UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RECONSTITUTION DES PALÉOTEMPÉRATURES HOLOCÈNES DE LA FORÊT BORÉALE CONIFÉRIENNE DE L'OUEST DU QUÉBEC BASÉE SUR UNE APPROCHE MULTI-INDICATEURS

THÈSE

PRÉSENTÉE

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PAR
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Cette thèse présente les résultats scientifiques de mon doctorat en cotutelle, réalisée à l'Université du Québec en Abitibi-Témiscamingue et à l'Université de Montpellier. Cette recherche s'articule autour de cinq parties : une introduction générale, trois chapitres, en lien avec des articles publiés, soumis et à soumettre dans des journaux scientifiques à comité de lecture et une conclusion générale. Le premier article (Chapitre 1) a pour objectif de comparer deux fonctions de transfert, la fonction de transfert Est canadienne modifiée de Larocque (2008) et la fonction de transfert canadienne (Fortin et al. 2015), toutes deux appliquées aux assemblages de Chironomidae du *Lac Aurélie* situé au centre du Québec (Canada). L'objectif du deuxième article (Chapitre 2) est d'évaluer la pertinence des assemblages de Chironomidae dans un lac peu profond (*Lac Lili*) situé à l'ouest du Québec (Canada). Le troisième article (Chapitre 3) a pour but de présenter une approche croisée Chironomidae/pollen afin d'augmenter la robustesse des reconstitutions quantitatives des paléotempératures. Ces chapitres peuvent être lu indépendamment, ce qui peut parfois engendrer des redondances, et contenir des informations supplémentaires référencées dans les appendices de la thèse.

Chapitre 1 – Bajolle, L., Larocque-Tobler, I., Gandouin, E., Lavoie, M., Bergeron, Y., Ali, A.A. (2018). *Major postglacial summer temperature changes in the central coniferous boreal forest of Quebec (Canada) inferred using chironomid assemblages.* Journal of Quaternary Science (DOI: 10.1002/jqs/3022)

Chapitre 2 – Bajolle, L., Larocque-Tobler, I., Ali, A.A., Lavoie, M., Bergeron, Y., Gandouin, E. (2018). *A chironomid-inferred Holocene temperature record from a shallow boreal lake: potentials and pitfalls.* Journal of Paleolimnology (DOI: 10.1007/s10933-018-0045-9)

Chapitre 3 – Bajolle, L., Peyron, O., Girardin., M.P., Fréchette., B., Gandouin, E., Grondin, P., Bergeron, Y., Remy, C.C., Ali, A.A. (2018). *August temperature variability over the past 8000 years in the western Québec boreal forest (Canada): a combined approach based on chironomids and pollen data.* Quaternary Science Reviews (à soumettre).

Je suis la première auteure de chaque article de ce manuscrit. Les diverses étapes de cette recherche (échantillonnage, acquisition des données Chironomidae-pollen, écriture et soumission des articles) ont été menées sous le suivi et la contribution de mes directeurs et co-directeurs Yves Bergeron, Adam A. Ali, Emmanuel Gandouin et Martin Lavoie. Pour le chapitre 1, Isabelle Larocque-Tobler a fourni l'intégralité des données Chironomidae du *Lac Aurélie* ainsi que sa fonction de transfert Est canadienne (Larocque 2008). Pour la réalisation du chapitre 3, Verushka Valsecchi m'a procuré les données pollen du *Lac Aurélie* (acquises durant un projet postdoctoral) et Bianca Fréchette la base de données modernes pollen de l'Est du Canada. Martin Girardin, Bianca Fréchette et Odile Peyron ont collaboré à l'élaboration de l'approche croisée de ce chapitre. Enfin, Pierre Grondin m'a fait bénéficier de son expertise pour mieux comprendre la dynamique paysagère des écosystèmes boréaux

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AA	Avant aujourd'hui
AD	Anno domini
AMS	Accelerator Mass Spectrometry
CATR	Combined quantitative august temperature reconstruction
CCA	Canonical correspondence analysis
CONISS	Constrained incremental sum of squares
DACP	Dark Age Cold Period (Period froide de l'Âge somber)
DC	Drought code (Indice de sécheresse)
DCA	Detrended correspondence analysis
FS index	Regional fire size
HTM	Holocene Thermal Maximum
k cal a BP, cal yr BP, cal BP	kilo calibrated years before present, calibrated years before present, calibrated before present
LIA	Little Ice Age
LOESS	Locally weighted scatterplot smothing
LOI	Loss on ignition
MAT	Modern Analogue Technique
MCA	Medieval Climate Anomaly
PANN	Précipitations annuelles totales
PAR	Pollen accumulation rate
PCA	Principal component analysis
RegBB	Regional biomass burned
RegFF	Regional fire frequency
RMSE	Root-mean-square error
RWP	Roman Warm Period
SCD	Square chord distance
SJJA	Mean sunshine for Juin, July, august
WA	Weighted Average
WA-PLS	Weighted Average Partial Least Square

RÉSUMÉ

Un futur climat planétaire plus chaud avec une sècheresse plus marquée durant toute l'année est aujourd'hui prévus, en particulier pour les hautes latitudes de l'hémisphère nord. Ces changements environnementaux seraient marqués par des fréquences et des intensités plus importantes des perturbations naturelles, qui pourraient menacer l'intégrité de certains écosystèmes forestiers boréaux. L'une des conséquences prévisibles serait une augmentation significative de l'occurrence des feux de forêt qui est déjà et deviendrait davantage encore l'élément perturbateur majeur de ces écosystèmes. Le devenir des écosystèmes boréaux suscite donc de nombreuses interrogations et des incertitudes, ce qui amène à souligner la nécessité d'une bonne caractérisation des changements climatiques spatio-temporels et de leurs conséquences sur ces écosystèmes.

