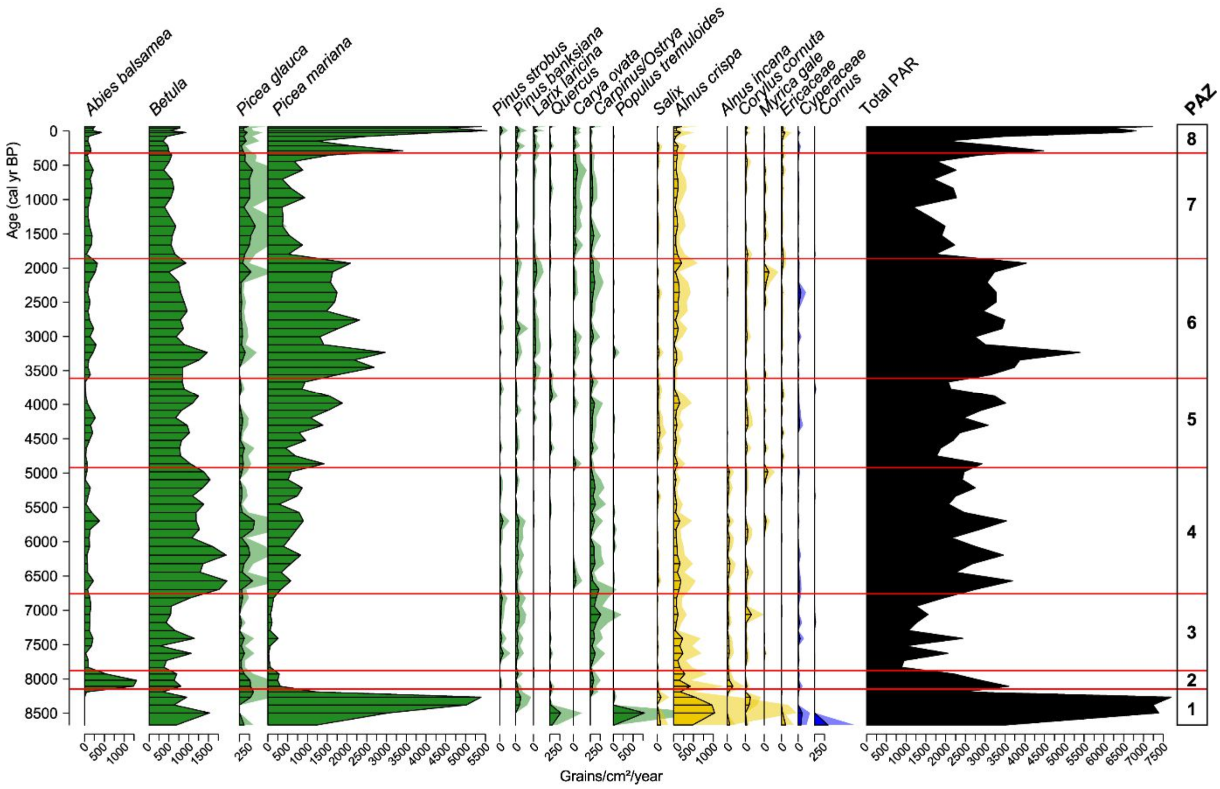
(c) Medeiros et al. (2022)



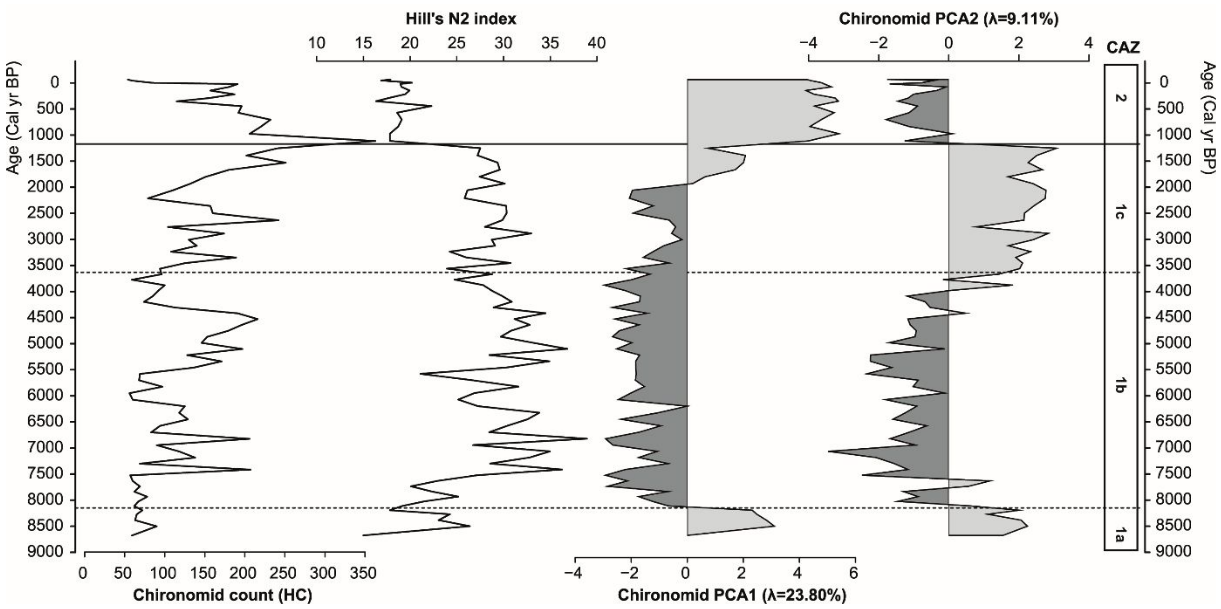
Supplemental Material S2.2c Chironomid-inferred August temperature reconstructions at lake Mista; with the transfer function of (a) Larocque (2008) in solid black line; (b) Fortin et al. (2015) in solid green line; (c) Medeiros et al. (2022) in solid blue line. Present day August temperature (13.5°C; Régnière et al. (2017)) in vertical dashed red line.



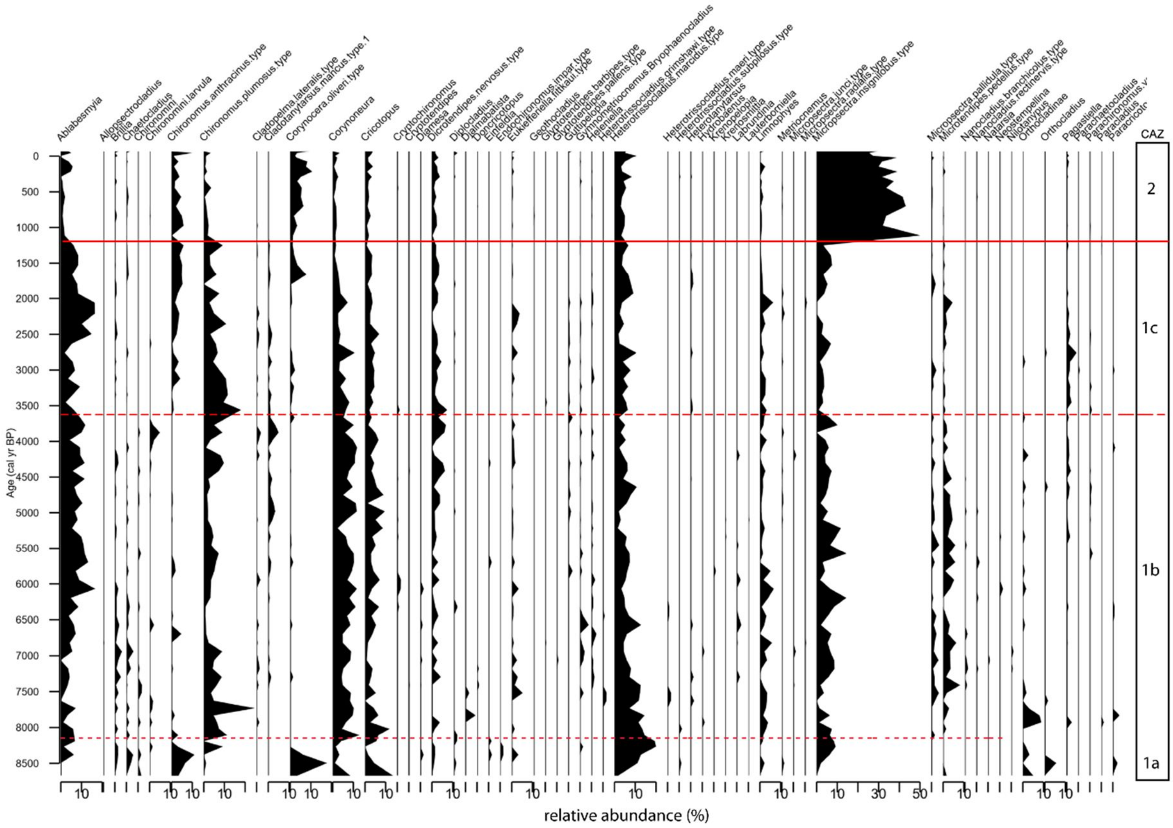
Supplemental Material S2.3 Simplified pollen influx diagram, with total pollen accumulation rate (PAR, black) trees (green), shrubs (yellow), herbs (blue), pollen assemblage zone (PAZ; in horizontal solid lines)

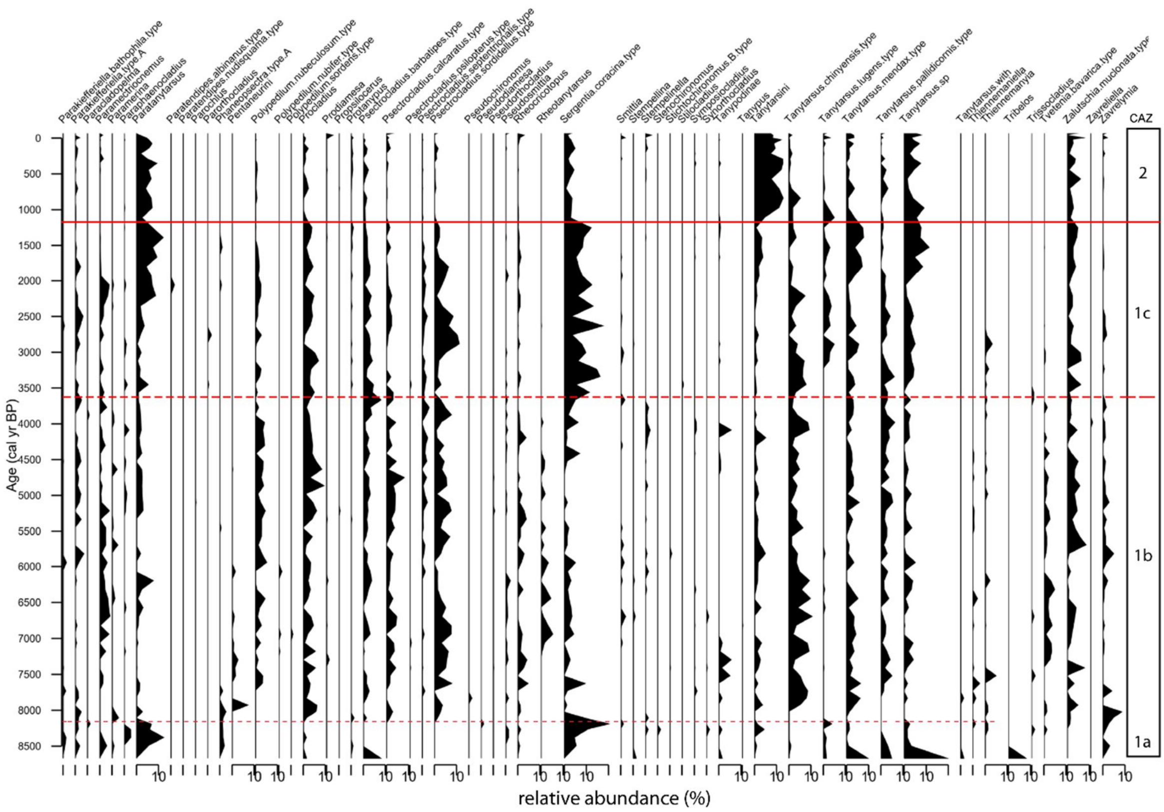


Supplemental Material S2.4a Chironomid count, chironomid species richness (Hill's N2 index), chironomid PC axis 1 and 2 sample scores (λ indicates the proportion of variance explained by the PC axis of the fossil data), chironomid assemblage zone (CAZ; in horizontal solid black line; sub-biozones horizontal dashed black lines).

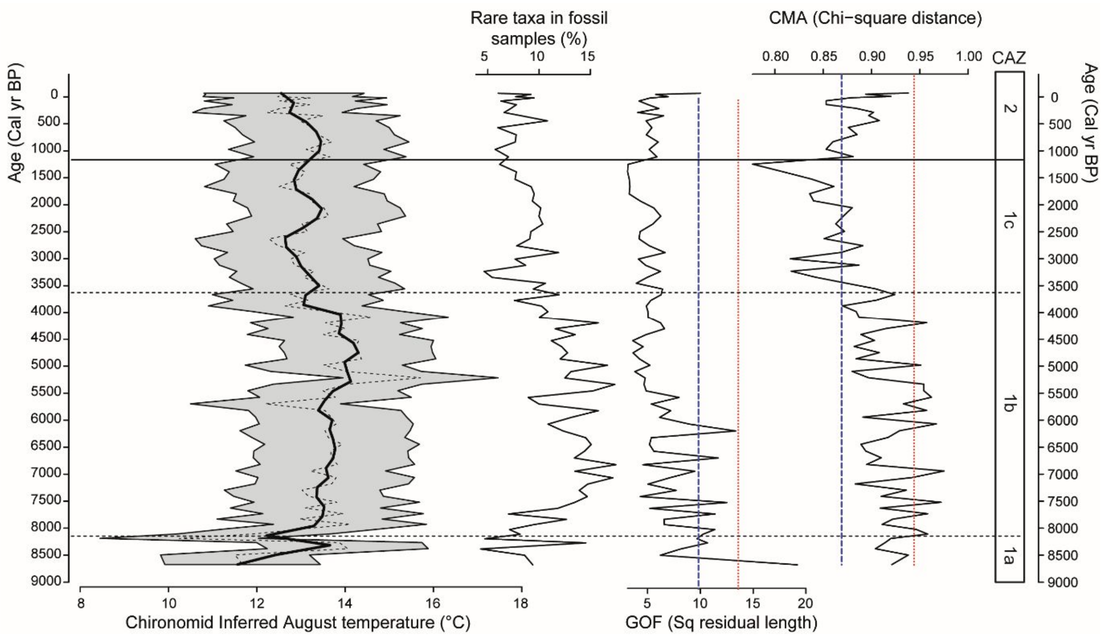


Supplemental Material S2.4b Detailed chironomid percentage diagram, chironomid assemblage zone (CAZ; in horizontal solid red line, sub-biozones in horizontal dashed red lines), constrained incremental sum of squares (CONISS).





Supplemental Material S2.4c Chironomid inferred August temperature (in dashed black line; with a LOESS smoother in solid black line (span=0.073), with the grey area delimiting the minimum and maximum sample-specific estimated standard error of prediction (eSEP)), fossil samples taxa absent or rare in modern dataset, goodness-of-fit (GOF) of fossil samples with temperature (samples with very poor fit exceed vertical dashed red line while those with poor fit are beyond vertical dashed blue line), fossil samples closest modern analogs (CMA) in modern dataset (samples with no close modern analog exceed vertical dashed red line while those with poor close modern analogs are beyond vertical dashed blue line), chironomid assemblage zone (CAZ; in horizontal solid black line; sub-biozones in horizontal dashed black lines).



References of Supplemental Materials

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Chapitre 3

Chironomid-inferred postglacial climatic changes along an east-west transect in the coniferous boreal forest of Québec, eastern Canada

Augustin Feussom Tcheumeleu, Thomas Suranyi, Olivier Blarquez, Damien Rius, Adam Ahmed Ali, Yves Bergeron, Pierre Grondin, Sylvie Gauthier, Lisa Bajolle, Laurent Millet

Prêt à soumettre

3.1 Abstract

In North America, the Holocene millennial scale climate variability was predominantly driven by orbital-induced insolation changes, solar irradiance, atmospheric greenhouse gas concentration and the early-Holocene deglaciation of the Laurentide Ice Sheet. The spatial and temporal complexity of the Holocene climate and some inconsistencies (in timing, amplitude, duration) observed at regional and global scales in recent reconstructions of major Holocene climatic periods (e.g., Holocene thermal maximum, Neoglacial) and events (e.g., Roman Warm Period (RWP), Dark Age Cold Period (DACP), Medieval Warm Period (MWP), Little Ice Age (LIA)), suggest that spatiotemporal climate patterns should be investigated across regions. In order to document the spatiotemporal changes in the climate in Québec, we studied chironomid assemblages as climate proxies along three records distributed along an east-west transect across the black spruce–moss bioclimatic domain. Our results suggest in particular the existence of a strong contrast in summer temperatures between east and west Québec before 7000 cal yr BP. In the east, during this period, the indirect influence of the decaying Laurentide Ice Sheet and ocean surface conditions counterbalance the maximum insolation to induce cooler summer conditions. In the east, the maximum summer temperature is only reached between 6000 and 5000 cal yr BP. The west of Quebec is little or not affected by these influences and the evolution of temperatures parallel the decrease of insolation during summer, with a maximum of temperatures around 7500 cal yr BP. We also highlight a strong climatic variability over the last 3000 years, with the succession of alternatively warm and cold events. Although these events appear generally synchronous between the three records, the chronological and analytical resolution does not allow us to compare with certainty this dynamic with the RWP, DACP, MWP, and LIA successions, and additional analyses are necessary to draw robust conclusions on this point.

3.2 Résumé

En Amérique du Nord, la variabilité climatique à l'échelle millénaire de l'Holocène a été principalement déterminée par les changements d'insolation induits par l'orbite, l'irradiance solaire, la concentration de gaz à effet de serre dans l'atmosphère et la déglaciation de l'inlandsis laurentidien au début de l'Holocène. La complexité spatiale et temporelle du climat de l'Holocène et certaines incohérences (p.ex., le timing, l'amplitude, la durée) observées à l'échelle régionale et mondiale dans les reconstructions récentes des principales périodes climatiques de l'Holocène (p.ex., le maximum thermique de l'Holocène, le Néoglaciaire) et des événements (p.ex., la période chaude romaine (RWP), la période froide de l'âge sombre

(DACP), la période chaude médiévale (MWP), le petit âge glaciaire (LIA)), suggèrent que les schémas climatiques spatio-temporels devraient être étudiés dans les différentes régions. Afin de documenter les changements spatio-temporels du climat au Québec, nous avons étudié les assemblages de chironomes en tant que proxies climatiques pour trois sites sélectionnés le long d'un transect est-ouest à travers le domaine bioclimatique de la pessière à mousses. Nos résultats suggèrent notamment l'existence d'un fort contraste de températures estivales entre l'est et l'ouest du Québec avant 7000 ans AA. Dans l'est, durant cette période, l'influence indirecte des vestiges de l'inlandsis laurentidien et les conditions de surface de l'océan contrebalancent l'insolation maximale pour induire des conditions estivales plus fraîches. Dans l'est, la température estivale maximale n'est atteinte qu'entre 6000 et 5000 ans AA. L'ouest du Québec est peu ou pas affecté par ces influences et l'évolution des températures est parallèle à la diminution de l'insolation pendant l'été, avec un maximum de températures autour de 7500 ans AA. Nous mettons également en évidence une forte variabilité climatique au cours des 3000 dernières années, avec une succession d'événements alternativement chauds et froids. Bien que ces événements semblent généralement synchrones entre les trois enregistrements, la résolution chronologique et analytique ne nous permet pas de comparer avec certitude cette dynamique avec les successions RWP, DACP, MWP et LIA, et des analyses supplémentaires sont nécessaires pour tirer des conclusions solides sur ce point.

3.3 Introduction

Boreal forests are ecosystems that are naturally subject to strong constraints, such as a short growing season, a 6 to 8-month freezing period, permafrost, etc., and their structure and functioning are mainly controlled by climate, fires, pests, and their interactions (Burton et al., 2010; Seidl et al., 2017; Subedi et al., 2023). The ongoing and future climate change will have significant and multiple consequences on the boreal forest and the associated goods and services (Gauthier et al., 2015; Gauthier et al., 2023). Climate predictions indicate that during the 21st century, the boreal biome is at risk of experiencing the strongest temperature increase compared to other forest biomes (IPCC, 2013). All projections indicate a very probable increase in fires and insect outbreaks in the boreal forest during the coming decades (Gauthier et al., 2015; Navarro et al., 2018; Aakala et al., 2023). Ultimately, through cascading effects, including its impact on the fire regime, climate change could even lead to a reversal of the carbon balance of boreal forests, which could become sources rather than sinks of carbon, with positive feedbacks on climate warming (Pan et al., 2011; Walker et al., 2019; Ameray et al., 2021; Girona et al., 2023a). Given the socio-economic and ecological importance of boreal forests, understanding and modeling the complex interactions between climate, fires, and vegetation is identified as a major research challenge in the context of ongoing and future global change (Girona et al., 2023b). In this context, paleoecological approaches complement current observation data by documenting ecosystem trajectories over the long-term, from the secular to the multi-millennial scale. This retrospective approach sheds new and often original light on initial equilibrium states, functional tipping mechanisms, system resilience, and vulnerability to global change, and has been successfully implemented to address the issue of fire/climate/vegetation relationships in the Canadian boreal forest (Reyer et al., 2015). The Holocene is a particularly suitable chronological window for this type of approach since it is characterized by low (Holocene Thermal Maximum, Neoglacial) and high-frequency climate variability (Roman Warm Period, Dark Ages Cold Period, Medieval Warm period, Little Ice Age) and certain periods are marked by temperatures that were probably warmer than today, allowing exploration of the effects of warming on ecosystems.

In North America, the Holocene millennial scale climate variability was predominantly driven by orbital-induced insolation changes, solar irradiance, atmospheric greenhouse gas concentration (Mayewski et al., 2004; Wanner et al., 2015) and the early-Holocene deglaciation of the Laurentide Ice Sheet (Renssen et al., 2009). The lower summer insolation that began in the Northern Hemisphere around 5000 cal yr BP (Berger and Loutre, 1991) partly explain the neoglacial cooling of the climate in North America (Viau et al., 2006; Marcott et al., 2013). Depending on the region, there is the influence of internal factors that modulate the timing and therefore the amplitude of the Holocene Thermal Maximum (Renssen et al., 2009). Although part of Canada was no longer covered by the Laurentide Ice Sheet around 10000 cal yr BP (Dyke, 2004; Dalton et al., 2020), its remnants, centered in Québec-Labrador, continued to influence atmospheric circulation dynamic and to exert strong cooling effects on the climate of nearby Québec-Labrador regions until ca. 6000 cal yr BP (Viau and Gajewski, 2009; Fréchette et al., 2021). These local and regional influence of the Laurentide Ice Sheet remnant resulted in a spatial and temporal discrepancies in the timing and amplitude of the Holocene Thermal Maximum across boreal Canada (Kaplan and Wolfe, 2006; Viau and Gajewski, 2009; Bajolle, 2018)), and asynchronous postglacial onset of the vegetation development (Blarquez and Aleman 2016; Fréchette et al., 2018; Fréchette et al., 2021).