Afin de maintenir ces paysages forestiers dans les limites de leur variabilité naturelle, le Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) se propose, dans un contexte d'aménagement écosystémique pour un aménagement durable (ADF), d'établir un Registre des états de référence. Dans cette perspective, l'objectif de recherche de cette thèse était de *produire des reconstitutions des paléotempératures holocènes les plus robustes possibles au sein de la pessière à mousses de l'ouest du Québec.* La recherche a porté sur une approche multi-indicateurs incluant les Chironomidae et le pollen contenus dans les sédiments des deux lacs retenus.

Les résultats mettent en évidence la pertinence des capsules céphaliques de Chironomidae pour reconstituer à haute résolution temporelle, les paléotempératures holocènes du mois d'août provenant du *Lac Aurélie* à l'aide de deux Fonctions de Transfert (FT). La FT Est canadienne s'est avérée plus en accord avec le signal régional que la FT canadienne. De surcroit, les assembalges de Chironomidae du *Lac Lili* ont donné une reconstitution surestimée des paléotempératures en raison de la faible profondeur de ce lac. Enfin, la reconstitution quantitative combinée (chironomide et pollen) des paléotempératures du mois d'août a souligné trois périodes principales: (i) 8500-4500 ans AA, identifiée comme le Maximum Thermique de l'Holocène (HTM) durant laquelle les températures d'août sont plus chaudes que les températures actuelles; (ii) 4500-1000 ans AA, marquée par le début de la période Néoglaciaire froide, où les températures oscillent autour des valeurs actuelles et (iii) les derniers 1000 ans AA, caractérisés par une diminution générale des températures. Plusieurs événements climatiques courts ont également été identifiés pour chaque période : (i) l’évènement froid de 8200 ans AA ; (ii) l’évènement chaud de 4200 ans AA ; (iii) la période chaude dite Romaine (RWP, 1900-1700 ans AA) ; (iv) la période froide de l’Âge Sombre (DACP, 1700-1500 ans AA) ; (v) l’Anomalie Climatique Médiévale (MCA, 1100 ans AA) et (vi) le Petit Âge Glaciaire (LIA, 500-250 ans AA). Une série d’événements froids est également observée vers 5900, 4300, 2800 et 400 ans AA, se référant probablement aux évènements « Bond ». La durée et l’amplitude observées des événements climatiques rejoignent les enregistrements régionaux, nord-américains et plus largement ceux de l’Hémisphère Nord.

Par ailleurs, la synthèse soulignant les relations entre climat-végétation-feu confirme l’influence d’une instabilité climatique sur les changements des régimes des feux, principalement causée par les variations saisonnières des précipitations et de l’irrégularité des épisodes de sécheresse. Toutefois, notre reconstitution combinée des paléotempératures indique que les grands feux coïncident avec l’évènement ponctuel de 4200 ans AA et ceux survenus à partir de 2000 ans (RWP, DACP, MCA et LIA). La température estivale conjuguée à d’autres variables climatiques (sécheresse estivale, ensoleillement estival, et précipitations annuelles) joue donc un rôle important dans la variation du régime des feux à l’ouest du Québec.

Mots clés : dépôts lacustres, Chironomidae, pollen, fonction de transfert, changements climatiques

INTRODUCTION GÉNÉRALE

Il est maintenant bien reconnu par la communauté scientifique que le climat de la planète se réchauffe (IPCC 2014). Selon les scénarios les plus pessimistes, les conséquences à long terme de ce processus induit par les activités humaines sur la composition, la structure et le fonctionnement des écosystèmes boréaux apparaissent inévitables et importantes (Price et al. 2013). Selon Price et al. (2013), une augmentation de 4 à 5 °C de la température moyenne est attendue sur l'ensemble de la zone boréale canadienne d'ici 2100. L'une des conséquences serait une augmentation significative de l'occurrence des feux de forêt (Girardin et al. 2013).

Les feux naturels structurent les paysages boréaux (Bergeron et al. 2010), jouant un rôle déterminant dans la dynamique des sols, dans les processus de régénération des espèces végétales ou encore au niveau du bilan global du carbone (Bond et al. 2004; Cyr et al. 2009; Price et al. 2013). Il est important de rappeler que la forêt boréale constitue le plus grand réservoir de carbone terrestre, conférant à ce biome une importance capitale dans l'équilibre climatique de la planète (Dixon et al. 1994; Bonan et al. 1995).

Puisque la forêt boréale canadienne constitue aussi l'un des plus larges écosystèmes encore vierge, il est essentiel de bien connaitre les processus naturels qui la façonne de façon à ce que l'utilisation des ressources naturelles puisse être durable et respectueuse de sa biodiversité (Harvey et al. 2003; Gauthier et al. 2008). La caractérisation du lien entre le climat et les incendies de forêt est au centre des préoccupations scientifiques, alimentées ces dernières années par l'occurrence de grands feux de forêt qui laissent, après leur passage, des paysages extrêmement calcinés où la végétation peine à revenir. Quel est et sera le niveau de résilience de la forêt boréale face à l'effet cumulatif des incendies et des perturbations liées aux activités humaines (foresterie, agriculture, urbanisation, etc.) ? Autrement dit, y a t-il un risque qu'au cours des prochaines décennies, les principaux processus écologiques qui régissent le fonctionnement de la forêt boréale (régime de feu, cycle du carbone et dynamique de végétation) soient altérés (voire remplacés par d'autres) ? Pour répondre à ces interrogations, il est indispensable de mettre en place des travaux de recherche permettant, sur une longue échelle temporelle, de distinguer la variabilité naturelle des processus écologiques qui contrôlent le fonctionnement des écosystèmes forestiers.

Au Québec, afin de maintenir les paysages forestiers boréaux dans les limites de leur variabilité naturelle, le concept d'aménagement écosystémique pour un aménagement durable des forêts (ADF) a été formulé et développé (Gauthier et al. 2008; Varady-Szabo et al. 2008). Il vise à réduire les écarts entre les caractéristiques de la forêt naturelle et celles de la forêt aménagée (Harvey et al. 2002; Gauthier et al. 2008; Boucher et al. 2009), de manière à maintenir à la fois l'intégrité écologique (Lindenmayer et Franklin 2002; Gauthier et al. 2008) et la productivité forestière (Grenon et al. 2010).

C'est dans cette approche écosystémique que le Ministère des Forêts, de la Faune et des Parcs du Québec (MFFP) se propose d'établir un registre des états de référence. Selon Grenon et al. (2010), un état de référence se base sur le portrait d'un paysage naturel à partir de reconstitutions historiques et de la compréhension de ses processus écologiques. Ces écarts provoqués par l'aménagement forestier peuvent être identifiés à l'aide de ce portrait référentiel qui représente un état du paysage naturel parmi une gamme d'états naturels possibles (Boucher et al. 2009). L'ensemble de ces états possibles permettra de caractériser et de comprendre le fonctionnement des paysages forestiers boréaux du Québec (*i.e.* variabilité naturelle de la dynamique de la végétation) sous l'effet du milieu physique, des changements climatiques en cours et des régimes de perturbation.

Pour mener à bien ce projet, il est nécessaire de caractériser la dynamique des paysages forestiers à différentes échelles spatiales (locale à régionale) et temporelles (décennale à pluriséculaire) et le cadre climatique associé. Cela implique le développement de travaux de reconstructions paléoclimatiques permettant de caractériser les changements majeurs du climat survenus depuis la déglaciation.

L'interglaciaire Holocène a été ponctué de plusieurs épisodes climatiques apparus à l'échelle globale tels que le Maximum Thermique de l'Holocène (HTM), l'Anomalie Climatique Médiévale (MCA) ou encore le Petit Âge Glaciaire (LIA) (Bergeron et Archambault 1993; Hunt 2006; Mann et al. 2009; Renssen et al. 2012; Holmquist et al. 2016 ; Andres et Peltier 2016). Cependant, des interrogations persistent sur la durée, l'amplitude, et l'impact des oscillations climatiques, de même que leurs impacts sur le fonctionnement des écosystèmes et les incendies de forêt.

De manière générale, les reconstitutions paléoclimatiques réalisées à ce jour dans l'est du Canada sont essentiellement fondées sur des données polliniques à l'aide de la méthode des analogues modernes (Muller et al. 2003; Fréchette et al. 2008; Viau et Gajewski 2009; Paquette et Gajewski 2013; Lafontaine-Boyer et Gajewski 2014; Ladd et al. 2017). Ces travaux ont montré que depuis 9000 ans AA (avant aujourd'hui, années étalonnées), une transition climatique est survenue vers 5000 ans AA, avec un refroidissement de 1 °C et une augmentation des précipitations annuelles d'environ 150 mm/an. L'Holocène inférieur (~9000–4500 ans AA) était caractérisé par un climat plus chaud et plus sec qu'aujourd'hui (Ali et al. 2012; Fréchette et al. 2018). Des modélisations climatiques récentes portant sur les 7000 dernières années pour l'ouest du Québec (Hély et al. 2010; Ali et al. 2012; Oris et al. 2014; Blarquez et al. 2015) ont révélé que le HTM (~7000–5000 ans AA) a été marqué par des conditions hydroclimatiques plus sèches. Selon Renssen et al. (2012), cet épisode climatique semble avoir été d'une durée variable selon les régions du Canada, soit de 2000 ans (~7000-5000 ans AA) jusqu'à 7000 ans (~10 000–3000 ans AA). Son amplitude aurait aussi été différente selon le lieu. Le MCA (~750–1050 ans AA) fut une période caractérisée par des conditions chaudes et des précipitations plus abondantes comparés à l'actuel (Hougton et al. 1990; Carcaillet et Richard 2000; Ali et al. 2012).

Toutefois, l'occurrence, l'amplitude, la durée et l'étendue spatiale de cet évènement ont fait l'objet de débats encore non résolus aujourd'hui (Mann et Jones 2003), notamment au Québec (Viau et al. 2006). En ce qui concerne le LIA (~650–100 ans AA), des travaux à l'ouest du Québec révèlent qu'il était plutôt froid et sec qu'aujourd'hui (Bergeron et Archambault 1993) tandis que d'autres études en Amérique du nord indiquent des conditions plutôt froides et humides à l'intérieur du continent et plus sèches le long des côtes est et ouest (Ladd et al. 2017; Hobbs et al. 2017).

Ces grandes variations du climat ont conduit, dans la région boréale du nord du Québec, à un allongement de la saison de feu vers 5000 ans AA, entraînant par le fait-même une augmentation de la fréquence des feux (Ali et al. 2012; Remy et al. 2017a). Ensuite, bien que le refroidissement graduel du climat s'est matérialisé par une diminution de la fréquence des feux, une augmentation de leur taille dû notamment à l'augmentation graduelle des températures printanières est survenue (Ali et al. 2012).

Au Québec, les travaux discutant des interactions pluriséculaires entre le climat et les incendies ont été essentiellement fondés sur des reconstitutions simulées du climat (Hély et al. 2010; Ali et al. 2012; Blarquez et al. 2015). Il y a un manque de données en ce qui concerne les reconstitutions des paléotempératures fondées sur des indicateurs autres que les grains de pollen. Par ailleurs, confronter les reconstitutions

de la végétation et du climat basées sur les mêmes assemblages polliniques peut amener un raisonnement circulaire (Fréchette et al. 2018).
Toutefois, plusieurs études en Europe et Eurasie (Peyron et al. 2005; Magny et al. 2006; Antonsson et al. 2006; Veski et al. 2015) ont prouvé la fiabilité de ces reconstitutions réalisées notamment à l'aide de la méthode des analogue modernes en les comparant avec d'autres reconstitutions fondées sur d'autres indicateurs comme les Chironomidae. Les données paléoclimatiques quantitatives font donc défaut au Québec, alors qu'elles sont indissociables du trio climat-feu-végétation (Fig. 0.1).