The spatial and temporal complexity of the Holocene climate (O'Brien et al., 1995; Renssen et al., 2009) and some inconsistencies (in timing, amplitude, duration) observed at regional (Mann and Jones, 2003; Viau et al., 2006; Renssen et al., 2009; Naulier et al., 2015; Bajolle et al., 2018) and global scales (Mayewski et al., 2004; Matthews and Briffa, 2005; Renssen et al., 2012; Neukom et al., 2019) in recent reconstructions of these major Holocene climatic periods and events, suggest that spatiotemporal climate patterns should be investigated across regions (Mayewski et al., 2004; Viau and Gajewski, 2009).

In eastern North America (e.g., Viau and Gajewski, 2009; Fréchette et al., 2018; Fréchette et al., 2021), most paleotemperature reconstructions are pollen-based reconstructions for multimillennial time periods. These paleoclimatic data are essential for explaining long-term vegetation dynamics. But, because of the longevity of trees, although each plant species is dependent on a climate type, vegetation does not respond quickly to climatic fluctuations (Davis, 1978) but also to disturbance regimes (Saucier et al., 2009; Grondin et al., 2023). As a result, temperatures reconstructed from pollen are often those of earlier periods, which can contribute to misinterpretation (Larocque and Hall., 2003).

Moreover, using climate interpretations from pollen data to understand vegetation dynamics from pollen data may lead to circular reasoning. The problem of circular reasoning can be avoided by the use of chironomid-inferred temperatures to explain the vegetation changes.

Chironomid subfossil assemblages are valuable paleoclimatic proxies in North America (Walker et al., 1991; Fortin and Gajewski, 2016; Bajolle et al., 2018; Medeiros et al., 2022) and Europe (Larocque et al., 2001; Heiri et al., 2011; Millet et al., 2012) because of their sensitivity and rapid responses to environmental changes and mainly to air and water temperatures (Larocque and Hall, 2003; Eggermont and Heiri, 2012).

In order to document the spatiotemporal changes in the climate in Québec, we studied chironomid assemblages as climate proxies along three records distributed along an east-west transect across the black spruce–moss bioclimatic domain. Indeed, in the black spruce-moss forest of Quebec, there is an east-west warming gradient in summer temperatures (Couillard et al., 2019). This study is based on the combination of existing chironomid data from lake Aurélie (Bajolle et al., 2018) and lake Mista (Feussom Tcheumeleu et al., 2023) and a new chironomid data from lake Adèle.

The aims of this paper are: (1) to present a new chironomid record from lake Adèle, (2) to contribute to document the spatiotemporal complexity of Holocene summer temperature changes in Québec using chironomid- based reconstructions from 3 sites distributed along an east-west transect in the coniferous boreal forest, and, (3) more specifically to provide evidences of the major Holocene climatic periods and phases (i.e. Holocene Thermal Maximum, Neoglacial, Roman Warm Period, Dark Ages Cold Period, Medieval Warm Period, Little Ice Age) recorded in the three studied sites.

3.4 Materials and methods

3.4.1 Study area and sites

The study area is the black spruce–moss bioclimatic domain (between 49 and 52°N, and 57 and 82°W; Saucier et al., 2009). The black spruce–moss forest (412,400 km^2 i.e. about 27% of Québec surface area) is the largest bioclimatic domain in Québec (Canada) of ecological and economic importance. We investigated three sites (lake Aurélie, lake Adèle, lake Mista; Fig.3.1; Table 3.1) along an east-west transect in the coniferous boreal forest of Québec, eastern Canada.

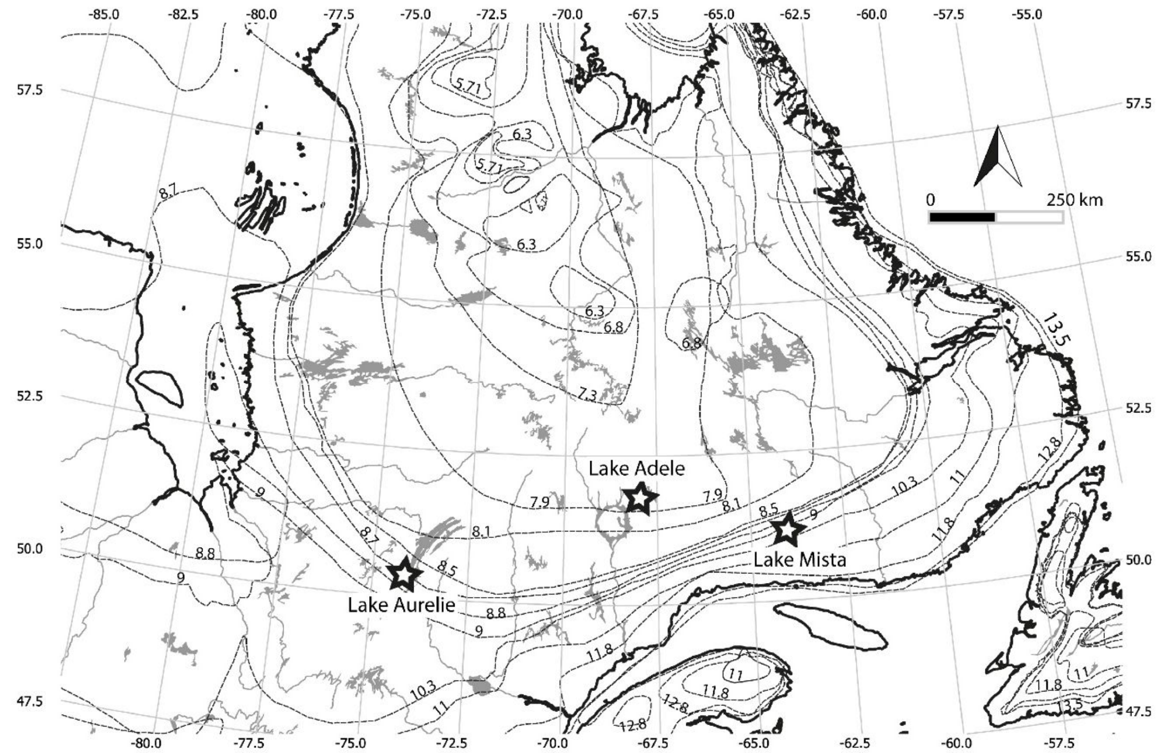

Figure 3.1 Location map of Lake Aurélie, Adèle and Mista. From South to North, the dashed grey lines represent the deglacial isochrones of the Laurentide Ice Sheet with ages in kyr BP (Dyke, 2004).

Lake Aurélie is located within the western portion of the black spruce–moss bioclimatic domain while lake Adèle and lake Mista are located in its eastern part (Saucier et al., 2009). The climate in the eastern part is colder (mean annual temperature (-2°C); Ministère des Ressources naturelles, 2013) and more humid (mean total annual precipitation (1000-1250 mm); Jobidon et al., 2015) than it is in the western portion (mean annual temperature (-0.5°C); mean total annual precipitation (651-1000 mm)). *Picea mariana* (Mill.) B.S.P. and *Pinus banksiana* Lamb are the dominant tree species in the West (Fréchette et al., 2018) while *Picea mariana, Abies* *balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss are the dominant tree species in the East (Fréchette et al., 2021).

The deglacial isochrones of the Laurentide Ice Sheet (Fig.3.1; Dyke, 2004; Dalton et al., 2020) suggest that lake Mista and Aurélie were deglaciated around 10300 and 8700 cal yr BP respectively, i.e. earlier before lake Adèle at ca. 7900 cal yr BP.

Table 3.1 Main characteristics of the lakes with details of the cores

Variable	Lake Aurélie	Lake Adèle	Lake Mista
Coordinates	50°25'12''N 74°13'47''W	51°50'10.72'' N 67°55'45.962''W	51°6'10.25'' N 63°26'34.82''W
Elevation (m a.s.l)	440	457	500
Lake area (ha)	1	2.23	0.27
Water depth (m)	10	6.25	5
Mean August air temperature (°C)	14.5	13.2	13.5
Sampling date	March 2010	September 2015	May 2017
Core length (cm)	335	320	373
References	El-Guellab et al. (2015) Bajolle (2018) Régnière et al. (2017)	Bastianelli (2018) Régnière et al. (2017)	Feussom Tcheumeleu et al. (2023) Régnière et al. (2017)

3.4.2 Coring and dating

Sediment cores were retrieved from the deepest point of each lake using a Kajak-Brinkhurst gravity corer for the sediment-water interface deposits, and a modified Livingstone-type square-rod corer for the subsequent long sediment cores. The chronology of our three lakes based on accelerated mass spectrometry (AMS) radiocarbon (^{14}C) and on gamma spectrometry (^{210}Pb) dating have already been published (Table 3.2). In this study, the radiocarbon dates were calibrated to calendar ages using IntCal20 (Reimer et al., 2020; age-depth model in Supplemental Material S3.1).

3.4.3 Geochemical analysis of Lake Adèle sediments

Determination of total organic carbon (TOC) and total nitrogen (TN) elemental dry-weight

Table 3.2 Radiocarbon dates from the three lakes

Lake	Material	Depth (cm)	Dates (^{14}C yr BP)	Calibrated age (yr BP)	Reference
Aurélie	Plant macro-remains	43-44	2870 ± 30	2993 (2879-3136)	El-Guellab et al. (2015)
	Plant macro-remains	111-112	3990 ± 35	4472 (4301-4570)	
	Plant macro-remains	163-164	4750 ± 35	5513 (5328-5584)	
	Plant macro-remains	220-221	6140 ± 40	7038 (6903-7161)	
	Plant macro-remains	236-237	6490 ± 40	7376 (7313-7480)	
	Plant macro-remains	326-327	7460 ± 50	8274 (8183-8371)	
Adèle	Sediment	0-2		-56	Bastianelli (2018)
	Sediment	2-4		-44	
	Sediment	4-6		-27	
	Sediment	6-8		-9	
	Sediment	8-10		9	
	Sediment	10-12		28	
	Sediment	12-14		45	
	Sediment	14-16		60	
	Plant macro-remains	36-38	1685 ± 15	1566 (1535-1687)	
	Plant macro-remains	98-100	2645 ± 15	2756 (2743-2768)	
	Plant macro-remains	148-150	3360 ± 15	3600 (3496-3685)	
	Plant macro-remains	198-200	3890 ± 15	4339 (4247-4410)	
	Plant macro-remains	248-250	4880 ± 15	5597 (5586-5651)	
	Plant macro-remains	288-290	6095 ± 15	6959 (6895-7149)	
Mista	Sediment	0-1.5		-67 ± 0	Feussom Tcheumeleu et al. (2023)
	Sediment	1.5-2.5		-54 ± 1	
	Sediment	2.5-3.5		-48 ± 1	
	Sediment	3.5-4.5		-27 ± 4	
	Sediment	4.5-5.5		-12 ± 7	
	Sediment	5.5-6.5		8 ± 11	
	Sediment	6.5-7.5		11 ± 9	
	Sediment	7.5-8.5		16 ± 8	
	Sediment	8.5-9.5		33 ± 11	
	Sediment	9.5-10.5		71 ± 18	
	Herbaceous stems	69-74	2103 ± 21	2064 (1997-2123)	
	Herbaceous stems	151-156	3694 ± 27	4036 (3928-4145)	
	Herbaceous stems	229-234	5109 ± 27	5812 (5751-5923)	
	Picea glauca cone	342-343	7472 ± 33	8283 (8193-8367)	
	Picea glauca cone	359-360	7741 ± 32	8511 (8430-8590)	

percentages in a given subsample by combustion was performed using a CN elemental analyzer (at the Environmental Chemical Analysis Unit of Chrono-environment laboratory) following drying, grinding and weighing of sediment subsamples taken at 4-5 cm intervals on the same core levels as for the chironomid analysis. Prior to measuring the TOC and TN, sediment subsamples were treated with hydrochloric acid in order to confirm the absence of carbonates. TOC and TN weight percentages were further used for the calculation of atomic C/N ratio in sediments. The C/N ratio help to trace sediment provenance, more precisely to distinguish in-lake (autochthonous) versus terrestrial (allochthonous) sources of organic matter (e.g. lacustrine algae versus terrestrial plants organic matter; Meyers, 1994, 2003).

The relationships between chironomid inferred August temperature, chironomid PC1 and 2 sample scores, TOC, TN and C/N ratio, were measured (Pearson's correlation coefficients) using the R Stats package. All statistical analyses were run with R 3.3.2 software (R Core Team, 2016).

3.4.4 Chironomid analysis and temperature reconstruction

Details on lake Aurélie and lake Mista coring and chironomid analysis are reported by Bajolle et al. (2018) and Feussom Tcheumeleu et al. (2023) respectively. The 164 sediment samples from lake Aurélie covered the past 8300 years. 79 other samples from lake Mista covered the past 8500 years.

For lake Adèle chironomid subfossil analysis, a total of 95 sediment samples were taken at 1-5 cm intervals depending on sedimentation rate. On each sample, between 0.5 and 1.7 g of wet sediments were processed for chironomid head capsules extraction using standard methods described in Brooks et al. (2007). Under a binocular stereomicroscope at 10x magnification, between 63 and 439 head capsules per subsample were handpicked using fine forceps and permanently mounted ventral side up between slide and coverslip in a drop of aquamount.

Chironomids identification was performed under a light microscope at 400x magnification with reference to taxonomic keys of Wiederholm (1983), Larocque and Rolland (2006), Brooks et al. (2007), Andersen et al. (2013) and Larocque (2014).

Chironomid percentage stratigraphic diagrams were plotted using strat.plot function in rioja R package (Juggins, 2014). The chironomid stratigraphies were zoned using the stratigraphically constraint cluster analysis CONISS (Grimm, 1987). The number of significant biozones was assessed by the Brocken-stick model (Bennett, 1996). A detrended correspondence analysis (DCA; Hill-Gauch, (1980)) with nonlinear rescaling and detrending by segments was performed on the chironomid percentage matrix using decorana command in the vegan R package (Oksanen et al., 2018) to assess the magnitude of species turnover. Since the DCA axis 1 gradient length was below 1.5 standard deviation units (SD) and thus requires the use of a linear method (Borcard et al., 2011), a principal component analysis (PCA) was performed on the chironomids square-root-transformed percentage matrix in order to explore changes in the chironomid assemblages through time (ter Braak and Prentice, 1988). Only chironomid taxa present in at least two samples and exceeding a threshold of 2% of the main chironomid sum were included in the analysis.

Mean August air temperatures were inferred using a chironomid-based temperature inference model (WA-PLS, 2 components; R^2_{boot}=0.73; $RMSE_{boot}$=1.84°C) based on a modern calibration dataset of 130 lakes and 130 taxa from eastern Canada and Newfoundland (Suranyi et al., in press) with August air temperature ranging from 7.1 to 21.8°C i.e. a gradient of 14.7°C.

The reliability of the chironomid-inferred temperature was assessed by calculating (1) the percentage of modern rare taxa per fossil sample (Hill's $N_2 < 2$; Hill, (1973)); (2) the chi-square distance to the closest modern assemblage (Overpeck et al., 1985); (3) the goodness-of-fit with temperature (Birks et al., 1990); (4) the statistical significance of the reconstructions using the palaeoSig package in R (Telford and Birks, 2011; Telford, 2019) with 999 random reconstructions. Analogue matching using chi-square distance as a measure of dissimilarity (Simpson, 2007) was used to assess whether the fossil chironomid assemblages had “good analogues” (if the chi-square distance lies in-between 1^{st}-5^{th} percentiles), “poor analogues” (if chi-square distance >10^{th} percentile and <20^{th} percentile) or “no analogues” (if chi-square distance >20th percentile). Goodness-of-fit with temperature was evaluated by passively fitting fossil samples to the canonical correspondence analysis (CCA) of the modern samples (ter Braak and Prentice 1988; Simpson, 2007). Fossil samples with a residual distance to CCA axis 1 above 90^{th} and 95^{th} percentiles of the residual distances of all modern samples were considered as having a “poor fit” and “very poor fit” respectively, with the inferred Mean August air temperatures (Birks et al., 1990). The percentage of chironomid taxa considered to be rare in the modern calibration dataset was estimated with the “compare” function in analogue R package (Simpson, 2007). Chironomid effective diversity (Hill’s N2 index) was measured using the “utility” function in rioja R package (Juggins, 2014).

Details on lake Mista and Aurélie chironomid-based temperature reconstruction diagnostics (i.e. percentage of fossil assemblage taxa missing from the calibration set, goodness-of-fit with temperature, analogue quality) are reported in Supplemental Material S3.2.

In order to assess the Holocene climatic variations across the boreal forest of eastern and western Québec, we did a multisite comparison of the spatiotemporal evolution of the climate during the Holocene in Québec. The inferred mean August temperatures from each lake were linearly interpolated to a constant annual temporal resolution then smoothed by LOESS method over a 1000-year window to screen century-scale fluctuations.

3.5 Results

3.5.1 Chironomids stratigraphy in lake Adèle

We counted between 63 and 439 chironomid head capsules (HC) per sample. In total, 83 chironomid taxa were identified in 95 samples from the sediment core of lake Adèle. The down-core changes in chironomid assemblages led to the identification of three statistically significant assemblage zones (CAZ-1 to CAZ-3; Fig.3.2) described as follows:

CAZ-1 (ca. 7100-4100 cal yr BP)

CAZ-1 is characterized by high relative abundance of taxa indicative of temperate to warm climatic conditions such as *Parakiefferiella* type A, *Ablabesmyia*, *Corynoneura*, *Polypedilum nubeculosum*-type, *Tanytarsus pallidicornis*-type and *Dicrotendipes nervosus*-type (Fig.3.3 with dominant chironomid taxa on the first and second axis of PC). Throughout this zone, PC1 sample scores were all negative (Fig.3.4). Most N2 diversity values of chironomid assemblages were above 25.

CAZ-2 (ca. 4100 to 2300 cal yr BP)

CAZ-2 is marked by a relative decline in the percentages of warm taxa characteristic of biozone 1 and the converse development of more temperate taxa like *Corynoneura*, *Procladius*, *Tanytarsus chinyensis*-type, *Paratanytarsus*, *Tanytarsus mendax*-type (Fig.3.3). The biozone is further characterized by a progressive increase in the relative abundance of the cold indicative taxa *Sergentia coracina*-type. From the start to the end of this biozone (Fig.3.4), chironomid N2 diversity gradually decreased from its highest value (32) down to 20. PC1 and 2 sample scores remained close to zero.

CAZ-3 (ca. 2300 to present)

CAZ-3 is characterized by high relative abundance of *Chironomus plumosus*-type, *Psectrocladius calcaratus*-type, *Corynocera oliveri*-type and *Sergentia coracina*-type (Fig.3.3). Chironomid N2 diversity reached its lowest value (15) for the whole sequence between ca. 1700-1800 cal yr BP before rising again (Fig.3.4). The shift of PC1 sample scores to values generally above 0 except around 1000 cal yr BP reflect changes in chironomid community from temperate climate indicating taxa to cold indicating taxa like *Corynocera oliveri*-type and *Sergentia coracina*-type.

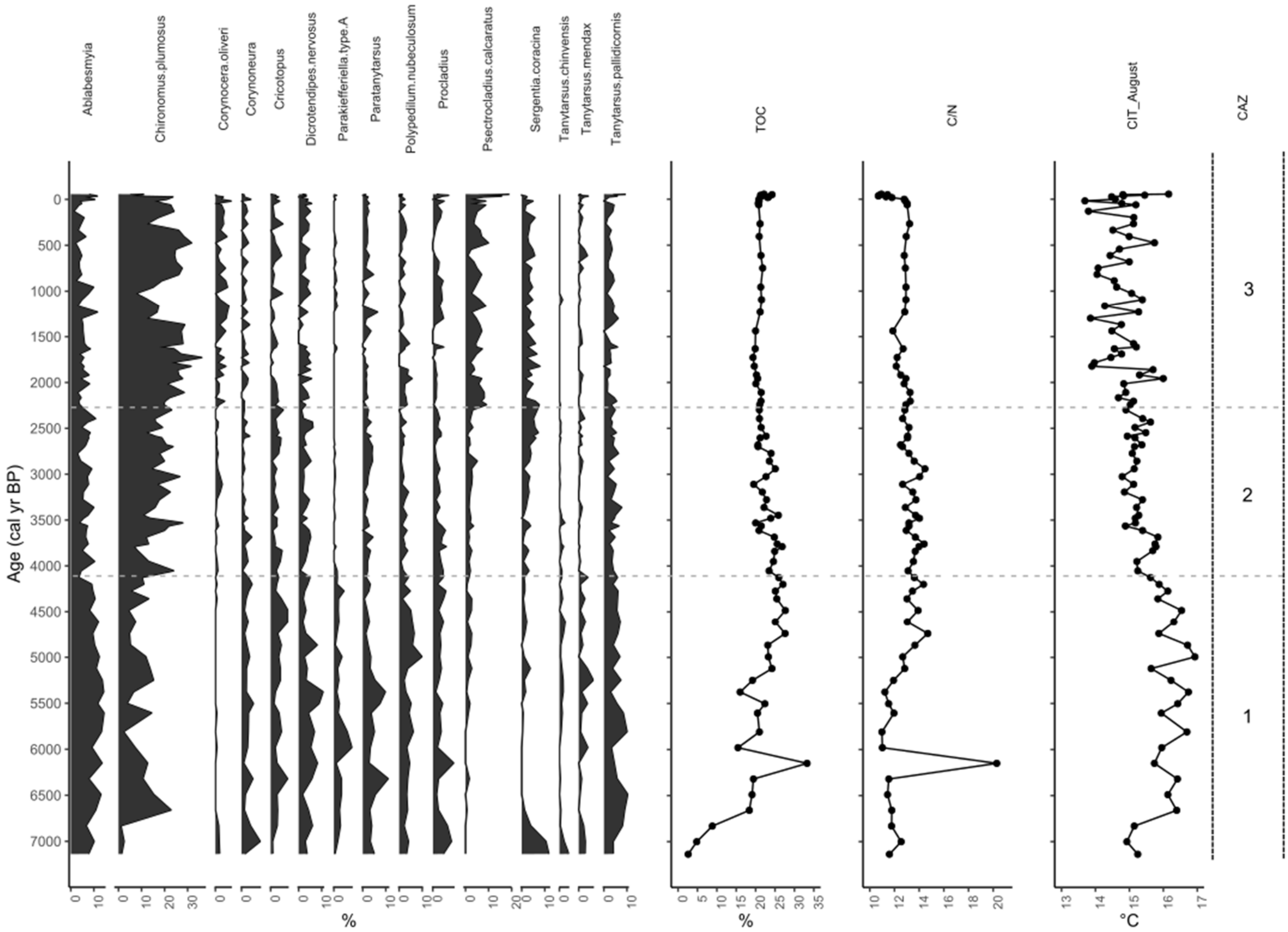

Figure 3.2 Lake Adèle: Simplified chironomid percentage diagram, chironomid assemblage zone (CAZ; in horizontal dashed grey lines), total organic carbon (TOC), C/N ratio and Chironomid inferred August temperature (CIT-August).

3.5.2 Geochemistry (TOC and C/N) in Lake Adèle

The TOC and C/N records from lake Adèle (Fig.3.2) show three distinct periods of changes in organic matter through time. From ca. 7100 to 5000 cal yr BP, the TOC (mean 17.8%; range 2.6-33.2%) and C/N (mean 12.3; range 11.4-20.2) mean values were low. Between ca. 5000 cal yr BP and AD 1950, the TOC (mean 22.4%; range 19.3-27.6%) and C/N (mean 13.2; range 11.8-14.7) increased and fluctuated around mean values. From AD 1950 to 2006, the TOC content of the sediments (mean 22.5%; range 21.2-24.2%) rose as oppose to the sharp decrease of C/N values (mean 11.1; range 10.7-11.7).

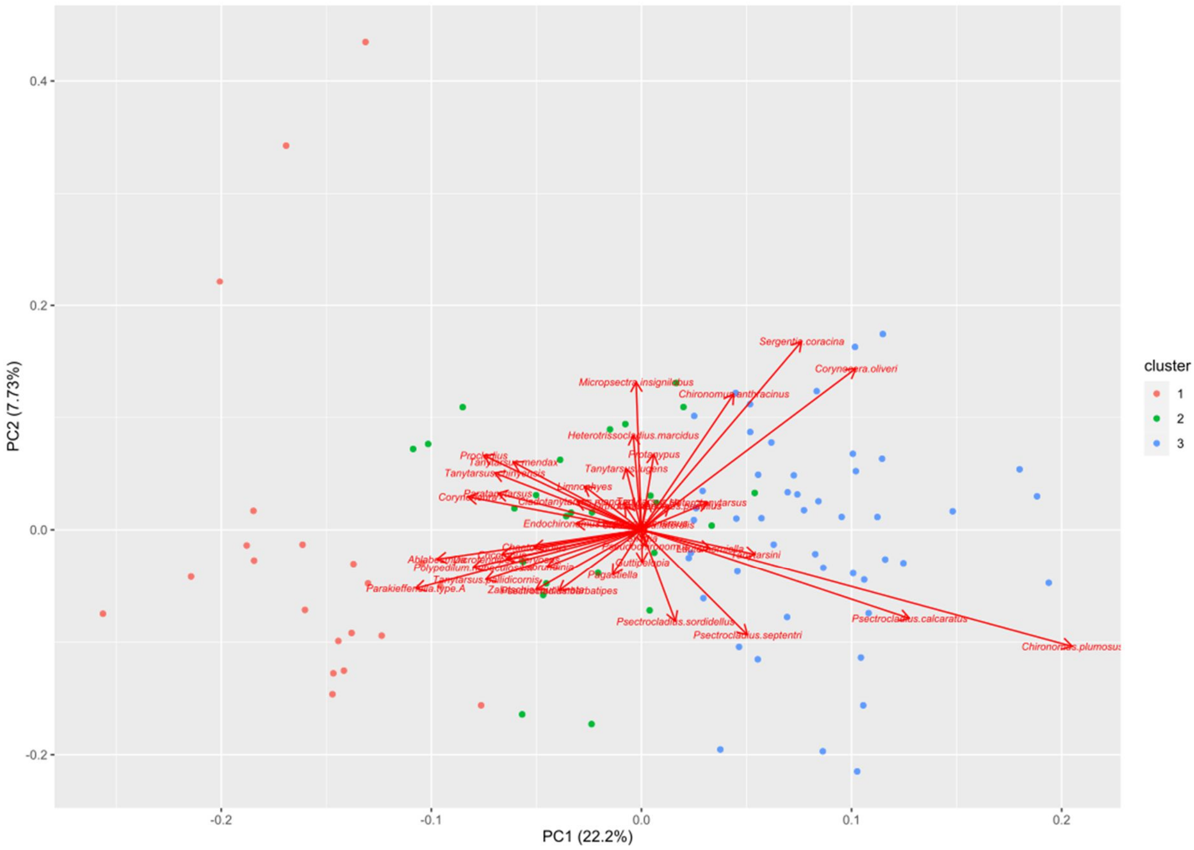

Figure 3.3 Lake Adèle: Samples (colored dots) and chironomid taxa principal component analysis plot. The clusters corresponding to the chironomid assemblage zones (red dots (CAZ 1), green dots (CAZ 2), and blue dots (CAZ 3)).

3.5.3 Chironomid-based temperature reconstruction from lake Adèle

All fossil samples contained less than twenty percent (range 1.25-4.72%) of rare taxa in the training set (Fig.3.4) as needed to obtain reliable estimation of temperature from a fossil sample (Brooks and Birks, 2001; Larocque-Tobler, 2010). Almost all samples have good fit with temperature excepted ten samples (five with poor fit and five other samples with very poor fit; Fig.3.4). All fossil samples had “good” analogues with the calibration dataset (Fig. 3.4). Our inferred temperatures failed the Telford test (Telford and Birks, 2011) when compared to 999 random reconstructions (p-value=0.16). However, the PC1 (λ=22.2%) and PC2 (λ=7.7%) scores are significantly correlated with inferred temperatures (Table 3.3).

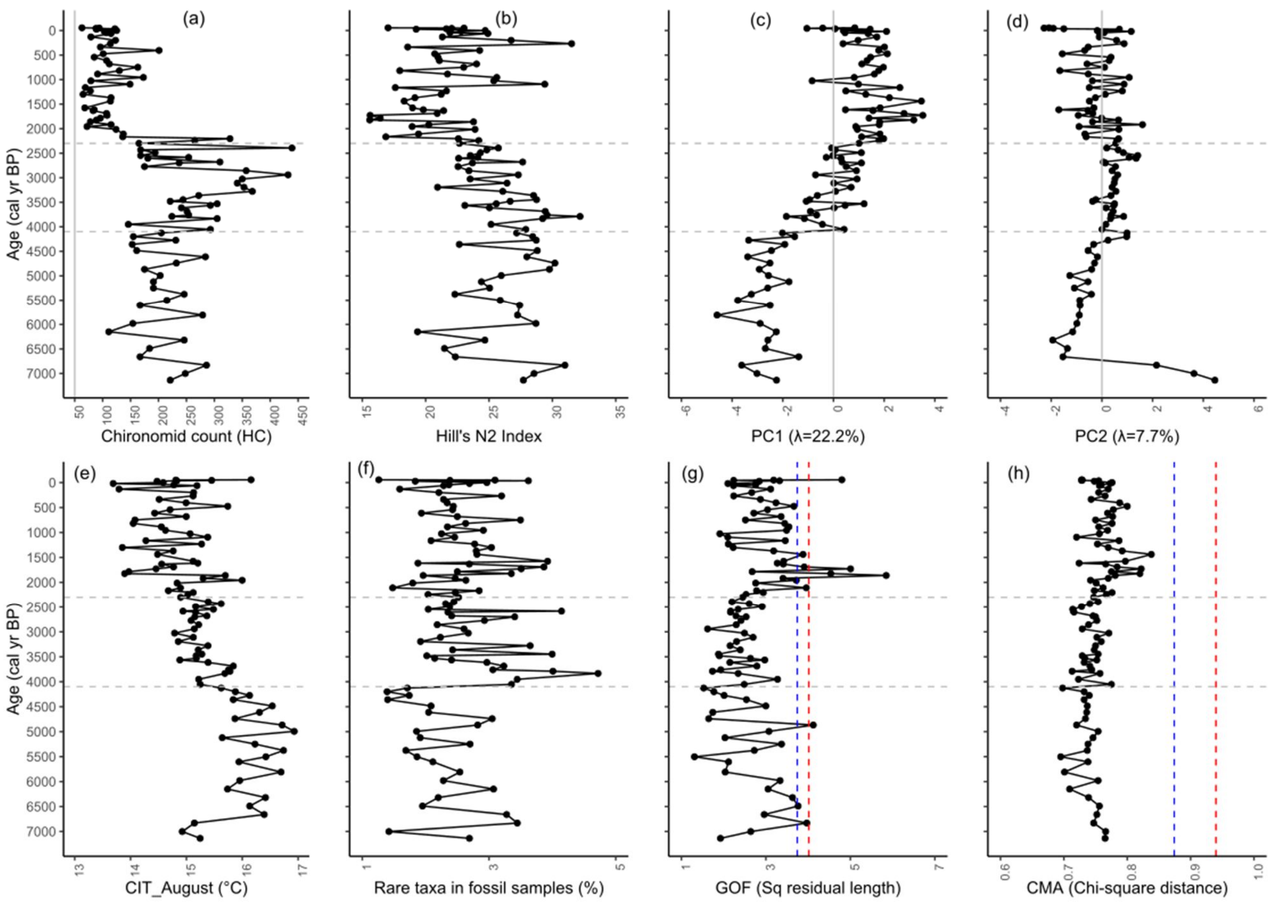

Figure 3.4 Lake Adèle: (a) chironomid count, (b) chironomid species richness (Hill's N2 index), (c) and (d) chironomid PC1 and 2 sample scores (λ indicates the proportion of variance explained by the PC axis of the fossil data), (e) chironomid inferred August temperature (CIT-August), (f) fossil assemblage taxa rare in modern dataset, (g) goodness-of-fit (GOF) of fossil samples with temperature (samples with very poor fit exceed vertical dashed red line while those with poor fit are beyond vertical dashed blue line), (h) fossil samples closest modern analogues (CMA) in modern dataset (samples with no close modern analog exceed vertical dashed red line while those with poor close modern analogs are beyond vertical dashed blue line), chironomid assemblage zone (CAZ; in horizontal dashed grey lines).

Three major periods can be distinguished from the lake Adèle chironomid-inferred August temperature graph (Fig.3.4):

- Period 1 (ca. 7100 to 4100 cal yr BP) marked by high temperature values (mean 16.06°C; range 14.92-16.93°C);

- Period 2 (ca. 4100 to 2200 cal yr BP) showing a gradual cooling trend with decreasing temperature values (mean 15.25°C; range 14.78-15.83°C);
- Period 3 (ca. 2200 cal yr BP to present) marked by a sharp cooling trend (mean temperature 14.78°C; range 13.68-16.15°C).

Table 3.3 Pearson's correlation coefficients and p-values between lake Adèle chironomid inferred August temperature, chironomid PC1 and 2 sample scores and geochemical variables (TOC, TN and C/N ratio). Asterisks indicate significant Pearson correlation test, with**: p value < 0.01 and ***: p value < 0.001.

	Inferred temperature	PC1	PC2	TOC	TN
PC1	-0.77***				
PC2	-0.36**				
TOC	0.15	0.03	-0.44***		
TN	0.18	0.06	-0.64***	0.86***	
C/N ratio	-0.015	0.003	0.15	0.57***	0.08

3.5.4 Multisite comparison of the post-glacial changes in summer temperatures across boreal Québec

The inferred mean August air temperatures based on chironomid assemblages from lakes Aurélie, Adèle and Mista show a generally similar trends starting with a warm period followed after 5000-4000 cal yr BP by a cooling period (Fig.3.5). Another common feature of all three records is the greater variability of reconstructed temperatures over the last 3 millennia, suggesting a succession of warm and cold secular events. However, the timing and magnitude of the reconstructed temperature changes differ between sites and their location.

While the sedimentary record from lake Adèle begins around 7000 cal yr BP, the cores from lake Mista and lake Aurélie document the earlier period, from 8700 and 8300 cal yr BP, respectively. For both records, the first half of the postglacial period can be subdivided into two phases. At lake Aurélie, located to the west of the transect, a first colder phase before 8000 cal yr BP is followed by the warmest summer temperatures of the entire record between 8000 and 6500 cal yr BP. The next phase between 6500 and 4800 cal yr BP is characterized by a slight decrease in summer temperatures, which nevertheless remain higher than during the period following 4800 cal yr BP. At lake Mista, located east of the transect, the climatic dynamic of the first half of the postglacial period is different. Indeed, a first colder phase between 8700 and 7000 cal yr BP is followed by a phase characterized by the warmest temperatures of the record between 7000 and 4000 cal yr BP. However, it should be noted that the reconstructed summer temperatures for the phase prior to the climate shift that occurred between 4000 and 5000 cal yr BP are equivalent for the 3 study sites and are around 16°C.

According to sedimentary records, the cooling that follows does not have exactly the same temporal dynamics. At lakes Mista and Adèle, the cooling is quite sharp and occurs around 4000 cal yr BP (4000 cal yr BP for Mista and 4100 cal yr BP for Adèle). At lake Aurélie, the transition is smoother and seems to occur slightly earlier, around 4800 cal yr BP, according to the available age-depth model, which is 800 years earlier than the two lakes located further east.

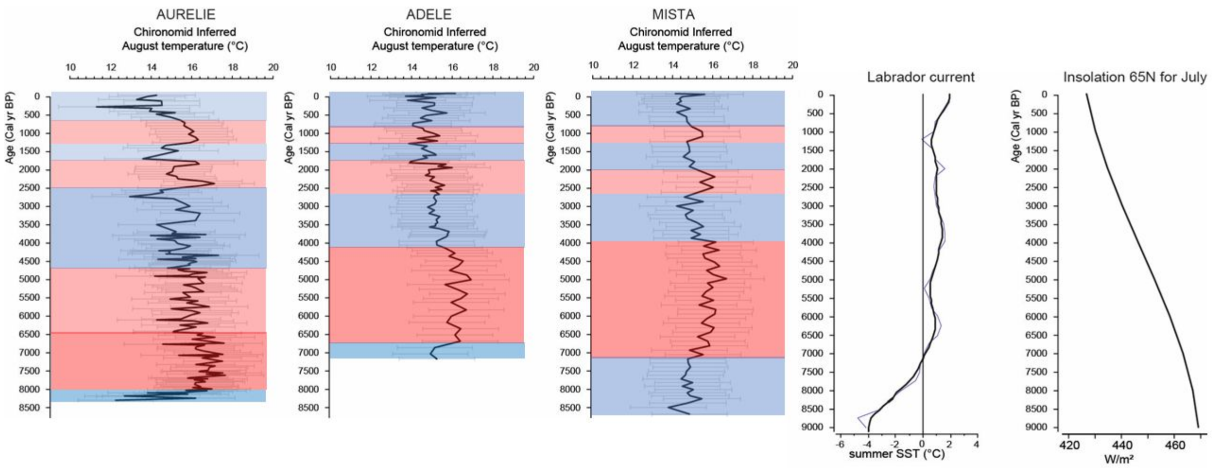

Figure 3.5 Chironomid inferred August temperature (in solid black lines; with the error bars delimiting the minimum and maximum sample-specific estimated standard error of prediction (eSEP)). Labrador current (summer Sea Surface Temperature (SST); Fréchette et al., 2021). Mid-month insolation 65N for July (Berger and Loutre, 1991).

Regarding the higher frequency climatic variability suggested by the three records for the last three millennia, it is still difficult to distinguish clearly a common pattern in the climatic dynamics given the analysis resolution of the different sequences and the accuracy of age-depth models. However, it could be suggested to recognize the occurrence of two globally warmer phases, the first one between 1800 and 2500 cal yr BP, and the second one between 1300 and 800 cal yr BP. These warmer phases were separated by a cold phase.

3.6 Discussion

3.6.1 Reliability of chironomid-based temperature reconstruction from lake Adèle

The reconstructed temperatures are likely to be reliable as (1) all fossil assemblages from lake Adèle had good analogs with the calibration dataset (ter Braak 1995) (2) the taxa in fossil assemblages are well represented in the modern assemblages (Birks 1998). However, the few assemblages that are poorly or very poorly fitted by temperature (Fig.3.4) should be interpreted cautiously. Six of the samples in question are distributed between 1600 and 2100 cal yr BP.

PC2 (λ=7.7%) significant correlation to TOC and TN (Table 3.3) suggest that in-lake variables such as quantity and quality of food source for chironomid larvae and/or oxygen conditions may have influenced short-term changes in chironomid assemblages (Velle et al. 2005; Brodersen and Quinlan 2006). Nevertheless, major changes in chironomid communities from lake Adèle seem to reflect changing climatic conditions. The contrasting temperature preferences of the main characteristic taxa of the different biozones, as well as the absence of a significant relationship between the reconstructed temperatures and organic matter (TOC and C/N; Table 3.3), suggest together that climate is most likely the primary direct or indirect driver of major changes in assemblage composition during the post-glacial period in lake Adèle record. Furthermore, the general pattern of chironomid-based temperature reconstructions from lake Adèle is coherent with other regional climate records as discussed in the next section.

3.6.2 Holocene climatic variations

Chironomid temperature inferences from the three study sites showed two major stages of long-term climate oscillations in eastern and western Québec.

Consistently for all three study sites, high summer temperatures were reconstructed during the mid-Holocene. These higher temperatures correspond to the Holocene Thermal Maximum known in the literature (Renssen et al., 2012). For all three sites, the Holocene Thermal Maximum is then followed, in late-Holocene, by a more or less gradual decrease in temperature which seems to correspond to the Neoglacial period (Fig.3.5; Viau et al., 2006). However, the timing, duration and amplitude of the temperature changes during the Holocene Thermal Maximum and the Neoglacial appear to be variable across the sites, distributed along an east-west gradient (Fig.3.5). While the reconstructed temperature curve at lake Aurélie parallels the summer insolation curve and thus suggests the predominant influence of orbital forcing on the evolution of summer temperatures, sites further east, particularly lake Mista, exhibit a slightly different climatic dynamic that probably results from the combined influences of external (insolation) and internal factors.

For the three chironomid-inferred temperature records, the 7000 to 4800 cal yr BP time window undoubtedly appears as a warm period whereas the 4800 to 4000 cal yr BP interval corresponds to the onset of Neoglaciation and the prevalence of colder conditions during summer across eastern and western Québec (Supplemental Material S3.3). Superimposed on this millennial-scale climate trend, Chironomidae-inferred temperatures suggest a higher-frequency secular-scale variability particularly over the last 3000 years characterized by the succession of the warm and cold events that could be only tentatively compared to the Roman Warm Period (RWP, Holmquist et al., 2016), the Dark Age Cold Phase (DACP, Helama et al, 2017), the Medieval Warm Period (MWP, Wang et al., 2022) and the Little Ice Age (LIA, Wang et al., 2022). Indeed, age model and analytical resolution does not allow us to compare with certainty this succession of warm and cold events with the RWP, DACP, MWP and LIA.

3.6.2a The Holocene Thermal Maximum

Chironomid-inferred temperatures at all three lakes (Aurélie, Adèle, Mista) show high values during the early and or mid-Holocene. This warm phase corresponds to the so-called Holocene Thermal Maximum period and seems strongly related to high orbital-induced insolation (Fig.3.5; Renssen et al., 2009; Wanner et al., 2015). The timing of Holocene Thermal Maximum in lake Aurélie (8300-4800 cal yr BP) is consistent with Fréchette et al. (2018) pollen-based temperature reconstructions which indicate a warmer than present temperatures for western Québec between 8500 and 4500 cal yr BP. The changes in reconstructed temperatures at lake Aurélie parallel the insolation curve, with the warmest phase of the Holocene occurring between 8100 cal yr BP and 6500 cal yr BP. Chironomid-inferred summer temperatures fluctuate around an average of 17°C, which is ca 2.5°C higher than today. At lake Mista, reconstructions based on Chironomidae suggest colder temperatures for the period from 8500 to 7100 cal yr BP, which nevertheless coincides with the peak of summer insolation. Fréchette et al (2021) also found a strong east-west contrast from pollen-based temperature reconstructions before 8000 and 7000 cal yr BP. This finding indicates the likely influence of local internal factors that counterbalance the influence of insolation. The distance between the decaying Laurentides Ice Sheet and the study sites does not explain this difference between the lake Mista and Aurélie records, since both sites are located at similar distances from the Laurentides Ice Sheet during the Holocene, and especially during the period 8500-7000 cal yr BP (see Fig.3.1). A strong contrast in climatic conditions between eastern and western Québec up to about 7500 cal yr BP was also highlighted by Frechette et al (2021) from pollen-based paleoclimate reconstructions. As suggested by these authors, colder climatic conditions at the more easterly lake Mista are probably influenced by oceanic conditions and atmospheric circulation prior to 7100 cal yr BP, linked to the decaying Laurentides Ice Sheet. First, the clockwise anticyclonic atmospheric circulation that resulted from katabatic winds over the remnant Laurentides Ice Sheet exerts a stronger cooling effect on the southeast side of the ice-cap. And secondly, before 7000, eastern Québec was probably under the cooling influence of the Labrador Inner Current, whose surface waters were colder due to meltwater inputs (Anderson et al., 2007; Frechette et al., 2021). Compared to lake Aurélie, the Holocene Thermal Maximum was delayed until ca. 4000 cal yr BP for lakes Adèle and Mista, i.e. ca 800 years after Aurélie. This difference lies well beyond the confidence interval of age estimation provided by the age-depth model of the 3 records and then may be considered as significant. This finding is also consistent with the pollen record of Fréchette et al. (2021) that suggests that the Holocene Thermal Maximum was also delayed in eastern Québec and Labrador by about 1000 years as compared to Fréchette et al. (2018) pollen-inferred temperatures for western Québec. At lake Adèle, this delay may be due partly to the proximity with the decaying Laurentide Ice Sheet (Kaufman et al., 2004), which locally offset the influence of high summer insolation. In Atlantic Canada where is located lake Mista, this delay was associated with the cooling effect of residual Laurentide Ice Sheet on the coupled atmospheric-oceanic circulation of the North Atlantic region (Kaufman et al., 2004).

3.6.2b The onset of Neoglaciation

Chironomid-based temperature reconstructions from eastern and western boreal regions of Québec (Fig.3.5) suggest an onset of the Neoglaciation between 4800 and 4000 cal yr BP. This is consistent with the pollen-based temperature reconstruction of Fréchette et al. (2018) and Fréchette et al. (2021), which highlighted the 4500 to 3500 cal yr BP time interval as the transitional period from Holocene Thermal Maximum to Neoglacial across the western and eastern boreal region of Québec. Magnan and Garneau (2014) peatland testate amoebae-based paleohydrological records near Havre St-Pierre suggest a cooling transition at ca. 3000 cal yr BP. The cooling down of temperatures following the Holocene Thermal Maximum is commonly associated with decreasing orbital-induced insolation (Wanner et al., 2015) from 469 to 452 W/m^2 (9000-5000 cal yr BP), between 452 and 440 W/m^2 (5000-3000 cal yr BP), then from 440 to 426 W/m^2 (3000 cal yr BP to present) (Fig.3.5; Berger and Loutre, 1991).