La présente thèse se propose donc de combler cette lacune pour un secteur de la région boréale au Québec. Dans cette optique, nous avons mis en place une approche pluridisciplinaire pour reconstituer le climat fondé sur l'analyse d'assemblages de Chironomidae (Insectes, Diptères) et de grains de pollen conservés dans les dépôts lacustres. L'analyse paléoclimatique reposant sur une approche croisée pollen-Chironomidae nous permettra de mieux cerner les interactions pluriséculaires entre le climat et les incendies de forêts et de mieux anticiper l'impact du changement climatique actuel et anticipé sur l'occurrence et la propagation des incendies dans l'Est du Québec.

L'originalité de la présente étude réside dans le croisement sur de mêmes sites de reconstitutions paléoclimatiques issues des assemblages subfossiles de deux bio-indicateurs. En effet, ce type d'approche constitue une première pour la région d'étude et le Québec en général, alors qu'elle a déjà donné des résultats très concluants dans d'autres régions du monde, telles qu'en Europe et Eurasie (Bigler et al. 2002; Peyron et al. 2005; Magny et al. 2006; Lotter et al. 2012), en Amérique du Sud (Massaferro et al. 2009) ou plus récemment encore dans l'archipel arctique canadien (Fortin et Gajewski 2016).

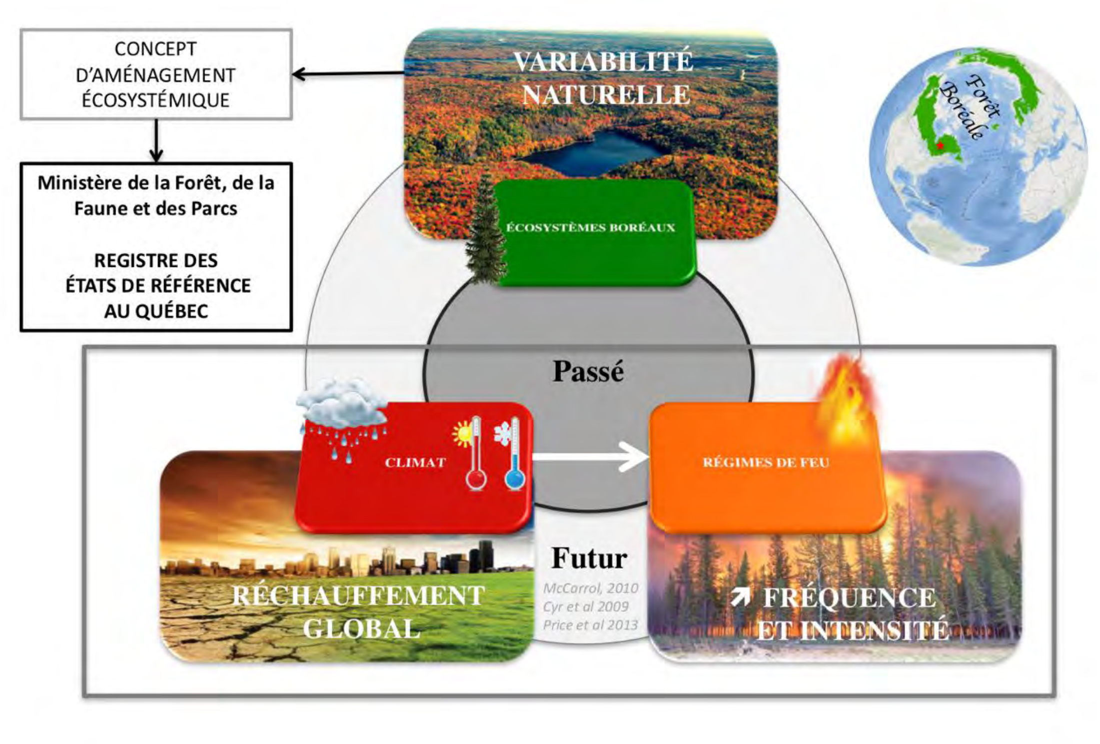

Figure 0.1 Interaction entre les compartiments climat-feu-végétation en forêt boréale. Le rectangle gris (climat-feu) attire l'attention sur l'objectif de la présente recherche dans la région d'étude (étoile rouge : la Jamésie à l'ouest du Québec (Canada)).

0.1 Les indicateurs thermiques paléoécologiques mis en œuvre

0.1.1 L'analyse des assemblages de Chironomidae dans les reconstitutions des paléotempératures

La famille des Chironomidae comprend une richesse taxonomique élevée qui se compose de près de 15 000 espèces (Brooks et al. 2007). En milieu d'eau douce, 211 genres et 1092 espèces ont été recensés à ce jour à l'échelle du Néarctique (Ferrington 2008). Leur cycle biologique court (~15 jours) débute par le développement d'une larve comprenant 4 stades aquatiques. Le cycle se poursuit par un stade nymphal (pupe) puis un stade adulte aérien sexué sous forme de moucheron (Fig. 0.2) (Walker 1987; Brooks et al. 2007). Les larves peuvent se développer sur différents substrats (sédiments, bois morts, etc.) et milieux aquatiques humides ou semi-terrestres (lacs, tourbière, marais, etc.) selon un gradient bathymétrique (Larocque et Rolland 2006). Leur temps de génération court et la capacité de dissémination des adultes volant font des Chironomidae des insectes répondant rapidement aux changements environnementaux (Walker et Mathewes 1989).

Durant le développement larvaire en milieu lacustre, chaque stade laisse derrière lui une capsule céphalique (CC) composée de chitine. Il s’agit d’une substance résistante à la dégradation, permettant à l’exosquelette de la larve d’être préservé dans les sédiments (Walker, 1987). En région boréale, les CC peuvent être abondantes dans les sédiments lacustres ; en effet, il est possible d’en trouver plusieurs centaines dans seulement quelques grammes de sédiment (Brooks et Birks 2000).