3.6.3 A higher climate variability during the last 3kyr.

Though the onset of neoglaciation was asynchronous (Fig.3.5) for all three paleoclimate records, the last 3000 years are characterized by greater high-frequency climate variability, with a succession of warm and cold events. Although the number of radiocarbon dates and the precision of the age models should lead to caution in interpreting these results, there seems to be some coherence in the reconstructed climatic succession for the three sites. Given the uncertainty associated with age estimates, comparing this succession of warm and cold events to the Roman Warm Period, Dark Ages Cold Period, Medieval Warm Period and Little Ice Age (Delwaide et al., 2021) sequence is possible but must remain speculative.

3.6.3a A possible warmer phase between 2500 and 1800 cal yr BP

The timing of a warm event that occurred around ca. 2500 cal yr BP seems to match at all three sites. The reconstruction of a warmer event during the 2500 and 1800 cal yr BP interval is consistent with the previous testate amoebae palaeohydrological record of Holmquist et al. (2016) which indicates that the Boreal Shield and James Bay Lowland regions of Ontario (Canada) also experienced warmer climate conditions between 2500 and 1600 cal yr BP. Based on tree-ring chronology of subarctic Québec *Picea mariana*, Delwaide et al. (2021) placed the Roman Warm Period between 1725 and 1550 cal yr BP. Considering the dating uncertainties of the chronology of our three lakes, and the delay that may perhaps occurred between climate changes and the ecological response of tree species, this can be a simultaneous event. The nature and causes of this warmth epoch in North America are not yet clearly understood (Holmquist et al., 2016)

3.6.3b A cold episode around 1500 cal yr BP

The inferred temperatures from all three sites show a synchronous multi-centennial coldness in western and eastern boreal Québec around ca. 1500 cal yr BP (Fig.3.5). The timing of this cold episode in the eastern and western boreal regions of Québec is coherent with pollen-based temperature reconstruction of O'Neill Sanger et al. (2021) which suggests a cold period (the Dark Age Cold Period) between 1550 and 1250 cal yr BP across southeastern Québec. This also agreed with the tree-ring chronology of Delwaide et al. (2021) which suggest that the Roman Warm Period was interrupted by a colder phase between 1550 and 1120 cal yr BP. In eastern North America, this climatic epoch was partly driven by decreased insolation and weakened ocean-atmospheric interactions including the negative phase of the North Atlantic Oscillation (Helama et al., 2017).

3.6.3c Around 1000 cal yr BP: The Medieval Warm Period?

The cold episode that occurred around 1500 cal yr BP was followed by a warmer phase recorded around 1000 cal yr BP across our study area. These findings are consistent with other studies that evidenced a warm interval around 1000 cal yr BP; e.g., tree-ring data from subarctic Québec (between 1120 and 840 cal yr BP; Delwaide et al., 2021), eastern Canadian boreal forest (between 1000 and 700 cal yr BP; Wang et al., 2022) and north-western Québec (between 1090 and 950 cal yr BP; Arseneault and Payette, 1997), the pollen-based studies in the boreal biome across North America (between 1250 and 950 cal yr BP; Viau et al., 2012) and the testate amoebae-based reconstruction near Havre St-Pierre (between 1100 and 600 cal yr BP; Magnan and Garneau, 2014) and in the Boreal Shield and James Bay Lowland regions of Ontario (between 1000 and 700 cal yr BP; Holmquist et al., 2016). This climatic episode was partly driven by increased ocean-atmospheric interactions including the persistent positive phase of the North Atlantic Oscillation characterized by enhanced warmth over interior North America (Trouet et al., 2009; Mann et al., 2009). Other studies (e.g., Gennaretti et al., 2014; Wang et al., 2022) suggested that volcanoes triggered the synchronization of eastern Canada with Northern Hemisphere Medieval Warm Period.

3.6.3d Post 1000 cal yr BP cooling phase

In lakes Mista and Aurélie, chironomid-inferred temperatures gradually get colder from 800-700 to 0 cal yr BP. At lake Adèle, the climate dynamic is less clear with a first cold phase between 1000 and 600 cal yr BP interrupted by a warmer phase around 500 cal yr BP. This colder phase suggested by the three records could hypothetically be compared to the Little Ice Age identified from the study of other records in Québec. Indeed, a similar temperature decline was observed in testate amoebae-based reconstruction from Hudson Bay Lowlands Canada (ca. 550-250 cal yr BP; Holmquist et al., 2016), at the eastern Canadian treeline (ca. 650-100 cal yr BP; Payette and Delwaide 2004), in the eastern Québec with permafrost growth in peatland (ca. 600; Dionne and Richard, 2006) and in northwestern Labrador with forest retreat (ca. 650-100 cal yr BP; Payette, 2007). The Little Ice Age was also documented in eastern Canadian boreal forest tree-ring data (500-100 cal yr BP; Wang et al., 2022) and near Havre St-Pierre peatland testate amoebae-based paleohydrological records (between 600 and 100 cal yr BP; Magnan and Garneau 2014).

The Little Ice Age was not clearly detected at lake Adèle. The chironomid assemblages and temperature relationship was possibly disturbed by other environmental variables operating on decadal to multi-century scale as supported by the significant correlations between chironomid PC2 and geochemical variables (TOC and TN; Table 3.3). The reconstructed surface temperature anomaly pattern of Mann et al. (2009) displayed apparent Little Ice Age warmth in part of northeastern Québec and northern Labrador between 550 and 250 cal yr BP. However, as illustrated by the divergent results obtained from lake Adèle, comparing this phase to the Little Ice Age is still uncertain and should be confirmed by higher resolution analyses and additional dating to refine the age model. This is also true for previous temperature variations reconstructed over the past 3000 years and their comparison to the Roman Warm Period, Dark Age Cold Phase, and Medieval Warm Period.

3.7 Conclusion

The summer temperature reconstructions from post-glacial chironomid stratigraphies of lakes Aurélie, Mista and Adèle provide new insight into the spatial pattern of Holocene climate at regional scales across the coniferous boreal forest of Québec. The results suggest in particular the existence of a strong contrast in summer temperatures between east and west Québec before 7000 cal yr BP. In the east, during this period, the indirect influence of the decaying Laurentide Ice Sheet and ocean surface conditions counterbalance the maximum insolation to induce cooler summer conditions. In the east, the maximum summer temperature is only reached between 6000 and 5000 cal yr BP. The west of Quebec is little or not affected by these influences and the evolution of temperatures parallel the decrease of insolation during summer, with a maximum of temperatures around 7500 cal yr BP. Our results also highlight a strong climatic variability over the last 3000 years, with the succession of alternatively warm and cold events. Although these events appear generally synchronous between the three records, the chronological and analytical resolution does not allow us to compare with certainty this dynamic with the RWP, DACP, MWP, and LIA successions, and additional analyses are necessary to draw robust conclusions on this point.

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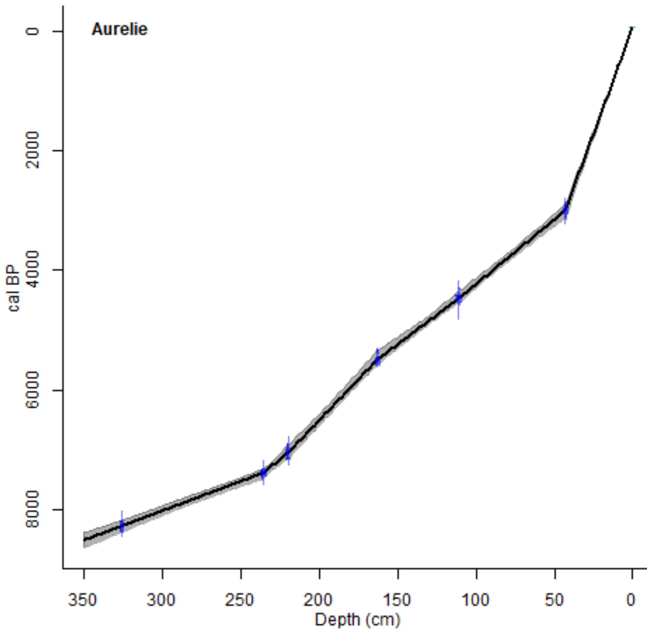
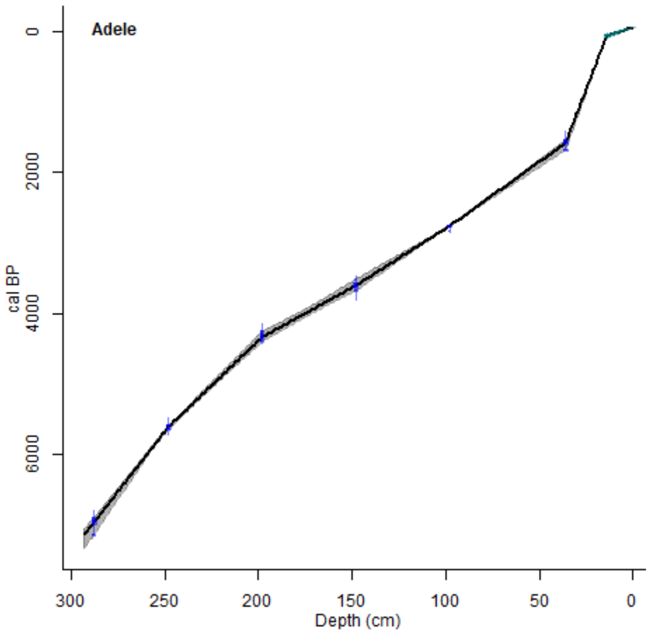
3.10 Supplemental Materials

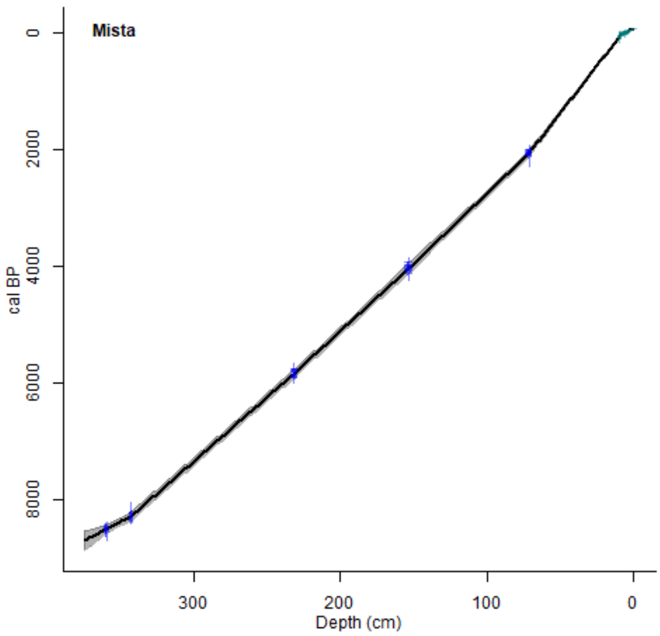
Supplemental Material S3.1a Age-depth model of Lake Aurélie based on ^{14}C dates (El-Guellab et al., 2015). Black line represents inferred chronology modeled using linear interpolation between dated levels. The 95% confidence intervals for the model are shown in grey.



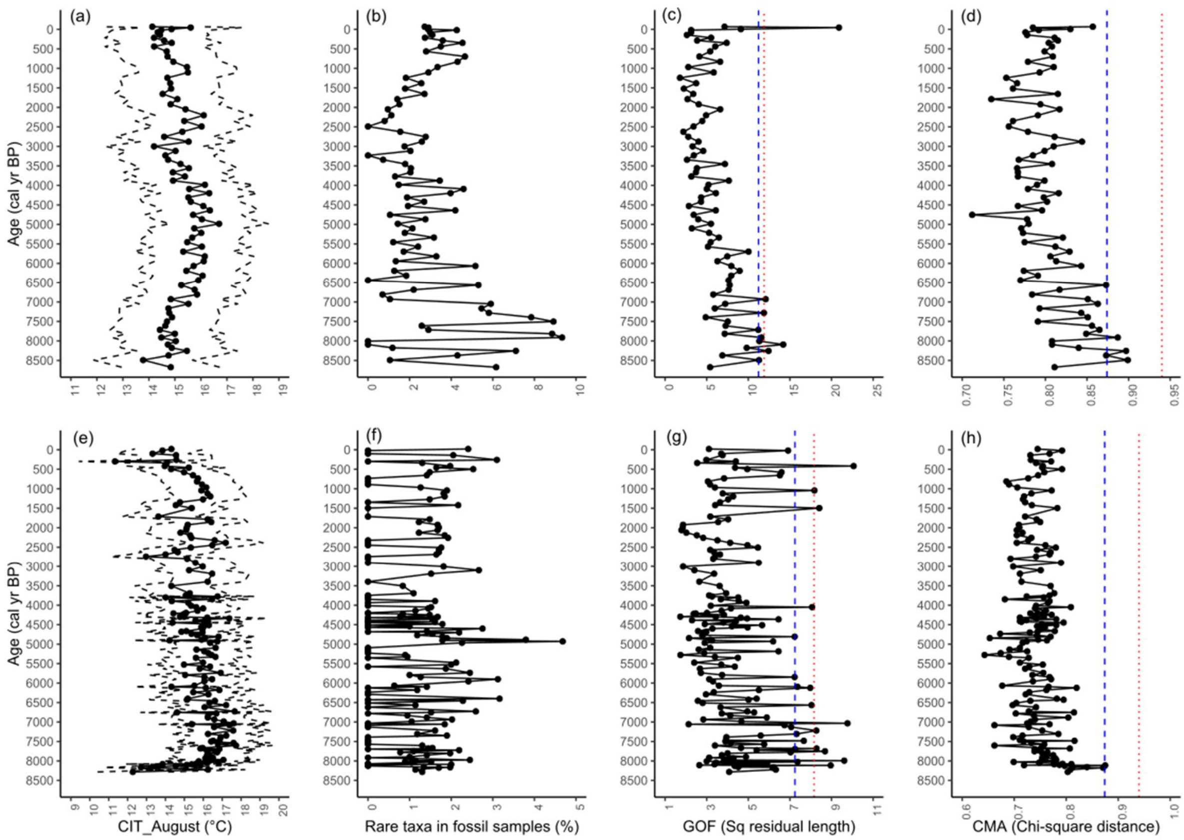
Supplemental Material S3.1b Age-depth model of Lake Adèle based on ^{14}C and ^{210}Pb dates (Bastianelli., 2018). Black line represents inferred chronology modeled using linear interpolation between dated levels. The 95% confidence intervals for the model are shown in grey.



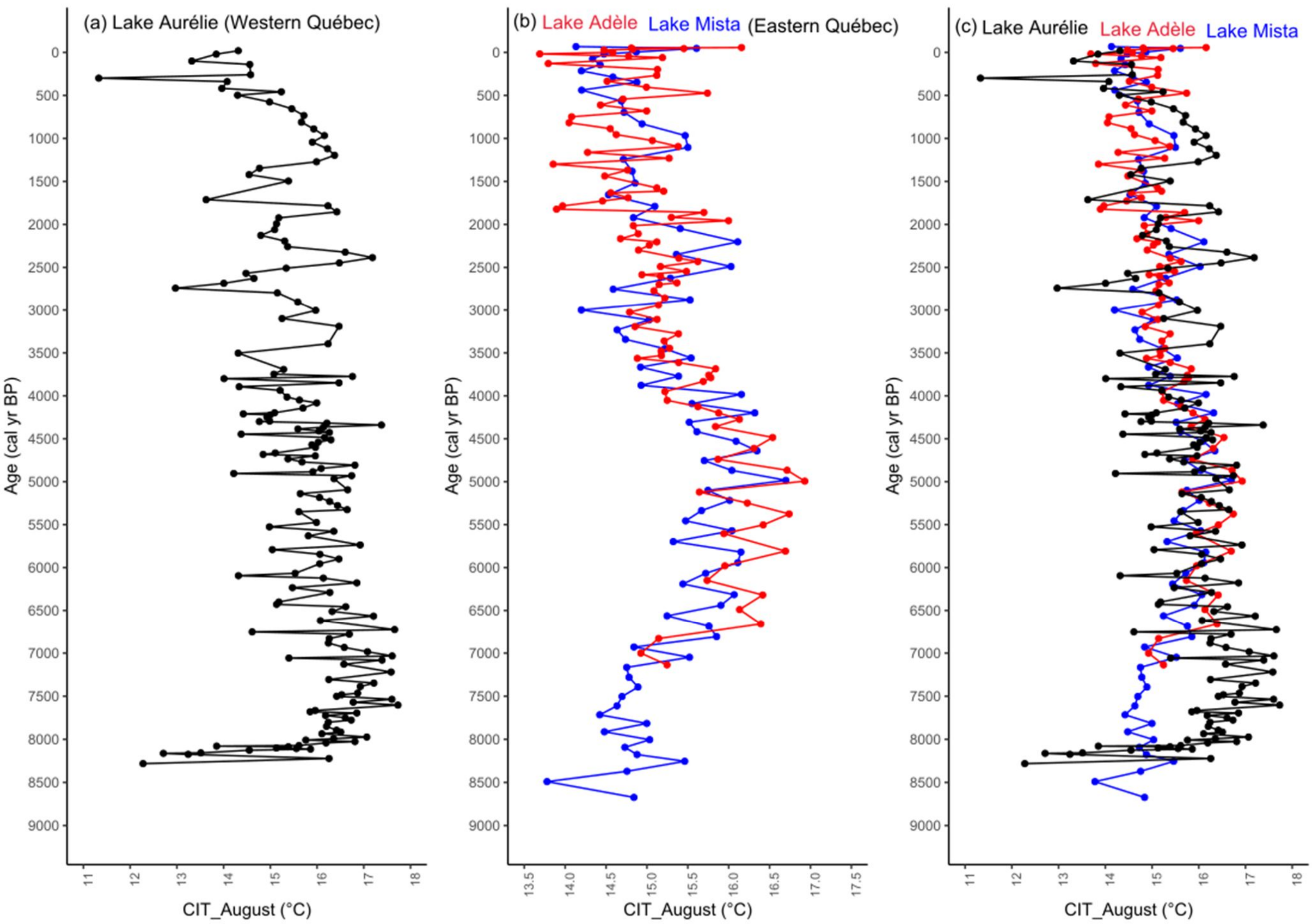
Supplemental Material S3.1c Age-depth model of Lake Mista based on ^{14}C and ^{210}Pb dates (Feussom Tcheumeleu et al., 2023). Black line represents inferred chronology modeled using linear interpolation between dated levels. The 95% confidence intervals for the model are shown in grey.



Supplemental Material S3.2 Details on lake Mista and Aurélie chironomid-based temperature reconstruction diagnostics (i.e. percentage of fossil assemblage taxa missing from the calibration set, goodness-of-fit with temperature, analogue quality).



Supplemental Material S3.3 Multisite comparison of the post-glacial changes in summer temperatures across eastern and western boreal Québec.



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Chapitre 4

A long (multimillennial) period of recurrent fires at short-intervals alters the resilience of black spruce moss forest in eastern Canada

Augustin Feussom Tcheumeleu, Damien Rius, Olivier Blarquez, Adam Ahmed Ali, Yves Bergeron, Pierre Grondin, Sylvie Gauthier, Laurent Millet

Prêt à soumettre

4.1 Abstract

Wildfire, climate, and their interactions are key drivers of boreal forests dynamics. According to global warming forecasts, high northern latitudes will be subject to the greatest temperature increases, as well as more severe and longer droughts. Over the last millennia, as a result of climate change, the fire regime has led to the opening of the landscape in Québec, with the transformation of closed-crown spruce-moss forests into lichen woodland. However, it is still poorly understood when and how lichen patches developed in the eastern closed-crown spruce forest subzone. We investigated the impact of fire return intervals and fire size/severity on multimillennial vegetation trajectories in two sites with very similar multimillennial summer temperature trend but contrasting modern vegetation. Our results suggest that changes in fire size and frequency control the long-term dynamics of black spruce-moss forests in eastern Québec. However, summer temperatures do not seem to directly control the fire regimes as the two studied sites displayed dissimilar trends in fire histories. Between 7000 and 3000 cal yr BP, both sites displayed similar vegetation trajectories whereas from 3000 cal yr BP to present, they exhibit different trajectories. At lake Adèle, the spruce-moss forest opened around 3000 cal yr BP. But, the resilience threshold of *Picea mariana* was likely exceeded around 1500 cal yr BP, leading to the transformation of black spruce-moss into spruce-lichen woodland. Recurrent fires at short intervals appear to be the main triggering mechanism. At lake Mista, the spruce-moss forest opened around 2000 cal yr BP, but shifted back to closed-crown forest during the last 300 years. Although the closed-crown forest appears resilient, it still remains in a precarious state of equilibrium as fire frequency could increase in the context of climate change and trigger the shifting of closed canopy forest to lichen woodland.

4.2 Résumé

Les feux, le climat et leurs interactions sont des facteurs clés de la dynamique des forêts boréales. Selon les prévisions de réchauffement climatique, les hautes latitudes de l'hémisphère Nord seront soumises aux plus fortes augmentations de température, ainsi qu'à des sécheresses plus sévères et plus longues. Au cours des derniers millénaires, sous l'effet des changements climatiques, le régime des feux a conduit à l'ouverture du paysage au Québec, avec la transformation des pessières à mousses en forêts de lichens. Cependant, on comprend encore mal quand et comment les forêts de lichens se sont développées dans le sous-domaine de la pessière à mousses de l'est. Nous avons étudié l'impact des intervalles de retour des feux et de la taille des feux sur les trajectoires multimillénaires de la végétation dans deux sites présentant des tendances de température estivale multimillénaires très similaires, mais une végétation

moderne contrastée. Nos résultats suggèrent que les changements dans la taille et la fréquence des feux contrôlent la dynamique à long terme des pessières à mousses dans l'est du Québec. Cependant, les températures estivales ne semblent pas contrôler directement les régimes de feux, car les deux sites étudiés présentaient des tendances dissemblables dans l'histoire des feux. Entre 7000 et 3000 ans AA, les deux sites présentent des trajectoires de végétation similaires, alors qu'entre 3000 ans AA et aujourd'hui, ils présentent des trajectoires différentes. Au lac Adèle, la pessière à mousses s'est ouverte vers 3000 ans AA. Mais le seuil de résilience de *Picea mariana* a probablement été dépassé vers 1500 ans AA, conduisant à la transformation de la pessière à mousses en pessière à lichens. Des incendies récurrents à intervalles rapprochés semblent être le principal mécanisme de déclenchement. Au lac Mista, la pessière à mousses s'est ouverte vers 2000 ans AA, mais elle s'est redensifiée au cours des 300 dernières années. Bien que la pessière à mousses semble résiliente, elle reste dans un état d'équilibre précaire car la fréquence des incendies pourrait augmenter dans le contexte du changement climatique et déclencher la transformation de la pessière à mousses en pessière à lichens.

4.3 Introduction

Boreal forests represent the world's largest terrestrial biome (Brandt et al., 2013; Girona et al., 2023a). They provide essential ecosystem services (Gauthier et al., 2015), and contain the largest reservoir of terrestrial carbon stored in soil and peatlands (Pan et al., 2011). At global level and over recent century, the boreal forest industries support 33% of sawn wood, 26% of paper on the market, and generate over a million direct jobs (Burton et al., 2010).

Wildfire, climate, and their interactions are key drivers of boreal forests dynamics (Payette, 1992). According to global warming forecasts, high northern latitudes will be subject to the greatest temperature increases (IPCC, 2014), as well as more severe and longer droughts (Trenberth et al., 2014; Spinoni et al., 2020). As a consequence, fire frequency and severity are likely to increase in North American's boreal forests (Flannigan et al., 2013). Also, model outputs predict that current global warming will induce an increase in fire frequencies and area burned in Canada (Flannigan et al., 2005). Consequently, the Canadian boreal forests and associated goods and services could be vulnerable to climate change, especially if feedbacks of fire-climate interactions cause ecosystems to cross thresholds (Gauthier et al., 2015; Girona et al., 2023b). Indeed, light or severe fires, successive fires and the cumulative effect of a spruce budworm outbreak followed by a fire, can lead to a transition from a closed-crown spruce forest to a lichen woodland (Payette et al., 2000; Girard et al., 2009), thereby modifying tree density and cover. Lichen woodlands are open-crown forests with low tree density (Rowe, 1984; Payette, 1992), generally considered in Canada to be unmanaged low-productivity ecosystems with no commercial timber harvesting (Kurz et al., 2013).

The vegetation zonation in Québec is determined mainly by climatic factors (Saucier et al., 2009; Grondin et al., 2023). The south-north temperature cooling gradient distinguishes the vegetation zone, whereas the east-west decreasing precipitation gradient divides the vegetation zones into subzones (Fig.4.1; Saucier et al., 2009; Couillard et al., 2019). Changes in precipitation patterns and induced fire frequencies and cycles influence the longitudinal composition of vegetation, both in mixed boreal forests and in coniferous boreal forests (Gauthier et al., 2001; Remy et al., 2017a). In general, the fire regime varies with latitude (Portier et al., 2016), the type of forest stand (Blarquez et al., 2015), topography (Cyr et al., 2007), and continentality (Portier et al., 2016; Remy et al., 2017a, b). Carcaillet et al. (2001) suggested that climate was the key process triggering fire over the eastern boreal forest during the Holocene. Moreover, major vegetation changes over the eastern boreal forest during the Holocene were mostly controlled by regional climate trends (Carcaillet et al., 2010) and fire size (Remy et al., 2017b) rather than by fire frequency.

In the closed-crown spruce-moss bioclimatic domain, there are disparities between intra and inter-regional (hereafter subzone) fire regimes (Remy et al., 2017a, b; Hennebelle et al., 2018; Couillard et al., 2022). Knowing the historical intra- and inter-regional variability of fire regimes is therefore necessary in the definition of sustainable forest management strategies (Hennebelle, et al., 2018). The inter (between eastern and western subzones) and intra (within the western spruce-moss subzone) regional long-term histories of fire and vegetation are well documented by Remy et al. (2017a, b) and Hennebelle, et al. (2018) respectively.

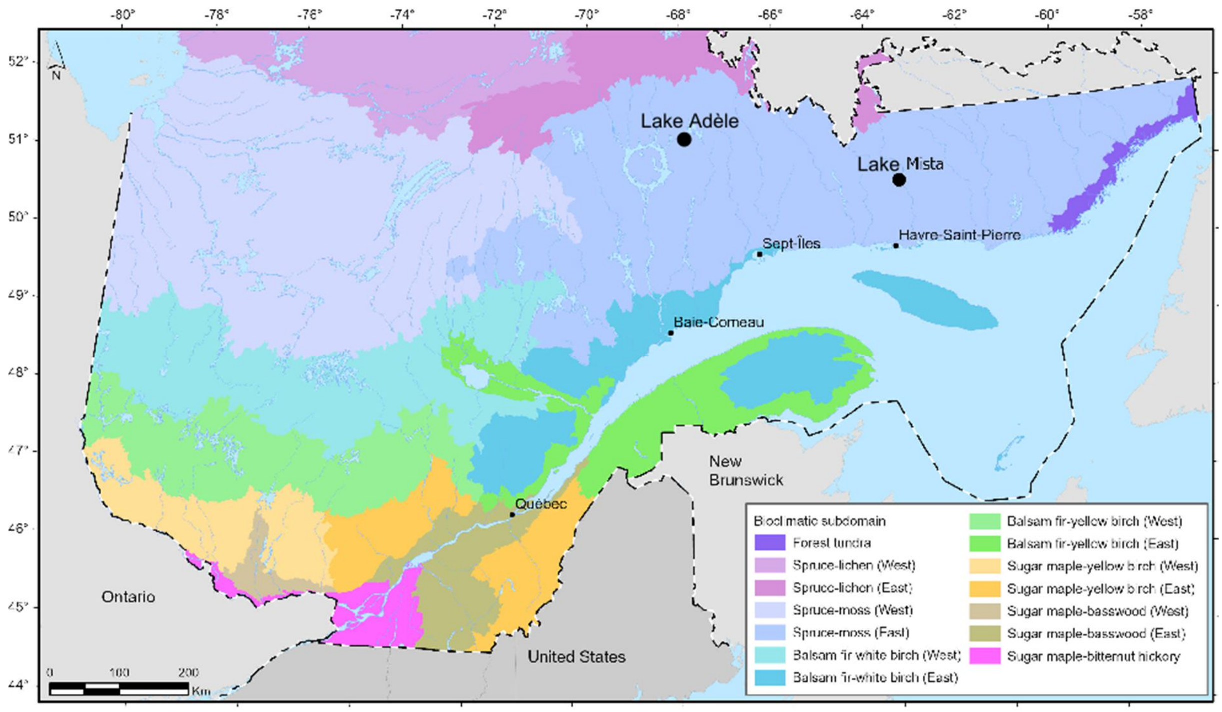

Figure 4.1 Location map of Lakes Adèle and Mista.

Over the last three millennia, as a result of climate change, the fire regime has led to the opening of the landscape, with the transformation of black spruce-moss forests into black spruce-lichen forests (Payette and Delwaide, 2018). However, it is still poorly understood when and how lichen patches developed in the eastern closed-crown spruce forest subzone (Bastianelli, 2018; Couillard et al., 2021; Fréchette et al., 2021).

Based on geochemical and charcoal analyses of lacustrine sediments, Bastianelli (2018) found that part of the eastern closed-crown spruce-moss forest shifted into lichen woodlands 4000-4500 years ago following recurrent fires at short intervals that disrupted the resilience capacity of the spruce-moss forest. This result needs to be supported by long-term vegetation history. Recent paleoecological evidence from maritime Québec (Couillard et al., 2021) suggests that a black spruce-lichen woodland stand developed 2000 years ago, mainly as a result of low-severity fires that prevented tree regeneration.

This study aimed to better understand the mechanisms triggering the development of open lichen woodlands within the closed-canopy black spruce–moss forests of eastern Québec, using fire return intervals (FRI; i.e., number of years between two consecutive fire events) and fire size/severity (FS; *sensu* Ali et al., 2012) from lakes Adèle and Mista (Fig.4.1). These two sites have a very similar multimillennial summer temperature trend, but are contrasting in modern vegetation: currently, lakes Adèle and Mista are surrounded by lichen woodland (Bastianelli 2018) and closed-crown forest (Feussom Tcheumeleu et al., 2023) respectively.

4.4 Materials and methods

4.4.1 Study area and sites

The study area is the eastern and maritime portion of the black spruce–moss bioclimatic domain in Quebec (Fig.4.1). We used two lacustrine records (Adèle and Mista; unofficial names) sampled within the eastern portion of the black spruce–moss bioclimatic domain to investigate long-term climate-fire-vegetation interactions. Lake Adèle is surrounded by lichen woodland ecosystems with *Picea mariana* as the dominant tree species (Bastianelli 2018) whereas lake Mista is surrounded by closed-crown black spruce forest with *Picea mariana, Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss as dominant tree species (Feussom Tcheumeleu et al., 2023). The climate at lake Adèle is colder and drier than at lake Mista. Indeed, the mean annual temperature is -2°C at lake Adèle and -1°C at lake Mista, and a total annual precipitation of 820 mm and 976.9 mm respectively (Régnière et al., 2017). For both lakes, the local topography is characterized by low-lying hills reaching a maximum altitude of 450 m at lake Adèle and 500 m at lake Mista. Fire is the main natural disturbance in the spruce-moss domain (Payette, 1992) with much longer fire cycle in its eastern portion (Gauthier et al., 2001).

Windthrow (Pham et al., 2004), spruce budworm (*Choristoneura fumiferana* Clemens; Morin et al., 2008) and hemlock looper (*Lambdina fiscellaria* Guenée) outbreaks (De Grandpré et al., 2008) are important secondary disturbances affecting mostly the eastern portion of the spruce–moss subdomain.

4.4.2 Sediment sampling and chronologies

Sediment cores were extracted from the deepest point of each lake using a Kajak-Brinkhurst gravity corer for the sediment-water interfaces, and a modified Livingstone-type square-rod corer for the subsequent long sediment cores. Chronologies were based on accelerated mass spectrometry (AMS) radiocarbon (^{14}C) and on gamma spectrometry ($^{210}Pb/^{137}Cs$) dating. The radiocarbon dates were calibrated to calendar ages using IntCal20 (Reimer et al. 2020). Age models for both lakes were previously published in Feussom Tcheumeleu et al., unpublished). The age-depth models from lakes Adèle and Mista suggest that their sediment cores cover the last 7100 and 8500 years respectively.

4.4.3 Records of past fire activity and fire history reconstructions

Fire history of lakes Adèle and Mista, were reconstructed from charcoal data available from Bastianelli (2018) and Feussom Tcheumeleu et al. (2023) respectively. The protocols for extracting charcoals are similar in the two studies. In brief, for each sedimentary sequence, contiguous subsamples of 1 cm^3 taken at 1 cm intervals were soaked in a bleach solution overnight. The subsamples were wet sieved through a 150 µm mesh then the macroscopic charcoal particles were counted (charcoal abundance) and measured (charcoal area) under a stereomicroscope coupled with WINSEEDLE 2016 software (Regent Instruments Canada Inc.). The macroscopic charcoal particles ($\geq$ 150 µm) were expected to come mainly from local fire events i.e. less than ten kilometers from the lakeshore (Oris, et al. 2014; Hennebelle et al. 2020).

Past burned biomass (hereafter BB; no unit) at each study site were estimated by transforming charcoal area measures into charcoal accumulation rates (CHAR; mm^2 cm^{-2} yr^{-1}) based on numerical age-depth models. These homogenized series were then pooled and smoothed (using the "paleofire" R package and a 500-year window; Blarquez et al., 2014) by (1) rescaling initial CHAR values using min-max transformation, (2) homogenizing the variance using Box-Cox transformation, and (3) rescaling the values to Z-scores (Power et al., 2008).

The dates of local fire events extracted from already published charcoal analysis results (Bastianelli 2018; Feussom Tcheumeleu et al., 2023) were used to calculate the past fire frequency (hereafter FF; fire. yr^{-1}) and fire return intervals ((hereafter FRI; yr) for each lake. The FF for each lake was calculated by pooling individual lake smoothed series using a kernel density estimation from the "paleofire" R package (Blarquez et al., 2014). For each lake, we used the ratio between BB and FF (fire size index; hereafter FS index; no unit; Ali et al., 2012) to characterize the temporal changes in fire size/severity at local scale. We added a constant equal to 1 to FS index in order to avoid having negative values (Ali et al., 2012). Following Ali et al. (2012), FS index values <1 are indicative of small fire size and/or low severity fire.

4.4.4 Vegetation history reconstructions

At lake Mista pollen data and vegetation history were already published in a previous paper (Feussom Tcheumeleu et al., 2023). At lake Adèle, the reconstruction of past changes in vegetation relied on the pollen analysis of 75 subsamples that were taken at 1-5 cm intervals along the post-glacial sediment record. Pollen grains were extracted from the sediment using standard methods (Fægri and Iversen, 1989). A known volume of an exotic marker (calibrated *Eucalyptus* pollen suspension) was added to each subsample before preparation in order to calculate pollen concentration (grains cm^{-3}; Benninghoff 1962) and pollen accumulation rate (PAR; grains cm^{-2} $year^{-1}$). A minimum of 300 pollen grains of terrestrial taxa was counted per subsample under a light microscope at 400x magnification. Pollen grains were identified to family, genus and species levels following Richard (1970), McAndrews et al. (1973) and the reference collection of the University of Montréal paleoecology lab.

Pollen signal is expressed as pollen influx to enable the estimation of the magnitude of pollen population changes within and among pollen taxa (Hicks, 1994). Indeed, pollen percentage diagrams can mask or distort the magnitude of many of the changes (Davis and Deevey Jr, 1964). Therefore, pollen influx records obtained from accurately dated lake sediment cores represent a potential proxy of changes in pollen population (Seppä et al., 2009). Higher pollen influx often reflects denser populations (Seppä et al., 2009).

The pollen diagrams were plotted using the strat.plot function in the rioja R package (Juggins 2014). Zonation of the pollen assemblages were defined using CONISS method (Grimm 1987). We determined the number of statistically significant assemblage zones by applying the broken-stick model (Bennett 1996).

4.4.5 Climate data

We used chironomid-based reconstructions of mean August air temperatures from lakes Adèle and Mista (Feussom Tcheumeleu et al., unpublished). Mean August air temperatures were inferred using a chironomid-based temperature inference model (WA-PLS, 2 components; R^2_{boot}=0.73; $RMSE_{boot}$=1.84°C) based on a modern calibration dataset of 130 lakes and 130 taxa from eastern Canada and Newfoundland (Suranyi et al., in press) with August air temperature ranging from 7.1 to 21.8°C i.e. a gradient of 14.7°C. The inferred August air temperatures were smoothed over a 1000-yr moving-window for comparison with fire histories and long-term vegetational changes.

4.5 Results

4.5.1 Climate variability and fire histories

Two sites, same summer temperature history …

The chironomid-based mean August air temperature reconstructions from lake Mista suggest a cold climate from ca. 8700 to 7000 cal yr BP (Fig.4.2a; Feussom Tcheumeleu et al., unpublished). From 7000 cal yr BP to present, the mean temperatures from lakes Adèle and Mista show a very similar trend. In brief, the summer temperature history is characterized by a warm phase between 7000 and 4000 cal yr BP (Fig.4.2a) followed, after 4000 cal. yr BP, by cooler summer temperatures (Fig.4.2a; Feussom Tcheumeleu et al., unpublished). Another common feature in the temperature records is the higher temperature variability suggested over the last 3000 years. Furthermore, chironomid-based summer temperature reconstructions suggest possibly two slightly warmer phases between 2500 and 1800 cal yr BP, and between 1300 and 800 cal yr BP (Fig.4.2a; Feussom Tcheumeleu et al., unpublished).

… but different fire regime history

At lake Mista, the FRI was most often around a mean value of 135 years (range 46-322 yrs) until ca. 5500 cal yr BP, then subsequently increased to a mean value of 269 years (range 69-575 yrs) between 5500 and 3500 cal yr BP (Fig.4.2b). From 3500 cal yr BP, the FRI dropped to a mean value of 169 years (range 69-460 yrs) before increasing during the last millennia (mean value 327 yrs; range 115-506 yrs). Fire size was smaller (FS index <1) before 5500 cal yr BP (Fig.4.2c). From 5500 cal yr BP, fires became larger (FS index > 1) until ca.2500 cal yr BP, before decreasing, but FS index values remained high. Between 1500 and 300 cal yr BP, fire size rose to reach maximum values as for the previous period between 5500 and 2500 cal yr BP. Starting from 300 cal yr BP to present, FS index was close to one.

Fire activity highly varied throughout the past 7000 years at lake Adèle (Fig.4.2b, c). Charcoal analysis indicated that between 7100 and 4500 cal yr BP, the FRI fluctuated around a mean value of 128 years (range 45-261 yrs), then decreased to a mean value of 87 years (range 18-

324 yrs) before rising again to a mean value of 199 years (range 90-306 yrs) after 1500 cal yr BP (Fig.4.2b). Small fires (FS index <1) were recorded before 6500 cal yr BP, and later between 4500-2500 cal yr BP. Large fires (FS index >1) were recorded between 6500 and 4500 cal yr BP, then also from 2500 cal yr BP to present (Fig.4.2c).

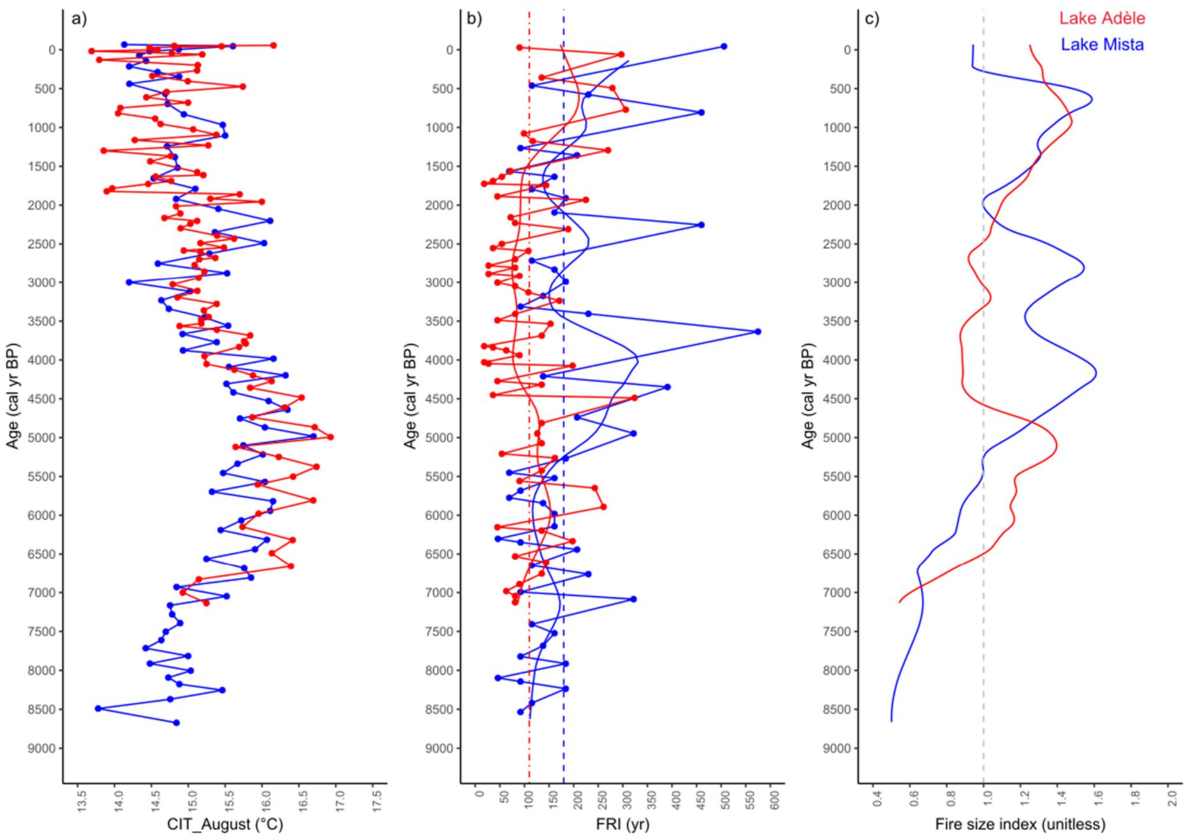

Figure 4.2 (a) chironomid inferred August temperature (CIT-August), reconstructed fire histories (b) fire return interval (smoothed over a 1000-year moving window (in solid lines); the dashed vertical lines indicate the mean values throughout the entire sequence from each site) **(**c) fire size (with threshold value of 1 in dashed vertical grey line; according to Ali et al. (2012), small size or low-severity fire when FS<1; large size or high-severity fire when FS>1).

During the past 7000 years, 63 fire events were detected at lake Adèle against 38 at lake Mista. Despite similar trends in reconstructed summer temperature records (Fig.4.2a), inter-site comparisons of charcoal analysis results from ca. 7000 cal yr BP to present, indicate a spatial variability in FRI and fires size index records inferred from lakes Adele and Mista (Fig.4.2b, c).

4.5.2 Vegetation history of lake Adèle

Three stages of postglacial vegetation development can be identified from changes in pollen assemblage composition and accumulation rates (Fig.4.3; supplemental materials S4.1a, b):

7100-6400BP: Forest tundra

At lake Adèle, *Alnus crispa*, *Betula*, *Picea mariana* and *Abies* gradually colonized ice-free areas (afforestation phase). Pollen assemblages highly dominated by *Alnus crispa* and *Betula* (likely *Betula papyrifera*, Fréchette et al., 2021) suggest the presence of a very open landscape, with forest-tundra like vegetation. *Abies* (likely *Abies balsamea*, Fréchette et al., 2021) settled around 6500 BP. *Picea mariana* is rare.

6400-3000 BP: Spruce-moss forest

The second stage of the postglacial vegetation development marks the beginning of the forest phase. *Abies* (likely *Abies balsamea*, Fréchette et al., 2021) is still present but rare. *Betula* (likely *Betula papyrifera*, Fréchette et al., 2021) population remained stable during this period, while *Picea mariana* continued its expansion as local vegetation became progressively dense, reaching maximum populations between 5000 and 3000 BP. *Pinus banksiana* gradually increased, reaching its highest values later.

This stage is overlain by a *Picea mariana* pollen zone, which can be subdivided into a *Picea mariana-Abies balsamea-Betula* forest subzone from 6400 to 5300 cal yr BP, and a closed-crown *Picea mariana* forest between 5300 and 3000 cal yr BP (Fig.4.3).

3000 BP to present: Spruce lichen woodlands

The third stage of the postglacial vegetation development is marked by a drastic drop of pollen accumulation rate, including the population regression of all taxa except *Pinus banksiana*. At the starting of this period, *Pinus banksiana* recorded its highest values, concomitant with a generalized opening of the closed-crown spruce-moss forest that seems to favor the representation of this taxon. There is no indication here of significant changes in the percentages of *Picea mariana* and *Betula* pollen within this zone (supplemental Material S4.1a).