Dans la présente étude, les capsules céphaliques ont été analysées selon une résolution temporelle variant, selon le site, entre 5 et 220 ans. Leur extraction a été réalisée à l’aide d’une méthode proche de celle décrite par Hoffmann (1986). L’identification taxonomique (sous microscope optique à 400-1000× de grossissement) a été menée à l’aide des clés taxonomiques de Oliver et Roussel (1983), Wiederholm (1983), Larocque et Rolland (2006) et Brooks et al. (2007), jusqu’au niveau de la famille, de la tribu, du genre et du morphotype d’espèce, quand leur état de conservation le permettait. Une centaine de capsules céphaliques a été comptée par échantillons. Au total, 180 échantillons (*Lac Aurélie*) et 116 échantillons (*Lac Lili*) ont été analysés. Le comptage des assemblages du *Lac Aurélie* a été réalisé par Isabelle Larocque-Tobler (Institut L.A.K.E.S, Lyss, Suisse).

Les assemblages de Chironomidae subfossiles représentent un outil paléo-environnemental robuste et fiable pour caractériser et reconstituer diverses variables limnologiques telles que le statut trophique et la chlorophylle-a (Langdon et al. 2006), l'influence du niveau d'eau sur la composition des assemblages (Greffard et al. 2012), la taille du lac et l'acidité (Mousavi 2002), le niveau d'oxygène (Heinis et Davids 1993) et tout particulièrement les températures de l'eau et de l'air (Walker et al. 1997). Ainsi, les Chironomidae ont la capacité de permettre des reconstitutions quantitatives et spatialisées des changements de la température estivale survenues pendant l'Holocène (Brooks 2006; Larocque-Tobler et al. 2015) à l'aide d'une fonction de transfert (Birks 1998).

De ce fait, plusieurs bases de données établies dans différentes régions au Canada (Larocque et al. 2006; Axford et al. 2009; Upiter et al. 2014; Saulnier-Talbot et al. 2015), en Europe (Brooks et Birks 2001; Heiri et al. 2007; Lotter et al. 2012; Larocque-Tobler et al. 2012), en Fennoscandinavie (Olander et al. 1999; Korhola et al. 2002; Seppä et al. 2002) et aux États Unis (Porinchu et al. 2002) ont démontré que la température de l'air et/ou de l'eau est un facteur majeur qui régi la distribution des Chironomidae.

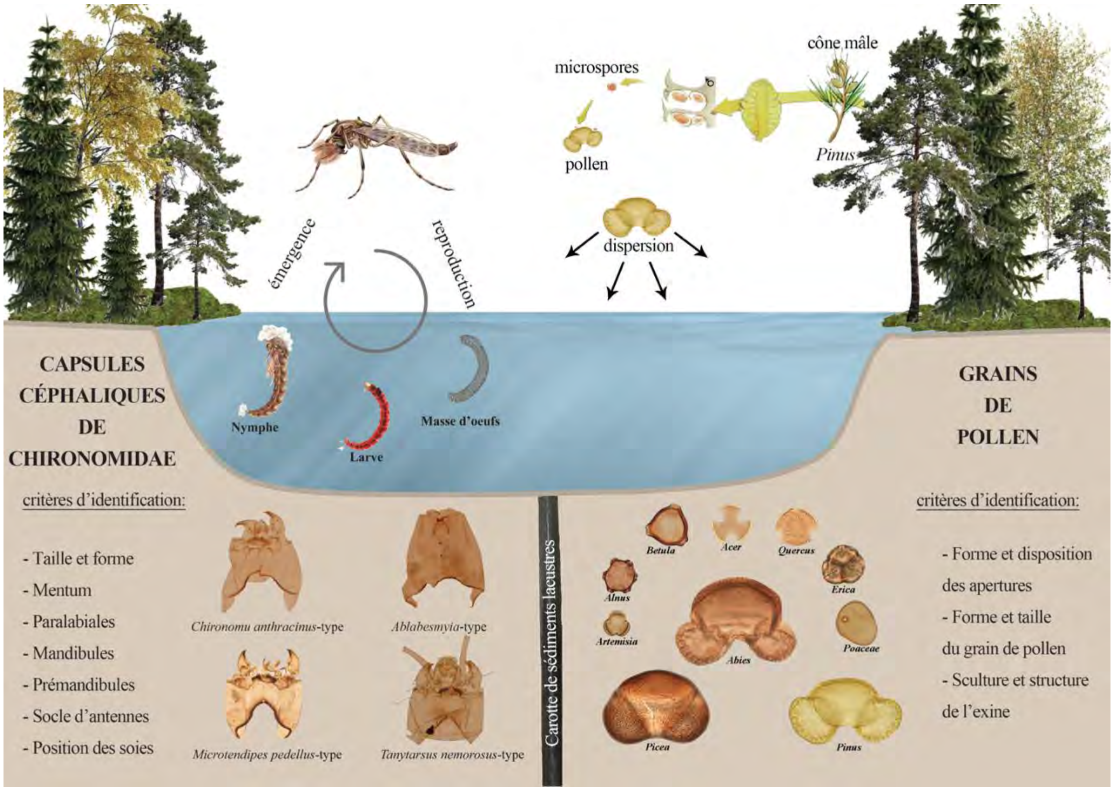

Figure 0.2 Caractéristiques des bio-indicateurs Chironomidae et pollen

Une fonction de transfert est créée à partir d'un échantillonnage de plusieurs lacs répartis selon un large gradient de température. Dans chaque lac, le sédiment de surface est prélevé, les CC extraites et des paramètres physico-chimiques et climatiques sont mesurés. La température de l'air est extrapolée *via* les stations météorologiques les plus proches du lac (Larocque et al. 2006). Une analyse de redondance (CCA) est ensuite utilisée pour déterminer lequel des paramètres explique le mieux la distribution des assemblages de Chironomidae. La température de l'air du mois d'août fait partie des variables qui expliquent le mieux cette distribution (Larocque 2008). À *posteriori*, une base de données modernes (référentiel actuel) peut être établie en corrélant la température et les assemblages modernes des Chironomidae. Ce dernier est par la suite utilisé par un modèle d'inférence développé sur la base de l'optimum et de la tolérance de chaque taxon de chironomide vis à vis de la température.