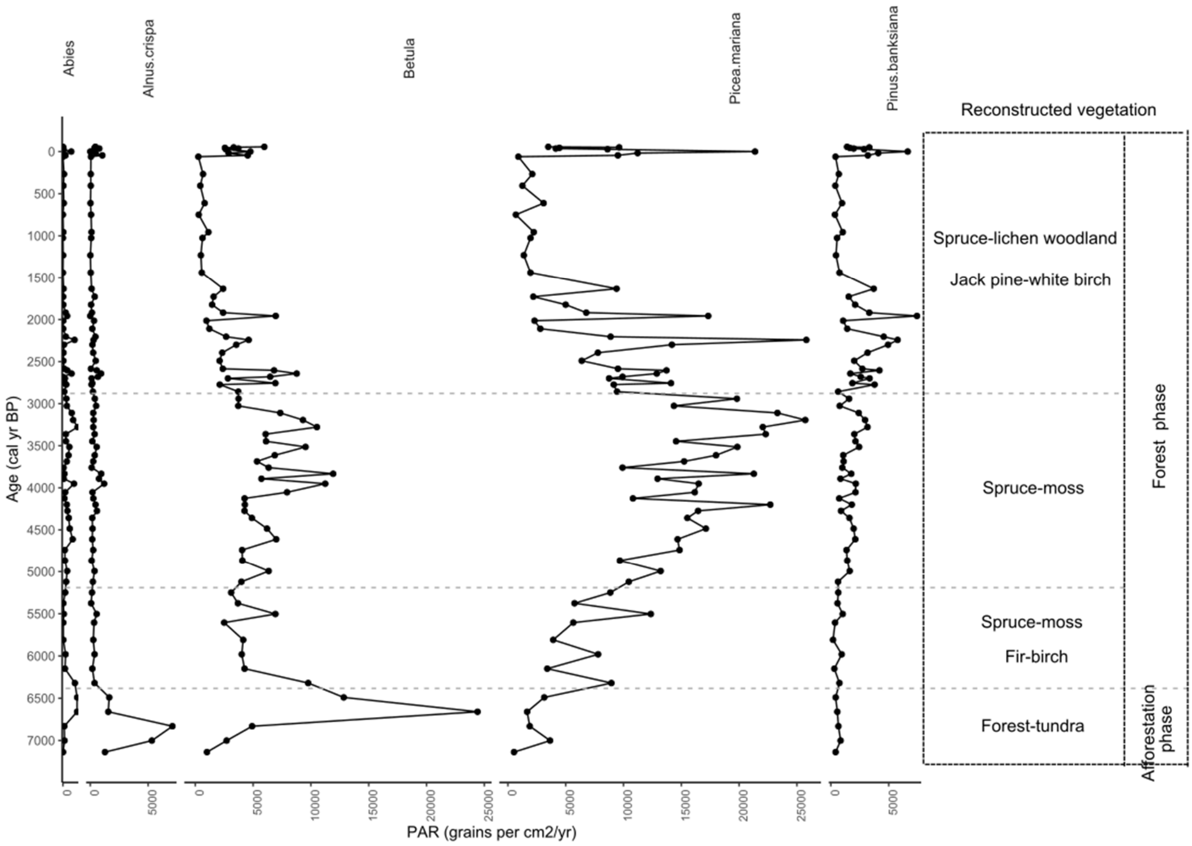

Figure 4.3 Simplified pollen influx diagram of lake Adèle, with vegetation zone in horizontal dashed grey lines.

This stage is overlain by a *Picea mariana* pollen zone, which can be subdivided into a *Picea mariana-Abies balsamea-Betula* forest subzone from 6400 to 5300 cal yr BP, and a closed-crown *Picea mariana* forest between 5300 and 3000 cal yr BP (Fig.4.3).

4.5.3 Inter-site spatial variability of vegetation

The vegetation histories of lakes Adèle and Mista can be compared from ca. 7100 cal yr BP to present.

The age of afforestation onset is asynchronous between lakes Adèle and Mista (Fig.4.3, Fig.4.4), probably due to a later time of deglaciation at lake Adèle (Feussom Tcheumeleu et al., unpublished). As the time span coved by individual lacustrine pollen records from lake Adèle and Mista is unequal, it seems hazardous to compare the duration of the afforestation phase at both sites. However, the time of transition from afforestation to forest phase appears to be close, i.e. around 6700 cal yr BP at lake Mista (Fig.4.4) and 6500 cal yr BP at lake Adele (Fig.4.3). Forest tundra and balsam fir-birch forest marked the end of afforestation at lake Adèle and lake Mista respectively (Fig.4.3, Fig.4.4).

During the forest phase, vegetation succession follows the same pathway at both sites until ca. 3000 cal yr BP (Fig.4.3, Fig.4.4; supplemental materials S4.1a, b; S4.2a, b). At both sites, the forest phase began with spruce-moss balsam fir-birch forest. As the *Picea mariana* population increase gradually, the spruce-moss balsam fir-birch forest shifted into closed-crown spruce-moss forest around 5300 cal yr BP at lake Adèle, then later around 4800 cal yr BP at lake Mista (Fig.4.3, Fig.4.4). Although the uncertainty of our age-depth models, both sites show a decreasing trend in pollen influx over the last 3000 years beginning at various times (Fig.4.3, Fig.4.4). At lake Adèle, the transition from closed-crown spruce-moss forest to spruce-lichen woodland occurred around 3000 cal yr BP, with *Pinus banksiana* as companion tree species to dominant *Picea mariana* till present (Fig.4.3; supplemental materials S4.1a, b). This transition was further indicated by a sharp regression in both total pollen influx and individual taxa pollen influx around 3000 cal yr BP (supplemental material S4.1b). At lake Mista, the decrease in total influx around 2000 cal yr BP, suggests an opening of the spruce-moss forest (supplemental material S4.2b). In contrast, the open spruce-moss forest observed at lake Mista, seems to have progressively shift back into closed-crown spruce-moss forest during the past 300 years (Fig.4.4; Feussom Tcheumeleu et al., 2023).

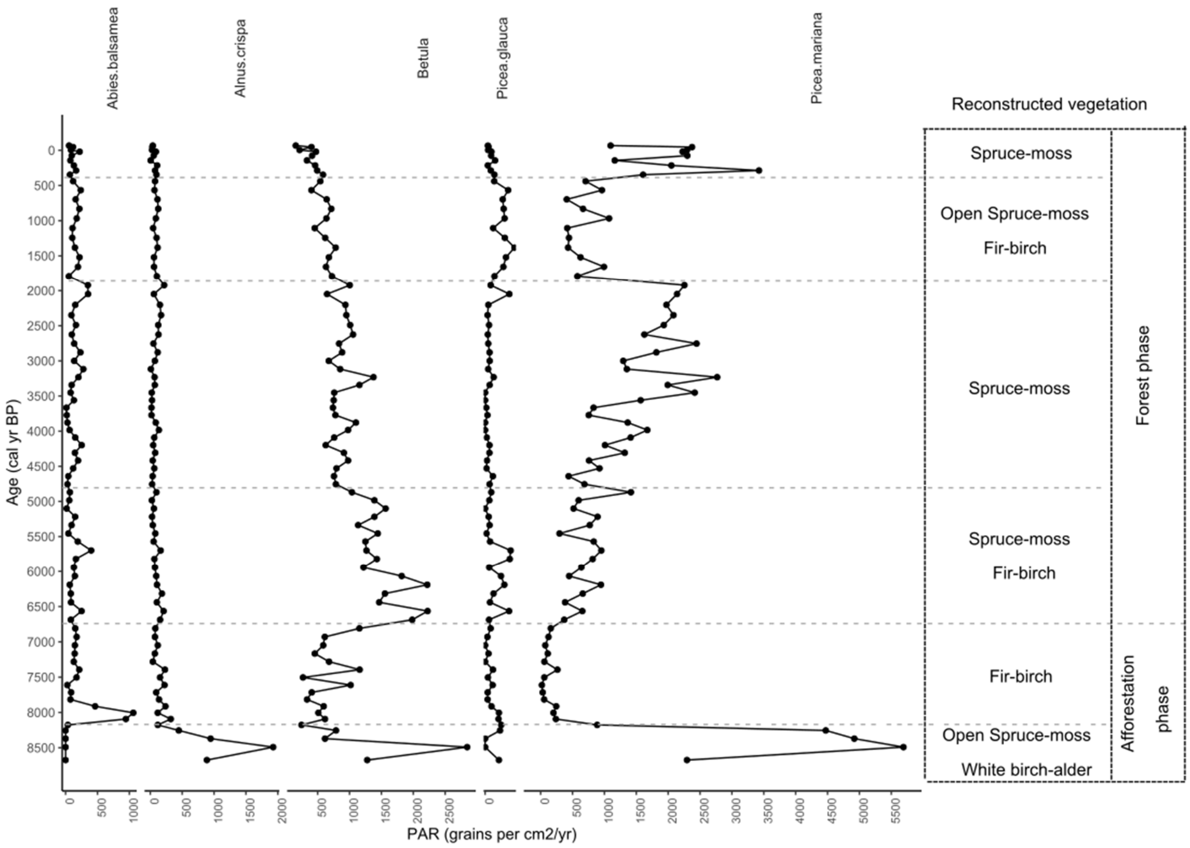

Figure 4.4 Simplified pollen influx diagram of lake Mista, with vegetation zone in horizontal dashed grey lines.

4.6 Discussion

4.6.1 Inter-site spatial variability in fire activity

Fire occurrence and size varied between the two sites studied. Summer temperatures do not appear to have directly triggered fires on lakes Adèle and Mista over the past 7000 years. Interestingly, FS index contrasted around 5000 cal yr BP, then becomes higher at lake Mista until 2500 cal yr BP. However, both sites have experienced infrequent but large fires in the last two millennia (Fig.4.2b, c), due probably to the warmer summers (Fig.4.2a; Feussom Tcheumeleu et al., unpublished) and the very dry climatic conditions that prevailed across the eastern and maritime Québec (between 2600 and 950 cal yr BP; Magnan and Garneau, 2014). These findings are plausible with the results of Remy et al. (2017a, b) indicating that largest fires were also recorded around 2500-2000 cal yr BP in the western and central regions of Québec, and around 1500-1000 cal yr BP in the eastern region.

At lake Mista, compared to the HTM period, the cooler Neoglacial climatic conditions seem less conducive to fires events (Fig.4.2a, b). Counterintuitively, at lake Adèle, fires occurred more frequently during the first half of Neoglacial, more precisely between ca. 4000 and 1500 cal yr BP (Fig.4.2a, b).

Although lakes Adele and Mista displayed similar summer temperature trends (Fig.4.2a), the fire histories reconstructed from lacustrine charcoal revealed major inter-site differences (Fig.4.2b, c). This finding highlights the possible influence of local factors, such as fuel loading and flammability, local weather, landscape connectivity (Cyr et al., 2007; Ali et al., 2009; Blarquez et al., 2015; Remy et al., 2017a, b; Hennebelle et al., 2018; Portier et al., 2019) on fire occurrence, and may explain the high spatial heterogeneity in the eastern Canada *Picea mariana* boreal forest fire histories. Furthermore, other climatic variables than summer temperature (e.g., warm springs, intra-seasonal variability in precipitation, fire season length and drought code; Remy et al., 2017a; Portier et al., 2019) could have a direct control on fire occurrence in eastern Québec. The modern meteorological conditions are drier at lake Adèle compared to lake Mista (Regnière et al., 2017). Indeed, in Québec, there is an east-west and south-north decreasing precipitation gradient (Saucier et al., 2009; Couillard et al., 2019) that could potentially explain the spatial heterogeneity in fire histories (Cyr et al., 2007; Portier et al., 2019). The wetter conditions in lake Mista, due to its maritime position, probably reduce fire ignition, spread and frequency compared to lake Adèle. However, paleohydrological data are needed to provide a better understanding of long-term differences in fire history at sites with similar summer temperature trends (Remy et al., 2017b). Unfortunately, to our knowledge, no paleohydrological data covering the past 7000 years do exist for the lake Adèle area.

Fire size increased on both sites during the transition from the afforestation phase to the forest phase (Fig.4.5, Fig.4.6). At lake Mista, fire size continued to increase with the expansion of flammable *Picea mariana* populations that might have overridden the effects of cooler climatic conditions that prevailed during the Neoglacial, then led to larger fires (Fig.4.6). Trend in FS index at lake Adèle contrasts with lake Mista from 5000 to 2500 cal yr BP (Fig.4.2c). Notwithstanding the maximum population of more flammable *Picea mariana* (Fig. 4.5), fires were moderate in size. The slight increase in *Betula* population (likely *Betula papyrifera*; Fréchette et al., 2021) which is less flammable (Sims et al., 1990), probably limited fire spread and burn (Blarquez et al., 2015). Differences in soil moisture could have a more local control on the size and occurrence of fires in eastern Canada (Portier et al., 2019). Indeed, fire occurrence would increase with decreasing moisture content of the upper layers of the forest floor, whereas fire size would increase with the dryness of the deeper layers (Portier et al., 2019).

4.6.2 Vegetation trajectories

Despite their dissimilar fire histories, the vegetation of lakes Mista and Adèle appears to have followed a similar successional trajectory between ca. 6500 and 3000 cal. BP, suggesting that during this period, major vegetation changes in both sites were primarily determined by regional climatic conditions.

Between 3000 and 1500 cal yr BP, the FRI at lake Adèle remained as short as between 4500 to 3000 cal yr BP. In contrast, *Picea mariana* population began to decrease around 3000 cal yr BP, perhaps as a result of regeneration failures that probably followed most fire burns (Payette and Delwaide, 2003). In fact, regeneration failure could occur when too-short intervals between wildfires (Fig.4.5) don't allow *Picea mariana* to reach sexual maturity (i.e. 50 years; Viglas et al., 2013), and/or where seeds, seedbeds and seedlings are of low-quality or insufficient, thus preventing vegetation recovery and re-establishment of the pre-fires tree density (Payette et al., 2000; Johnstone and Chapin, 2006a; Day et al., 2023). On the other hand, the population of fire-adapted *Pinus banksiana* increased slightly, maybe favored by highly frequent and large or high-severity fires (Fig.4.5). A similar scenario is also suggested for nearby lake Steeve (Remy et al., 2017b) which was affected as well by the largest fires around 2000 cal yr BP. The pollen data of King (1986), suggests that *Pinus banksiana* probably reached the northernmost lake Gras around 2200 cal yr BP. Indeed, frequent and large or high-severity forest fires are favoring the self-perpetuation of *Pinus banksiana* (Sims et al., 1990). In addition, the warmer (Fig.4.2a; Feussom Tcheumeleu et al., unpublished) and drier (Magnan and Garneau, 2014) climate combined with sandy superficial deposits (Remy et al., 2017b) are propitious environment for the establishment of *Pinus banksiana* (Sims et al., 1990; Boiffin and Munson 2013). Under harsh post-fire conditions (warm and dry weather), Boiffin and Munson (2013) observed critically low *Picea mariana* regeneration compared to high levels of *Pinus banksiana* seedling establishment in the closed-crown spruce forest of eastern Canada. Indeed, *Pinus banksiana* is an alternate conifer tree species better adapted to short intervals between fire than *Picea mariana* in eastern Québec (Baltzer et al., 2021).

Throughout the last 1500 years, *Picea mariana* population remains low despite the lengthening of the FRI. Other causal factors (e.g., spruce budworm outbreak reduces seed production; Payette and Delwaide, 2003; Simard and Payette, 2005; Girard et al., 2009) including high severity fires (Johnstone and Chapin, 2006b; Reid et al., 2023) recorded during this period, seem to have contributed in maintaining low the population of *Picea mariana*. In fact, the quantity of postfire seeds varies with the size of the pre-fire population (Greene and Johnson, 1999), while the postfire recruitment rate of *Picea mariana* depends on the availability of a good mineral seedbed (Johnstone et al., 2004; Reid et al., 2023). Postfire recruitment is therefore a critical determinant of forest regeneration (Johnstone et al., 2004).

It is likely that the opening of the spruce-moss forest took place around 3000 cal yr BP. But, the resilience threshold of *Picea mariana* was probably exceeded around 1500 cal yr BP, leading to the transformation of black spruce-moss into spruce-lichen woodland. Recurrent fires at short intervals appear to be the main triggering mechanism.

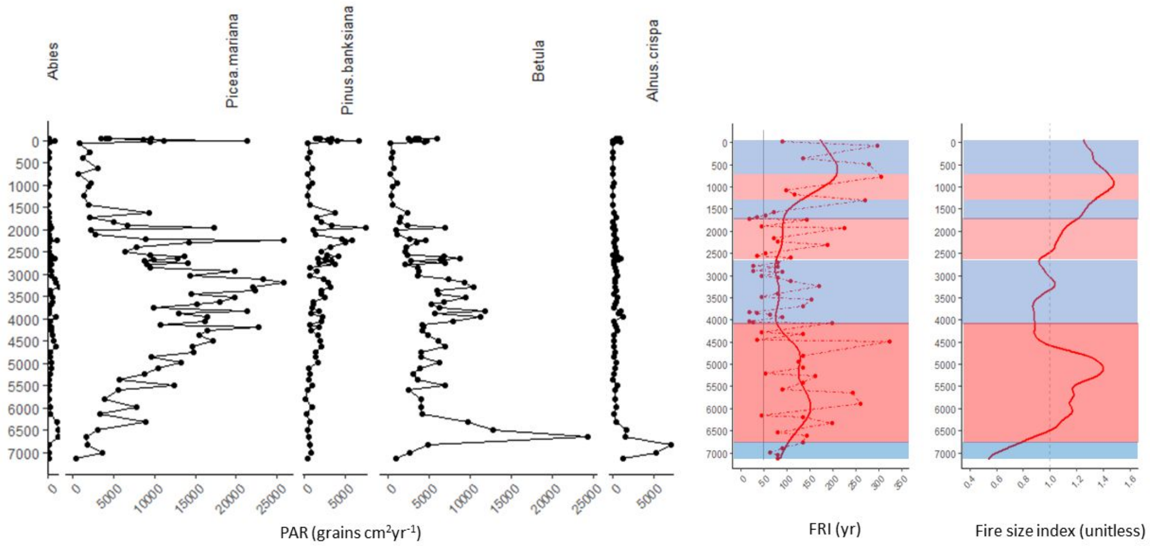

Figure 4.5 Lake Adèle: simplified pollen influx diagram; fire return interval (smoothed over a 1000-year moving window (in solid lines); the solid vertical grey line corresponds to 50 years); fire size (with threshold value of 1 in dashed vertical grey line; according to Ali et al. (2012), small size or low-severity fire when FS<1; large size or high-severity fire when FS>1). Background colors differentiate warm (red) and cool (blue) periods.

Compared with the results of sediment geochemistry analysis (Bastianelli, 2018), the spruce-moss forest did open up at lake Adèle between 4500 and 4000 cal yr BP (Fig.4.5), but only slightly. Despite this opening of the forest, the size of the *Picea mariana* population remained at least equal to that prior to 4500 cal yr BP. The longer recovery time (increased FRI) then allowed the forest to re-densify (Fig.4.5) between 4000 and 3000 cal yr BP. So, the date of transition to lichen forest suggested by Bastianelli (2018) is not concomitant with the vegetation history of lake Adèle. Indeed, the opening of the spruce-moss forest appears to have begun around 3000 cal yr BP and was pronounced from 1500 cal yr BP as earlier discussed. In southwestern Labrador (Fréchette et al., 2021), the lichen woodland seemingly developed around 2600 cal yr BP.

At lake Mista, the *Picea mariana* population continued to expand until around 2000 cal yr BP, when it began to decline. According to Feussom Tcheumeleu et al. (2023), shorter FRIs between 2000 and 1500 cal yr BP (Fig.4.6) coupled with very dry climatic conditions (between 2600 and 950 cal yr BP; Magnan and Garneau, 2014) probably limited tree cover (Hogg and

Wein, 2005), leading to gradual opening of the vegetation cover as suggested by the total influx decrease till ca. 1000 cal yr BP when it started rising again with wetter conditions (between 950 and 0 cal yr BP; Magnan and Garneau, 2014).

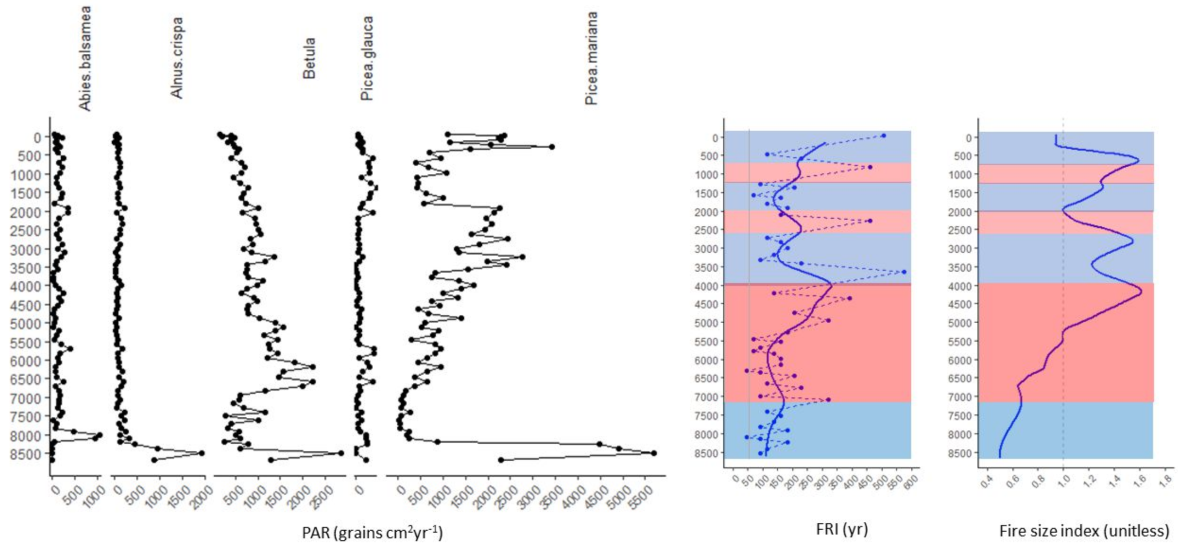

Figure 4.6 Lake Mista: simplified pollen influx diagram; fire return interval (smoothed over a 1000-year moving window (in solid lines); the solid vertical grey line corresponds to 50 years); fire size (with threshold value of 1 in dashed vertical grey line; according to Ali et al. (2012), small size or low-severity fire when FS<1; large size or high-severity fire when FS>1). Background colors differentiate warm (red) and cool (blue) periods.

4.6.3 Resilience of the black spruce-moss forest of Québec

From 6700 cal yr BP till present, black spruce maintains its dominance in the landscape throughout. The progressive expansion of *Picea mariana* populations, independently of changes in FRI until 3000 cal yr BP (lake Adèle) and 2000 ca yr BP (lake Mista), may reflect successful post-fire regeneration at both sites (Asselin and Payette, 2005). According to Johnstone and Chapin (2006a), the self-replacement of *Picea mariana* is generally successful when fire return intervals are between 50 and 150 years.

Lake Mista

Closed-crown spruce-moss forest similar to that observed today seems to have established around 4800 cal yr BP. Although fire size influenced vegetation trajectory at lake Mista as suggested at a regional scale by Remy et al (2017b), frequent fires probably contributed to forest openings. *Picea mariana* seems resilient as the opened spruce-moss forest shift back to closed spruce-moss forest during the last 300 years with decreased fire frequency and size (Fig.4.6). Nevertheless, the spruce-moss forest remains in a precarious state of equilibrium as fire frequency and size could increase in the context of climate change and trigger the shifting process.