Les reconstitutions quantitatives sont réalisées à l'aide d'une méthode (WA-PLS) de pondération basée sur un modèle à réponse unimodale dont l'optimum est estimé par une analyse des moyennes pondérées (ter Braak et Juggins 1993). Cependant, pour qu'une fonction de transfert soit fiable, elle doit répondre à certains critères :

(i) un échantillonnage robuste d'un grand nombre de lacs couvrant à la fois un large gradient moderne des températures et la gamme des températures passées rencontrées dans un lac (Birks 1998),

(ii) une distribution unimodale pour chaque taxon dans le but de calculer un optimum de température aussi réaliste que possible,

(iii) une identification taxonomique des CC menée jusqu'au plus haut niveau taxonomique possible afin d'obtenir l'optimum le plus proche de la réalité pour chaque taxon (Larocque 2008; Heiri et Lotter 2010).

D'un point de vue purement méthodologique, le présent travail sera l'occasion de mener une étude comparative de deux fonctions de transfert différentes : la fonction de transfert Est canadienne (Larocque 2008) et la fonction de transfert canadienne (Fortin et al. 2015) afin, d'une part, d'examiner les forces et faiblesses de chacune et, d'autre part, de retenir le modèle le plus fiable.

De plus, il est à noter qu'une grande partie des plans d'eau d'une de nos zones d'étude, soit la plaine de Matagami, comporte de nombreux lacs peu profonds qui ont la particularité d'être sensibles aux fluctuations du niveau d'eau et aux changements climatiques (Jeppesen et al. 2014 ; Smol 2016). Toutefois, dans les études paléolimnologiques, de tels lacs peuvent présenter certains verrous, d'une part en raison de la probabilité élevée d'habitats complexes à l'interphase sédiment-eau à cause des macrophytes aquatiques et, d'autre part, des problèmes pour caractériser les optimums écologiques des bio-indicateurs littoraux dominant ces milieux (Smol 2016).

En effet, plusieurs auteurs (Brodersen et Lindegaard 1997; Upiter et al. 2014) ont montré que les assemblages de Chironomidae dans ce type de milieu étaient majoritairement représentés par des taxons littoraux et/ou eutrophes. L'étude réalisée par Larocque-Tobler et al. (2015) a également mis en évidence que la plupart des taxons littoraux sont des taxons thermiques « chauds ». Par conséquent, une reconstitution en termes d'amplitude de températures pourrait être surestimée. Des études paléoclimatiques menées à l'échelle plurimillénaire sur ce type de milieu afin de vérifier la capacité des bio-indicateurs à enregistrer les changements climatiques sont d'ailleurs encore peu nombreuses.

En dépit des réserves précédentes, une étude pratiquée sur un site peu profond tel que le *Lac Lili* (1,40 m de colonne d'eau) nous est apparu nécessaire, de manière à vérifier si les assemblages de Chironomidae ont le potentiel de reconstituer au minimum en tendance et en amplitude de changement les paléotempératures régionales.

0.1.2 L'analyse pollinique dans les reconstitutions des paléotempératures

Les grains de pollen (angiospermes et gymnospermes) et les spores (fougères et lycopodes) sont abondamment présents dans les dépôts lacustres et tourbeux. Ils y sont conservés pendant plusieurs milliers d'années (Bennett et Willis 2002). Leur identification repose sur des critères morphologiques variés tels que la taille et la forme du grain de pollen, la sculpture et la structure de l'exine (réticulation par exemple), et la présence et la disposition des apertures (pores et sillons) (Fig. 0.2). Il est donc possible d'identifier les plantes productrices au niveau de la famille, du genre et, quelque fois de l'espèce (Richard 1970; McAndrews et al. 1973).

Pour un site d'étude donné, l'analyse des grains de pollen délivre un diagramme pollinique illustrant des spectres polliniques qui couvrent une période donnée telle que la période Holocène (Lavoie 2001). Ainsi, les courbes polliniques retracent l'histoire des variations d'abondance des taxons polliniques et par suite, l'histoire postglaciaire des populations des espèces végétales pouvant se décliner en trois phases successives de végétation : la phase non arboréenne, la phase d'afforestation et la phase forestière (Richard 1993).

De surcroit, la description des assemblages polliniques de la végétation fait cas de quelques taxons indicateurs de la région boréale en question. *Picea* (épinette)*, Abies* (sapin)*, Pinus* (pin)*, Populus* (peuplier)*, Betula* (bouleau)*, Thuja* (cèdre), par exemple, montrent des représentations polliniques différentes enregistrées par le milieu de dépôt. Toutefois, ces représentations polliniques ne reflètent pas directement leur abondance dans les peuplements développés autour du milieu de dépôt en question.

En effet, l'accumulation du pollen dans les sédiments est impactée par de nombreux biais taphonomiques incluant la production différentielle et la capacité de dispersion des taxons (Bradshaw et Webb III 1985). La production pollinique dépend entre autres de l'âge de l'individu, de son rythme de floraison et des conditions climatiques (Lavoie 2001). Par ailleurs, il est nécessaire de connaître les différentes sources polliniques enregistrées par le dépôt qui varient selon la taille du bassin de réception. Un petit bassin est riche en pollens provenant de taxons locaux (déposés près de la plante productrice ou provenant d'une source située à quelques mètres du point d'échantillonnage) et extra-locaux (<500 m). Un grand bassin (>300 m de diamètre) quant à lui est capable de récolter des pollens d'origine régionale (source située à plus de 500 m jusqu'à l'ordre du kilomètre) (Prentice 1985; Sugita 2007).