Lake Adèle

Compared to lake Mista, the forest opening occurred earlier at lake Adèle, around 3000 cal yr BP. This corresponds to the period when most landscape opened across northern Québec. The landscape opening in northern Québec began around 3000 cal yr BP and was more pronounced between 2000 and 900 cal yr BP (Asselin and Payette, 2005; Payette and Delwaide, 2018; Kouadio, 2021). Near Havre-Saint-Pierre (Fig.4.1), Couillard et al (2021) described, on the basis of botanically identified and ^{14}C dated soil charcoal remains, a black spruce forest stand that shifted to lichen woodland around 2000 cal yr BP following low-severity fires. At the landscape scale, the black spruce forests opening was not observed everywhere across the eastern spruce-moss subdomain of Québec as supported by dynamics of the other types of forest stand of this region (Bastianelli, 2018; Couillard et al., 2021).

At lake Adèle, the spruce-moss forest generally showed resilience in the face of fire over several millennia. But, during the past 3000 years, the shortening of fire return intervals, coupled with very dry climatic conditions, probably compromised *Picea mariana* regeneration, gradually degrading the resilience of black spruce-moss forests to fire (Whitman et al., 2019). Considering the regeneration potential of *Picea mariana* and the resilience capacity of the spruce-moss forest (Baltzer et al., 2021), the natural reversion of spruce-lichen woodland to spruce-moss forest very rarely occurs in the absence of fire (Jasinski and Payette, 2005; Payette and Delwaide, 2018), or for instance, if fires of unusually high severity could remove the lichen mat on seedbeds (Mallik and Kayes, 2018), and if suitable conditions for the expansion of the closed-crown forest are restored (Girard et al., 2008). Indeed, in lichen woodlands, the lichen matted seedbeds inhibit the regeneration of *Picea mariana* seedlings (Mallik and Kayes, 2018), contributing therefore to the self-perpetuation of lichen woodland. To our knowledge, no evidence of a natural conversion of lichen woodland to closed-crown forest is known (Payette et al., 2000; Girard et al., 2008; Côté et al., 2013; Mansuy et al., 2013). Only human-induced conversion case studies have been reported (Gonzalez et al., 2013; Hébert et al., 2014; Marty et al., 2023).

At lakes Mista and Adèle, while climatic conditions and fire size play an important role in determining long-term vegetation trajectories, recurrent fires at short intervals appear to be the main causal factor of the shifting process. Indeed, black spruce-moss forests seem resilient to changes in fire regimes until the resilience threshold of black spruce is likely exceeded.

4.7 Conclusion

We investigated the impact of fire return intervals (FRI; i.e., number of years between two consecutive fire events) and fire size/severity (FS; *sensu* Ali et al., 2012) on multimillennial vegetation trajectories in two sites with very similar multimillennial summer temperature trend but contrasting modern vegetation. Our results suggest that changes in fire size and frequency control the long-term dynamics of black spruce-moss forests in eastern Québec. However, summer temperatures do not seem to directly control the fire regimes as the two studied sites with similar trend in summer temperatures displayed dissimilar trends in fire histories. Between 7000 and 3000 cal yr BP, both sites displayed similar vegetation trajectories whereas from 3000 cal yr BP to present, they exhibit different trajectories. At lake Adèle, the spruce-moss forest opened around 3000 cal yr BP. But, the resilience threshold of *Picea mariana* was likely exceeded around 1500 cal yr BP, leading to the transformation of black spruce-moss into spruce-lichen woodland. At lake Mista, the spruce-moss forest opened around 2000 cal yr BP, but shifted back to closed-crown forest during the last 300 years. Empirically, this return to closed forest has not been observed (Jasinski and Payette, 2005), but seems possible and requires further study. Although the closed-crown forest appears resilient, it still remains in a precarious state of equilibrium as fire frequency could increase in the context of climate change and trigger the shifting of closed canopy forest to lichen woodland.

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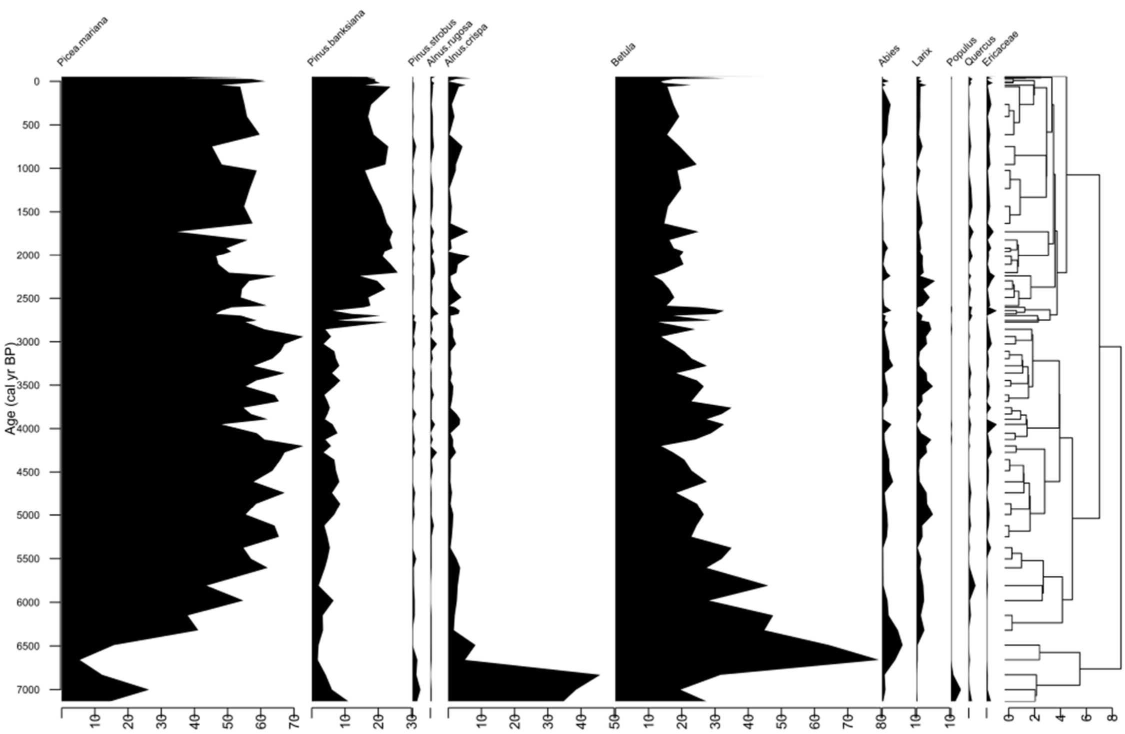
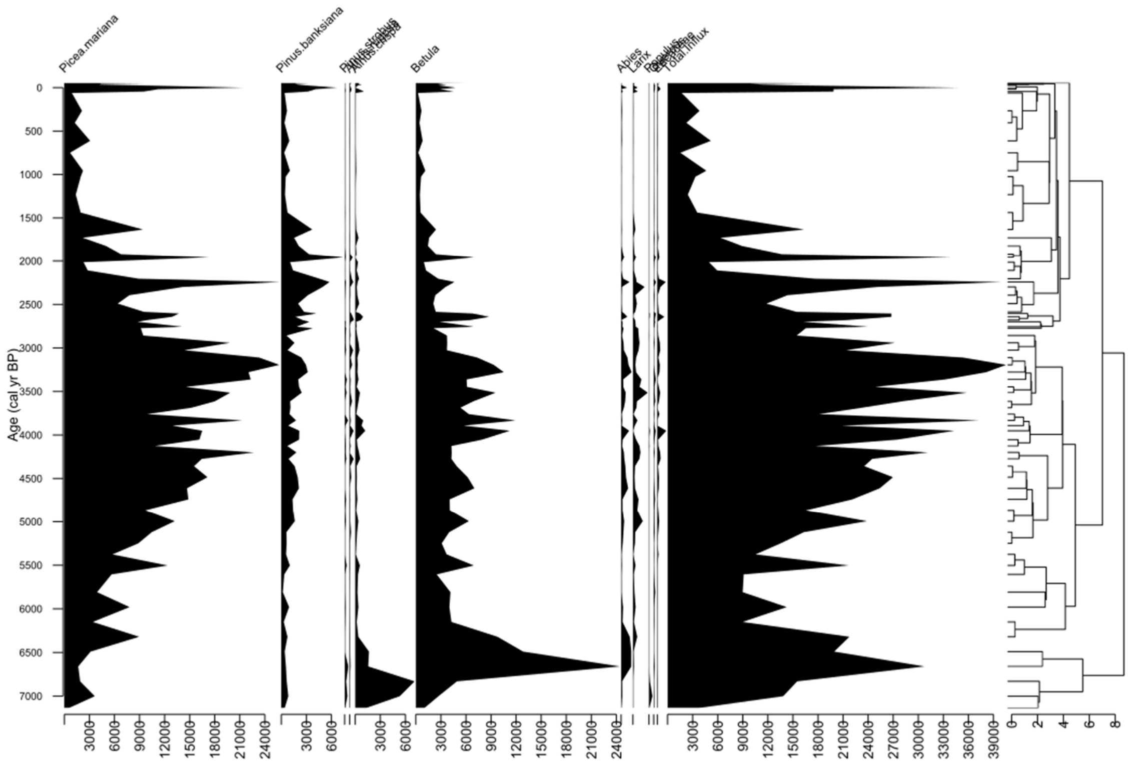
4.10 Supplemental Materials

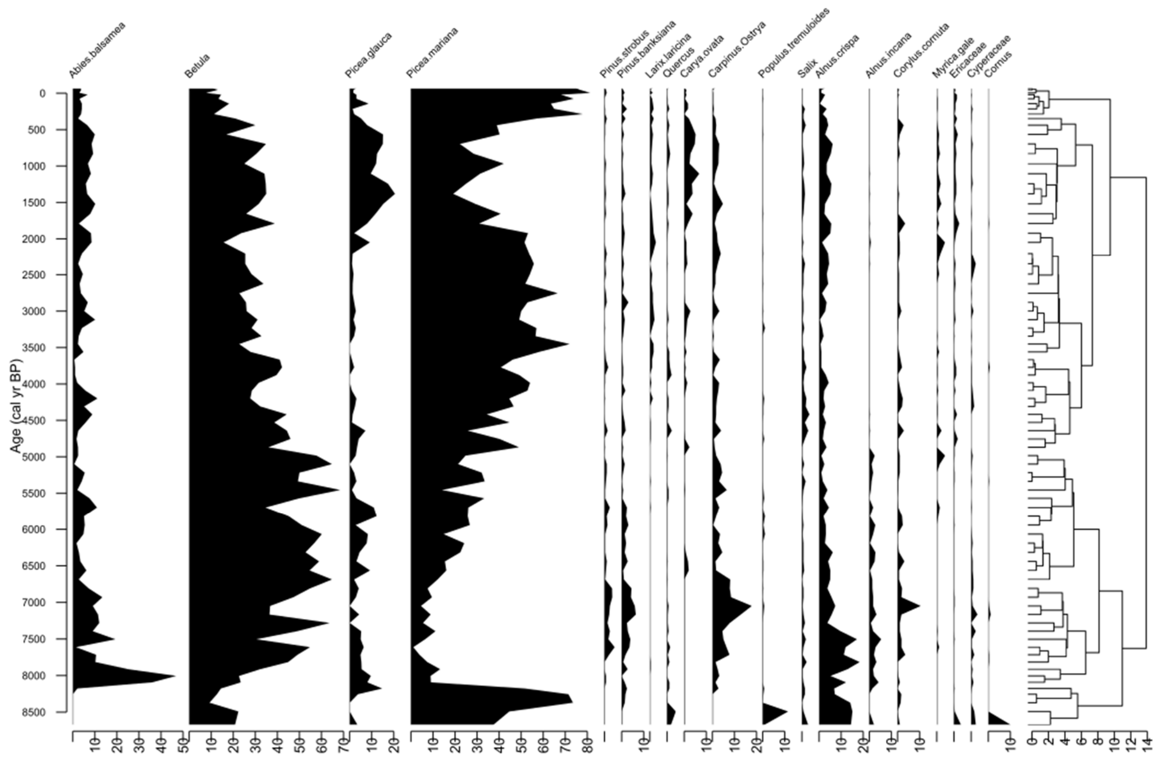
Supplemental Material S4.1a: Detailed pollen percentage diagram of lake Adèle



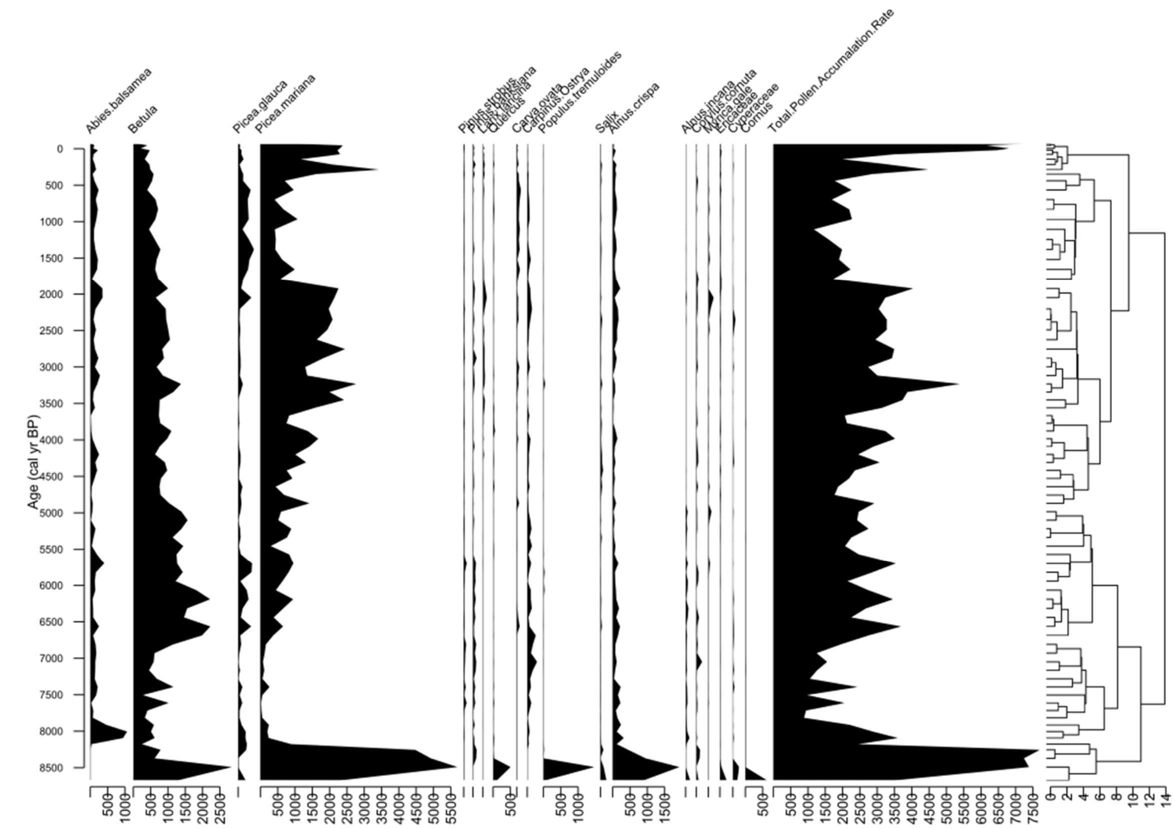
Supplemental Material S4.1b: Detailed pollen influx diagram of Lake Adèle



Supplemental Material S4.2a Detailed pollen percentage diagram of Lake Mista



Supplemental Material S4.2b: Detailed pollen influx diagram of Lake Mista



Chapitre 5

Synthèse et perspectives

L'objectif général de cette thèse était de compléter les reconstitutions postglaciaires du climat, des régimes de feux, et de la végétation à l'est du Canada, à partir de trois bioindicateurs archivés dans des sédiments lacustres, notamment les chironomes (paléotempératures), charbons de bois (feux) et pollen (végétation) pour in fine améliorer les connaissances et la compréhension des interactions climat-feu-végétation dans la forêt boréale du Québec.

Nous avons acquis des données originales et de qualités (chapitres 2, 3 et 4). Des interprétations spécifiques à chaque proxy ont été proposées, en particulier pour reconstituer le climat à partir des assemblages de Chironomidae (chapitres 2 et 3), la dynamique temporelle de la végétation à partir du pollen (chapitres 2 et 4) et les changements des régimes de feux à partir des charbons de bois (chapitres 2 et 4). L'analyse conjointe et croisée de cet ensemble de données et de reconstitutions a ainsi constitué une base solide pour explorer les interactions feux-végétation-climat au cours de la période postglaciaire.

5.1 Principaux résultats et contributions de cette thèse

5.1.1 Des données nouvelles sur l'histoire de la végétation, des feux et des températures au Québec maritime

L'analyse multiproxies de la séquence sédimentaire de Mista fournit les premières reconstitutions paléoécologiques de la relation entre la dynamique de la végétation et les changements temporels du climat et de l'activité des incendies au Québec maritime. Ainsi, les reconstitutions de paléotempératures, à partir des assemblages de chironomes, suggèrent que le climat régional était plus chaud entre 7000 et 4000 ans AA (période dite de maximum thermique de l'Holocène), puis s'est progressivement refroidi au cours des 4000 dernières années (période dite de néoglaciaire). Les conditions climatiques du maximum thermique de l'Holocène semblaient propices aux incendies. Les incendies et le climat ont tous deux influencé la succession végétale. Cependant, la composition de la végétation (forte abondance de *Betula* spp peu inflammable) ainsi que des conditions climatiques humides semblent avoir atténué les impacts du réchauffement (associé au maximum thermique de l'Holocène) sur la taille/sévérité des incendies, après quoi le changement de végétation (forte abondance de *Picea mariana* plus inflammable) a favorisé les grands incendies pendant le Néoglaciaire. Le changement climatique et les grands incendies ont favorisé l'expansion des pessières à mousses au détriment des sapinières à bouleaux.

A ce jour, aucune étude paléoécologique, alliant l'histoire postglaciaire du climat, des incendies et de la végétation, à partir des données empiriques issues d'un même site, n'avait été menée dans cette partie de la Côte-Nord. Les études paléoécologiques menées sur la Côte-Nord, fournissent des connaissances fragmentaires, de la végétation et du climat (Fréchette et al., 2021), puis des incendies (Payette et al., 2013 ; Portier et al., 2016) de la région. Par ailleurs, les études traditionnelles climat-feu-végétation utilisent l'approche pollen (Méthode des Analogues Modernes ; p.ex., Gajewski et al., 2021) ou l'approche modélisation à basse résolution (p.ex., Remy et al., 2017a, b) pour reconstituer les températures postglaciaires qui serviront par la suite à comprendre les relations climat-feu-végétation au Québec. Nos résultats (chapitres 2 et 4) fournissent des données indépendantes sur la température (chironomes), les incendies (charbons de bois) et la végétation (pollen) pour le même site, une première au Québec. La présente étude a justement comme originalité de définir les liens climat-feux-végétation sur la Côte-Nord à partir de trois proxies (chironomes, charbons, pollen) indépendants les uns des autres. Les chapitres 2 et 4 apportent des connaissances nouvelles sur la dynamique de la pessière à mousses de l'est du Québec déjà documentée par Richard et al. (2020), Couillard et al. (2021), Fréchette et al. (2021). Les résultats du chapitre 4 permettent d'une part de réviser l'âge de la pessière à lichens actuelle autour du lac Adèle à au plus 3000 ans. D'autre part, d'identifier les feux récurrents à intervalles rapprochés au cours du

Néoglaciaire comme étant le principal facteur susceptible d'avoir provoqué la transformation de la pessière à mousses en pessière à lichens.

5.1.2 Les assemblages des Chironomidae : marqueurs efficients des changements du climat

L'étude des interactions climat-végétation, à partir des paléotempératures et paléovégétation issues des mêmes assemblages polliniques, peut conduire à un raisonnement circulaire. Le raisonnement circulaire consiste à (1) reconstituer la végétation passée à partir des assemblages polliniques, puis (2) les paléotempératures à partir de la végétation passée, et enfin (3) l'interprétation à la lumière des paléotempératures, des changements observés à partir des assemblages polliniques. Pour des raisons d'indépendance du proxy, il est donc recommandé d'utiliser les données polliniques pour reconstituer soit la paléovégétation, soit les paléotempératures, et non les deux pour un même site (Fréchette et al., 2018, 2021).

Les chironomes se sont avérés des bioindicateurs climatiques intéressants et pertinents pour les reconstitutions des températures. Ils ont fonctionné comme outils de reconstitutions quantitatives dans différents contexte (des carottes différentes, des lacs différents ; chapitres 2 et 3). Ils donnent des résultats cohérents si on compare les séquences entre elles (ex. Mista versus Adèle ; matériel supplémentaire S3.3b, chapitre 3) ou si on compare avec l'histoire climatique reconstituée par d'autres proxies (ex. pollen, cernes d'arbres, thécamoebiens, chapitre 3). Malgré la possibilité de biais induit par d'autres facteurs internes au lac (p.ex., pH, oxygénation, salinité de l'eau ; Velle et al., 2005 ; Brodersen et Quinlan, 2006), nos résultats montrent que les chironomes fournissent des reconstitutions pertinentes. Ils sont capables de matérialiser les grands changements du climat (HTM, Néoglaciaire), mais leur sensibilité permet aussi de repérer des événements climatiques plus brefs et de plus faibles amplitudes comme le Petit Age Glaciaire, la Période Chaude Médiévale, la Période Froide de l'Age Sombre ou la Période Chaude Romaine. Pour finir, un autre avantage des chironomes en tant que proxy climatique, c'est son indépendance vis-à-vis de la végétation (Millet et al., 2008). Son utilisation permet de sortir du raisonnement circulaire de l'utilisation des assemblages polliniques.

La courbe de températures au lac Mista (chapitre 2) change (chapitre 3) parce que les fonctions de transfert (FT) utilisées diffèrent. En fait, dans le chapitre 1, nous avons utilisé trois fonctions de transfert, Larocque (2008), Fortin et al. (2015) et Medeiros et al. (2022). La première FT s'est avérée être celle ayant la meilleure performance statistique, susceptible de produire des reconstitutions précises. Bien que les courbes de températures générées par chacune des trois FT soient fortement similaires (matériel supplémentaire S2.1c ; chapitre 2), la FT de Larocque (2008) semble être mieux adaptée au site d'étude (lac Mista ; chapitre 2). Elle fournit des températures les plus proches de celles issues des données météorologiques pour la période de référence 1981-2010 (13,5°C ; Régnière et al., 2017). Pour le chapitre 3, nous avons utilisé la nouvelle FT de Suranyi et al. (in press). Comparée aux FT préexistantes (Tableau 1.1), la nouvelle FT de Suranyi et al (in press) inclut plus de sites au sud du Québec dont la température est supérieure à 19°C. Par ailleurs, la nouvelle FT de Suranyi et al (in press) contient de meilleurs analogues, et la courbe des températures reconstruites est similaire à celle de plusieurs enregistrements climatiques régionaux. En effet, les meilleurs analogues des assemblages du début et du milieu de l'Holocène (entre 11700 et 4200 ans AA) se trouvent probablement dans les lacs actuels situés au sud du Québec comme suggéré précédemment par Bajolle et al. (2018).