Par ailleurs, l'analyse des assemblages polliniques est d'autant plus complexe en raison des différences dans la production, le transport et la séquestration des grains de pollen dans les sédiments.En effet à titre d'exemple, selon Richard (1993) et Lavoie (2001), dans les forêts conifériennes et/ou mixtes au Québec-Labrador, *Abies balsamea* (sapin baumier) est connue pour être sous-représenté (<10 %) polliniquement malgré son abondance soutenue au sein des peuplements. Il en est de même pour *Populus tremuloides* (peuplier faux-tremble) et *Thuja occidentalis* (cèdre). *A contrario*, les genres *Betula* et *Pinus* sont sur-représentés polliniquement. Pour le genre *Picea,* la représentation pollinique de *Picea mariana* (épinette noire) se justifie particulièrement par la proximité des individus occupant les rives souvent tourbeuses des lacs étudiés, ou se développant sur les tourbières mêmes.

Dans la présente étude, les grains de pollen et les spores ont été extraits selon la méthode développée par Faegri et al. (1989). L'identification des grains de pollen et des spores a été faite sous microscope optique à un grossissement de 400× à l'aide des clés taxonomiques de Richard (1970) et de McAndrews et al. (1973). Selon leur état de conservation, ils ont pu être déterminés jusqu'au niveau de la famille, du genre et de l'espèce.

Au moins 300 grains de pollen produits par des plantes terrestres vasculaires ont été comptés par échantillons (somme pollinique). Au total, 79 échantillons ont été analysés pour le *Lac Aurélie* (résolution temporelle entre 40 et 300 ans) et 154 pour le *Lac Lili* (résolution temporelle entre 20 et 100 ans). Les analyses polliniques du *Lac Aurélie* ont été réalisées par Verushka Valsecchi dans le cadre d'un projet postdoctoral réalisé sous la direction du Pr. Adam A. Ali.

Les changements à l'échelle plurimillénaire des proportions des différents types de grain de pollen et spores conservés dans les dépôts lacustres ont permis de reconstruire à la fois la végétation passée et les fluctuations climatiques (Viau et al. 2006). Ainsi, différentes variables climatiques telles que la températures et les précipitations estivales peuvent être obtenues à l'aide de la méthode des analogues modernes, laquelle est fréquemment utilisée en Amérique du Nord (Fréchette et al. 2008; Viau et Gajewski 2009).

La reconstitution de la végétation ou du climat par l’intermédiaire d’un assemblage pollinique subfossile (postglaciaire) est généralement basée sur la comparaison avec un référentiel actuel (analogue). Autrement dit, l’assemblage pollinique subfossile est comparé à divers assemblages polliniques actuels (ou modernes) et l’environnement (en termes de végétation et climat) associé au meilleur assemblage pollinique actuel est extrapolé à l’assemblage pollinique subfossile. Pour ce faire, une base de données modernes est utilisée afin d’établir les liens entre un assemblage pollinique moderne et un assemblage subfossile.

Dans une base de données modernes, les assemblages polliniques des sites sont comparés les uns par rapport aux autres et regroupés selon leur ressemblance à l’aide d’une technique de regroupement. La méthode des analogues modernes (Guiot 1990) est ensuite utilisée pour reconstituer le climat à partir d’un assemblage pollinique. Elle repose sur le postulat qu’*a priori*, si les assemblages de deux échantillons sont similaires à des périodes différentes, les grains de pollen les constituant proviennent d’une végétation semblable et témoignent donc d’un climat similaire. Ainsi, le lien pollen-climat se base sur la relation pollen-végétation et végétation-climat. La recherche d’assemblages polliniques actuels comparables à ceux subfossiles s’effectue grâce à des mesures de dissimilarité (la mesure de corde au carré, SCD, « *squared chord distance* ») (Overpeck et al. 1985). L’estimation de la température de chaque assemblage subfossile est calculée à partir de la moyenne pondérée des valeurs climatiques correspondant aux meilleurs des assemblages modernes sélectionnés (avec la différence la plus basse).

Le référentiel actuel utilisé pour les reconstitutions des paléotempératures dans cette thèse s’appuie sur la base de données modernes de l’Est du Canada, qui compte 1010 sites localisés à l’est de la longitude 100°O et au nord de la latitude 44°N. Elle comprend 52 taxons polliniques (22 arboréens, 12 arbustifs et 18 herbacés) et 70 variables climatiques et bioclimatiques. Cette base de données modernes compilée par Fréchette et al. (2018) est-elle même tirée de la base de données modernes nord-américaine compilée par Whitmore et al. (2005). Quinze groupes de sites ont été identifiés avec le programme *K*-means (Legendre et Legendre 1998) et 5 analogues modernes ont été retenus pour la reconstitution des paléotempératures. Ces reconstitutions ont été analysées avec le package « bioindic » (Guiot et Gally 2014) développé sur le programme R (R Core Team 2016).

0.1.3 Approche croisée pollen/Chironomidae pour renforcer la robustesse des reconstitutions paléoclimatiques

En raison d'un réseau d'interactions complexes dans un écosystème forestier boréal, mais également pour des raisons de taphonomie différentielle entre organismes, il est indispensable d'étudier plusieurs bio-indicateurs afin d'obtenir la vision la plus large et complète possible des changements climatiques (Birks et Birks 2006). Les comparaisons disponibles entre les modèles de différents indicateurs climatiques sont un point focal de la recherche paléoclimatique (Renssen et al. 2001).

Comme nous l'avons précisé précédemment, les différents indicateurs retenus peuvent être influencés par d'autres facteurs que la seule température (Mann 2002). Ainsi, le niveau d'eau et les macrophytes ont eu même aussi une influence sur les assemblages de Chironomidae en milieu lacustre (Brodersen et al. 2001). C'est également le cas pour les régimes de feu sur la végétation productrice de pollen (Remy et al. 2017b). La procédure de l'approche croisée permet de mettre en évidence les forces et faiblesses de chaque indicateur. En les comparant, les points forts peuvent être exploités et les faiblesses identifiées (Mann 2002; Birks et Birks 2006).