5.1.3 Des nouvelles reconstitutions quantitatives de températures estivales pour le Québec

Nos différentes reconstitutions (chapitres 2 et 3), permettent d'avoir les premières données de paléotempératures de la région de la Romaine (Mista) et de Manicouagan (Adèle). Ces résultats contribuent à améliorer l'état des connaissances paléoclimatologiques pour l'est du Québec et de compléter les cartes paléoclimatiques du Canada.

Ces nouvelles reconstitutions quantitatives inférées d'après les assemblages de Chironomidae combinées à celles disponibles sur le lac Aurélie donnent un nouvel aperçu des changements spatiotemporels des températures postglaciaires au Québec. Les reconstitutions des températures postglaciaires le long d'un transect est-ouest en forêt boréale du Québec, ont confirmé l'existence d'un contraste de températures entre l'est et l'ouest du Québec avant 7000 ans AA (matériel supplémentaire S3.3, chapitre 3) comme suggéré par avant par Fréchette et al. (2021). Avant 7000 ans AA, à l'est (Québec maritime), les influences indirectes des vestiges de l'Inlandsis Laurentien et de la température estivale des eaux océaniques de surface atténuent les effets d'une insolation maximale, ce qui induit des conditions estivales plus fraîches. A l'opposé, le climat était plus chaud à l'ouest (Québec continental), avec des températures maximales autour de 7500 ans AA, probablement peu ou pas affectées par ces influences. Entre 7000 et 4800 ans AA, le climat était chaud simultanément dans l'est et l'ouest du Québec. Dans l'est et l'ouest du Québec, la transition climatique a eu lieu entre 4800 et 4000 ans AA qui marque le début du Néoglaciaire. Les reconstitutions des températures estivales inférées d'après les assemblages de Chironomidae des 3 enregistrements (Mista, Adèle et Aurélie) mettent également en évidence une forte variabilité climatique au cours des 3000 dernières années, avec une succession d'événements tour à tour chauds et froids, généralement synchrones entre l'est et l'ouest du Québec, et probablement comparables aux périodes chaudes romaine et médiévale, aux périodes froides de l'âge sombre et du petit âge glaciaire. De manière générale, tous ces évènements climatiques ont été également mis en évidence, de l'est (Magnan et Garneau, 2014) à l'ouest (Holmquist et al., 2016 ; Delwaide et al., 2021), du nord (Arseneault et Payette, 1997) au sud (O'Neill Sanger et al., 2021) du Québec par d'autres bioindicateurs (pollen, thécamoebiens, cernes d'arbres ; voir chapitre 3). Bien que le nombre de dates radiocarbone et la précision des modèles d'âge incitent à la prudence dans l'interprétation de nos résultats, le timing de ces évènements semble correspondre assez bien aux résultats livrés par d'autres bioindicateurs climatiques. Toutefois, la résolution d'analyse est un peu faible pour mettre en évidence les variations de températures d'ordre séculaire.

5.1.4 Le rôle (minime) des températures estivales dans la dynamique postglaciaire de la végétation et des feux à l'est du Québec

D'après nos résultats (Fig.5.1 ; Fig.5.2), les changements de températures estivales pendant la période enregistrée par les archives à Mista et Adèle ne semblent pas jouer un rôle prépondérant sur la dynamique forestière et l'histoire des feux à l'est du Québec. A Mista et Adèle, suite au réchauffement postglaciaire, les températures sont au-dessus d'un seuil qui permet l'afforestation. Apparemment, tout au long de la période postglaciaire, les températures ne descendent jamais en dessous d'un seuil qui induirait une réponse de la végétation. Donc pas limitant dans ce contexte. L'occurrence des incendies à l'est du Québec semblent indépendante des variations de températures estivales. D'autres facteurs climatiques sont sans doute plus prégnants comme, les précipitations printanières et estivales, la variabilité hydrologique interannuelle (Remy et al., 2017a), l'indice de sécheresse (Portier et al., 2019), ainsi que des facteurs non climatiques, tels l'inflammabilité de la végétation et la connectivité paysagère (Blarquez et al., 2015), et la topographie (Remy et al., 2017a).

A l'opposé des sites à l'est du Québec, à Aurélie (ouest du Québec ; Fig.5.3), les feux semblent moins récurrents avec le refroidissement de la température estivale. Bajolle (2018) note une forte abondance d'espèces thermophiles comme *Pinus strobus*, *Thuja occidentalis* au cours de la période chaude dite de maximum thermique de l'Holocène (températures estivales au maximum). Ensuite, ces espèces vont considérablement régresser avec le refroidissement néoglaciaire (baisse de la température estivale). A l'ouest du Québec, il y a une relation entre les variations de température estivale et la végétation. Il y a donc un contraste entre l'est et l'ouest sur les processus de contrôle de la végétation.

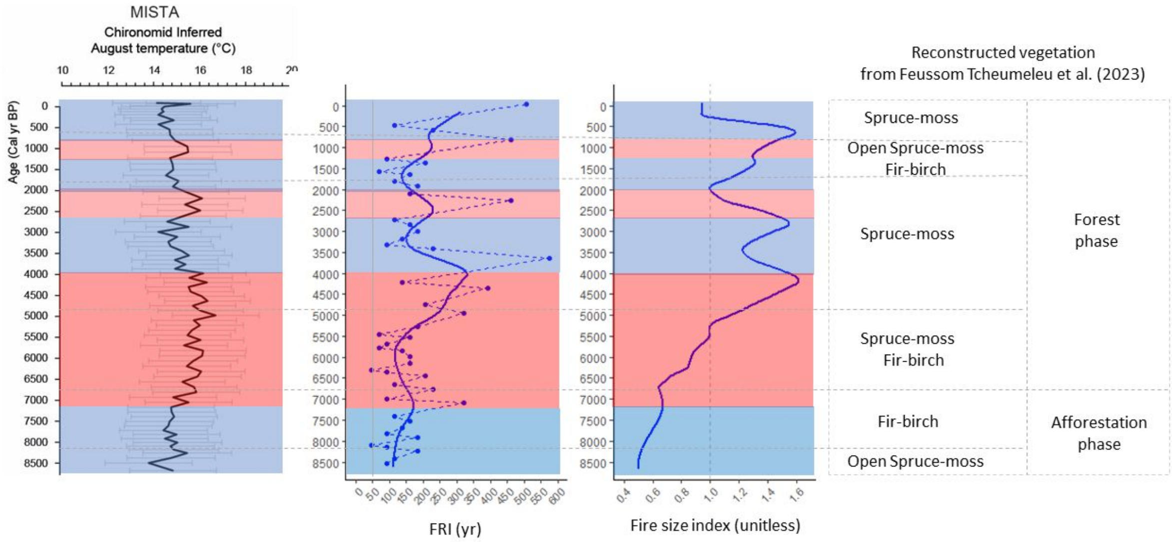


Figure 5.1 Chironomid inferred August temperature, reconstructed fire and vegetation histories of Lake Mista.

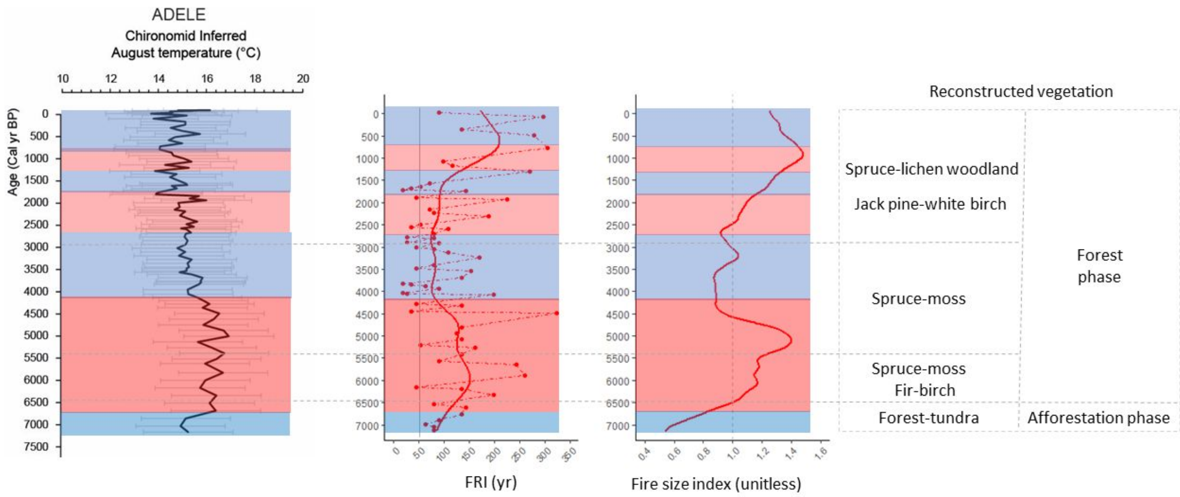


Figure 5.2 Chironomid inferred August temperature, reconstructed fire and vegetation histories of Lake Adèle.

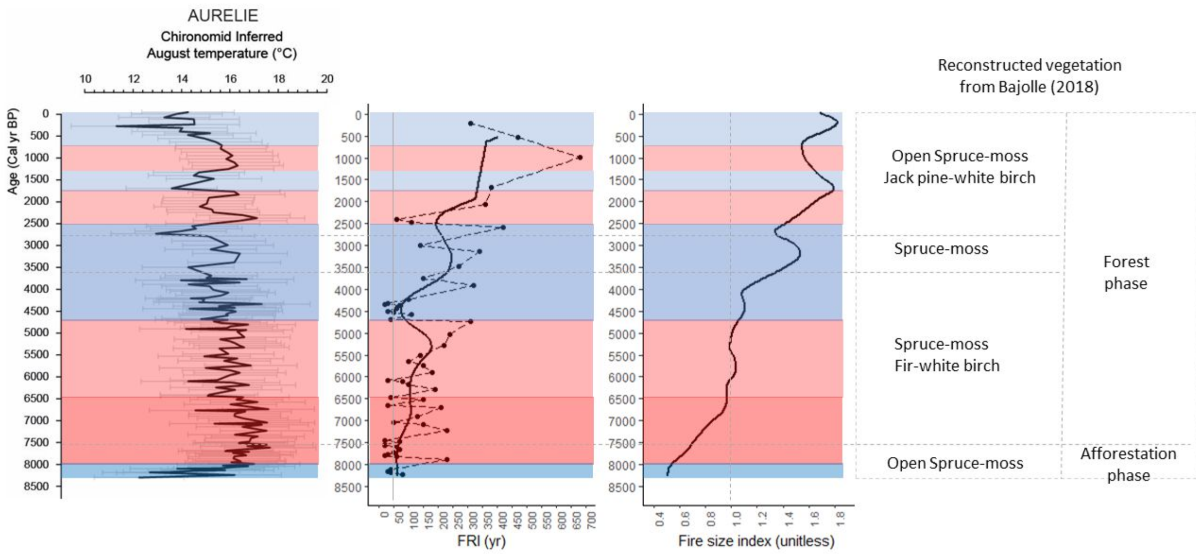


Figure 5.3 Chironomid inferred August temperature, reconstructed fire and vegetation histories of Lake Aurélie.

5.1.5 Le rôle prépondérant des régimes de feux sur la pessière

Les variations de la taille et de la fréquence des feux semblent contrôler la dynamique à long terme de la pessière à mousses du Québec maritime. Dans la partie nord de la pessière à mousses de l'est (lac Adèle), la végétation commence à s'ouvrir autour de 3000 ans AA, suite à des feux récurrents à intervalles rapprochés qui provoqueraient la multiplication des échecs de régénération de l'épinette noire. La pessière à mousses ouverte persistera, avec la participation des conditions climatiques très sèches entre 2600 et 950 ans AA qui pourraient limiter le développement de l'épinette noire (Boiffin et Munson, 2013), mais finira par basculer en pessière à lichens vers 1500 ans AA. Les conditions climatiques très sèches au Québec maritime, rapportées par Magnan et Garneau (2014), couplées à des intervalles de retour des feux courts, vont également contribuer à l'ouverture de la végétation environnante du lac Mista vers 2000 ans AA. Le rallongement des intervalles de retour des feux et des conditions climatiques plus humides, vont permettre à la pessière mousses ouverte de se redensifier autour du lac Mista au cours des 500 dernières années. Bien que les feux soient devenus peu récurrents, les conditions climatiques humides plus propices, la pessière à lichens autour du lac Adèle va se maintenir à travers une auto-régénération. En effet, dans les pessières à lichens, les lits de germination recouverts de lichens inhibent la croissance des graines et semis de l'épinette noire (Mallik et Kayes, 2018), contribuant ainsi à l'autoperpétuation de la pessière à lichens. Contrairement aux résultats d'analyses géochimiques et anthracologiques de Bastianelli (2018) qui révèlent que la pessière à lichens actuelle autour du lac Adèle daterait de 4000 à 4500 ans, les reconstitutions de végétation à partir d'analyses polliniques suggèrent que cette pessière à lichens serait vielle d'au plus 3000 ans.

D'après les données regroupées de Remy et al. (2017b), les changements de trajectoires à long terme de la végétation à l'est du Québec seraient dus principalement à la taille des incendies plutôt qu'à leur fréquence. Nos résultats ont contribué à montrer que sur certains sites (p.ex., lac Adèle ; chapitre 4), les incendies récurrents à intervalles rapprochés semblent être le principal facteur de modification de la trajectoire à long terme de la végétation dans la pessière à mousses de l'est. Comparés aux conclusions de Remy et al. (2017b), nos résultats confirment l'existence de disparités intrarégionales dans les relations feu-végétation dans la pessière à mousses de l'est.

5.1.6 Trajectoire de la végétation le long du transect est-ouest

L'histoire de la végétation des trois sites étudiés comporte deux phases. Une phase d'afforestation de 8500 à 7500 ans AA (à l'ouest ; lac Aurélie ; Fig.5.3) et de 8500 à 6500 ans AA (à l'est ; lacs Mista et Adèle ; Fig.5.1 ; Fig.5.2), suivie par une phase forestière de 7500 ans AA à aujourd'hui (à l'ouest ; lac Aurélie ; Fig.5.3) et de 6500 ans AA à aujourd'hui (à l'est ; lacs Mista et Adèle ; Fig.5.1 ; Fig.5.2). Pendant la phase d'afforestation et une partie de la phase forestière, des végétations contrastantes se développaient à l'est (lac Mista) et à l'ouest (lac Aurélie) du domaine de la pessière à mousses. Autour du lac Mista, une végétation de sapinière à bouleau précède la phase forestière. La pessière à mousses fermée similaire à celle observée aujourd'hui semble s'être mise en place à l'ouest du Québec autour de 3600 ans AA (lac Aurélie) puis à l'est vers 5000 ans AA (lacs Mista et Adèle). Aux lacs Aurélie et Mista, l'avènement des grands feux coïncide avec la fermeture de la pessière à mousses (Fig.5.1 ; Fig.5.2) et l'augmentation de l'inflammabilité du paysage suite à l'expansion de *Picea mariana*.

Vers 3000 ans AA, les grands feux (Fig.5.2 ; Fig.5.3) contribueront à l'ouverture du couvert forestier, permettront l'installation de *Pinus banksiana* (espèce pyrophile) aux lacs Aurélie et Adèle. L'ouverture du couvert forestier sera tardive (2000 ans AA) autour du lac Mista. À l'échelle du domaine de la pessière à mousses moderne du Québec, l'ouverture de la pessière à mousses fermée semble synchrone entre les lacs Aurélie (à l'ouest) et Adèle (à l'est), puis asynchrone entre les lacs précédents et le lac Mista (à l'est). La végétation moderne autour de chacun des sites étudiés, démontrent que la pessière à mousses ouverte s'est soit maintenue (lac Aurélie), à basculer vers la pessière à lichens (lac Adèle), s'est redensifiée (lac Mista).

Les conditions climatiques chaudes (Fig.5.3) et sèches (Fréchette et al., 2018) du maximum thermique de l'Holocène au lac Aurélie (chapitre 2 ; Fig.5.3), semblent propices à des incendies récurrents à intervalles rapproché. Cependant, ces feux sont de petites tailles, leur propagation étant limitée probablement par une forte abondance de feuillue tel *Betula* (Bajolle, 2018) qui sert de coupe-feu (Blarquez et al., 2015). Contrairement à la période du maximum thermique de l'Holocène, le climat frais (Fig.5.3) et humide (Fréchette et al., 2018) du Néoglaciaire (chapitre 2 ; Fig.5.3) sera moins propice aux incendies. Nonobstant, ce seront des grands feux.

A l'opposé des sites à l'est (lacs Mista et Adèle), l'intervalle de retour des feux à l'ouest (lac Aurélie) semble s'allonger avec le refroidissement de la température estivale (Fig.5.1 ; Fig.5.2 ; Fig.5.3). Comparé à la fréquence des feux, la taille des feux semble être le principal facteur de modification de la trajectoire à long terme de la végétation dans la pessière à mousses de l'ouest comme l'ont suggéré Remy et al. (2017b).

Dans un contexte où les changements climatiques en cours augmentent les risques d'incendies, une hausse de la fréquence des feux constitue une menace pour les populations locales (qualité de l'air, risques sanitaires, décès, etc.), les ressources forestières (déforestation, baisse de volume bois, etc.) et l'environnement (perte d'habitats naturels, hausse des émissions de CO_2, pollution diverse, etc.). Sur un territoire comme Adèle (chapitre 4), lorsque l'intervalle de temps entre deux feux se raccourcit beaucoup, les épinettes noires (*Picea mariana*) n'ont pas le temps d'atteindre la maturité sexuelle (c-à-d 50 ans ; Viglas et al., 2013), et donc la pessière à mousses de se régénérer (chapitre 4). Une fois le point de bascule de l'épinette noire franchi, nous assistons à des accidents de régénération qui provoquent la transformation de la pessière à mousses en pessières à lichens. Suite aux changements climatiques, l'augmentation de la fréquence des incendies risque d'entraver la croissance du couvert forestier qui est essentiel pour, protéger la biodiversité dont certaines espèces comme *Rangifer tarandus caribou* (Caribou forestier) sont vulnérables, et répondre aux besoins des industries forestières en ressources bois.

Savoir comment les changements de températures estivales postglaciaires au Québec ont affecté les régimes de feux et la dynamique de la végétation à différentes échelles spatiales et temporelles, pourra servir de directive à la définition de stratégies d'aménagement forestier durable inspirées de la variabilité naturelle des régimes de perturbation, puis aider certainement les gestionnaires forestiers à mieux évaluer la résilience des forêts boréales face aux changements climatiques futurs.

5.2 Perspectives de recherches futures

Cette thèse apporte de nouvelles connaissances sur le climat postglaciaire, les relations climat-feu et les interactions climat-feu-végétation en forêt boréale au Québec. Toutefois, les disparités (ex. végétation, température, précipitation, relief, dépôts de surface et sols ; Saucier et al., 2009 ; Grondin et al., 2023) qui existent au Québec ne permettent pas de généraliser nos conclusions à d'autres sites sans extrapoler. D'autres études paléoécologiques devraient être menées afin de compléter les cartes paléoclimatiques (paléotempérature, paléohydrologie) et de la paléovégétation, d'améliorer notre compréhension des relations entre le climat, les incendies et la végétation au Québec. Pour capter les évènements climatiques ponctuels (RWP, DACP, MWP, LIA) lors des études paléoécologiques futures, plus d'échantillons sélectionnés objectivement le long des séquences sédimentaires, devraient être datés, afin d'obtenir des dates moins extrapolées et beaucoup plus précises. D'autres études régionales fondées sur une approche à haute résolution temporelle des échantillons, devraient être menées. Cela facilitera également la validation des reconstitutions de températures basées sur les chironomes par des données dendrochronologiques.

Dans plusieurs études multiproxies (charbon, pollen) des relations feu-végétation au Québec (Blarquez et al., 2015 ; Remy et al., 2017b), l'hypothèse des arbres du genre *Betula* jouant le rôle de pare-feu est souvent émise pour justifier des feux peu étendus ou peu sévères enregistrés au cours du maximum thermique de l'Holocène (chapitres 2 et 4) en présumant qu'il s'agit des arbres de *Betula papyrifera*. Ceci en s'inspirant de la végétation actuelle qui pourtant pourrait être différente de la végétation passée (Fréchette et al., 2018, 2021). Pour lever cette équivoque, il serait pertinent de distinguer les espèces arborescentes et arbustives, en mesurant le diamètre des grains de pollen du genre *Betula* tel que décrit par Richard (1970).

Au Canada, les données paléoclimatiques (températures, précipitations) aident à comprendre les relations climat-feu pendant la période postglaciaire (ex. Ali et al., 2012 ; Remy et al., 2017a ; Gaboriau et al., 2020). Plusieurs études des relations climat-feu durant l'Holocène suggèrent que les feux étaient plus fréquents lorsque le climat était sec, au cours du maximum thermique de l'Holocène (Ali et al., 2012 ; Remy et al ; 2017a) ou du Néoglaciaire (Carcaillet et Richard, 2000 ; Ali et al., 2008). Cependant, ces conclusions résultent souvent de la comparaison entre des données paléofeux et paléohydrologiques provenant des sites différents. C'est le cas pour les chapitres 2 et 4 où les données paléohydrologiques de Magnant et Garneau (2014) nous ont permis de comprendre les relations climat-feu-végétation à l'est du Québec. Dans un contexte de changement climatique où les variations de températures et de précipitations ne cessent d'inquiéter les populations, décideurs et pouvoirs publics, des analyses comparatives multisites et multiproxies (chironomes (paléotempérature), thécamoebiens (paléohydrologie), charbons (paléofeux)) permettrait de mieux comprendre les mécanismes de contrôle des feux de forêt à différentes échelles temporelles et spatiales, afin d'adapter les stratégies de gestion durable.

Nos résultats (chapitres 2 et 4) suggèrent que l'ouverture de la végétation notée autour de 3000 ans AA, serait due à des conditions climatiques arides (Hogg et Wein, 2005) ou à des perturbations majeures (feux récurrents, légers ou sévères (Chapitre 4 ; Girard et al., 2009)) ou secondaires (épidémie de la tordeuse de bourgeons de l'épinette (TBE ; chapitre 4 ; Girona et al., 2018 ; Navarro et al., 2018a, b)) voire à un effet cumulé, épidémie de la TBE suivie d'incendies (Girard et al., 2009)). Des études supplémentaires d'une séquence sédimentaire couvrant les 3000 dernières années, permettraient de tester l'hypothèse de l'épidémie de la TBE, à travers une approche croisée (pollen, charbons, écailles et ADN sédimentaire de la TBE) de la dynamique de la végétation (pollen) *versus* celles des incendies (charbons de bois) et des épidémies de la TBE (écailles et ADN sédimentaire de la TBE).

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