Dans le présent travail de thèse, l'approche croisée Chironomidae/pollen devrait ainsi nous permettre de mieux vérifier la concordance des reconstitutions des paléotempératures obtenues à partir de chacun des deux bio-indicateurs et surtout de mieux caractériser les différentes oscillations du climat qui ont ponctué notre zone d'étude au cours de l'Holocène.

0.2 Objectifs de la thèse

La finalité de cette thèse est de documenter le cadre paléoclimatique d'un secteur de la forêt boréale du Québec à l'aide de deux bio-indicateurs complémentaires (pollen et Chironomidae) contenus dans des dépôts lacustres. Au-delà de ce volet méthodologique climatique, cette information nous permettra de discuter autour des conséquences du changement climatique sur l'occurrence des feux et d'alimenter en données quantitatives les futures stratégies visant à minimiser l'impact environnemental et socio-économique des incendies de forêt au Canada. La thèse s'articule en trois chapitres qui traitent à la fois d'aspects méthodologiques et de reconstitutions quantitatives du climat au cours de l'Holocène

Dans un premier chapitre, nous comparons les résultats de deux fonctions de transfert, la fonction de transfert Est canadienne modifiée de Larocque (2008) et la fonction de transfert canadienne (Fortin et al. 2015) appliquées aux assemblages de Chironomidae du *Lac Aurélie* situé dans la forêt boréale au centre du Québec (Jamésie, Canada) afin de retenir la meilleure reconstitution des paléotempératures.

Dans un deuxième chapitre toujours méthodologique, nous présentons les résultats du *Lac Lili* sur des assemblages de Chironomidae. Le *Lac Lili* situé dans la forêt boréale à l'ouest du Québec (Jamésie, Canada), étant un lac peu profond, il offre l'occasion de tester la pertinence d'une telle approche dans ce genre de milieu à forte contrainte locale vis-à-vis des fluctuations bathymétriques.

Le troisième chapitre présente une approche croisée Chironomidae/pollen pour augmenter la confiance des reconstitutions quantitatives des paléotempératures afin de produire la meilleure courbe climatique de synthèse régionale. Ce chapitre a permis d'ouvrir une discussion générale sur les périodes et évènements climatiques clés qui ont ponctué l'Holocène.

Pour conclure, une synthèse portée sur les relations potentielles existantes entre le régime des feux et les conditions climatiques a été menée afin de répondre à la question suivante : *les températures estivales influencent-elles à elles seules directement les changements du régime des feux dans l'ouest du Québec ?*

0.3 Région d'étude : la pessière à mousses de l'Ouest de la Jamésie

La forêt boréale canadienne s'étend de Terre-Neuve jusqu'à la frontière de l'Alaska, globalement entre les 45^{e} et 145^{e} degrés de longitude ouest, et les 45^{e} et 60^{e} degrés de latitude nord. Représentant 30 % de la forêt boréale mondiale, elle se distingue par des assemblages mixtes de conifères et de feuillus au sud, et des assemblages majoritairement dominés par différentes espèces conifériennes plus au nord (Bergeron 2000).

Au Québec, les paysages naturels sont le résultat d'une dynamique de végétation complexe généralement lente, consécutive au dernier retrait de l'inlandsis Laurentidien (11 700 à 8200 ans AA) (Walker et al. 2012). Les derniers lambeaux de glaces ont disparu du centre de la péninsule du Québec-Labrador vers 6000 ans AA (Payette, 1993; Dyke 2004). La flore qui a suivi le retrait du glacier s'est enrichie dans le temps en constituant des associations diverses structurées par les modifications climatiques et l'incidence des perturbations naturelles (Richard, 1995; Richard et Grondin 2009).

Les lacs faisant l'objet de cette thèse sont situés dans la région la Jamésie (ouest du Québec, Canada), un territoire de 350 000 km^2 localisé entre les 49^e et 55^e degrés de latitude nord au nord-ouest du Québec (Fig. 0.3). Deux lacs ont été étudiés.

Le *Lac Aurélie* (*nom non officiel* ; 50°25'12''N ; 74°13'47''O), situé à 440 m d'altitude, est localisé au sud-est de cette région, à 66 km au nord de la ville de Chibougamau. Il est d'une superficie d'un hectare et sa profondeur d'eau maximale est d'environ 10 m. Il est situé dans la plaine du lac Mistassini à l'intérieur du domaine bioclimatique de la pessière à mousses de l'ouest (Saucier et al. 2009). Le couvert forestier repose sur des dépôts de surface tels que du till, de l'argile et parfois du sable. La végétation est dominée par des peuplements forestiers d'épinette noire (*Picea mariana* Mill.) et de pin gris, (*Pinus banksiana* Lamb.) (Blouin et Berger 2005). La température moyenne annuelle de la station météorologique la plus proche (Chapais 2 : 1971–2000) est de 0.0 ± 1.3 °C avec une moyenne du mois le plus chaud (août) de 14.9 ± 1.4 °C. Les précipitations moyennes annuelles sont de 660 mm (Environnement Canada 2017).

Le *Lac Lili* (*nom non officiel* ; 49°10'25.501''N ; 79°22'26.931''O) est localisé au sud-ouest de la Jamésie, à 110 km au nord de la ville de Rouyn-Noranda en Abitibi-Témiscamingue à une altitude de 320 m (Fig. 0.3). Il est d'une superficie de 10 ha et sa profondeur maximale d'eau est d'environ 1,40 m. Le *Lac Lili* est situé dans la plaine du lac Matagami à l'intérieur du domaine bioclimatique de la pessière à mousses de l'Ouest, à la limite actuelle des forêts boréales et mixtes (Saucier et al. 2009). Les forêts sont constituées par des peuplements de peuplier faux-tremble (*Populus tremuloides* Michx.), d'épinette noire et de pin gris (Blouin et Berger 2005). La température moyenne annuelle de la station météorologique la plus proche (La Sarre : 1971-2000) est de 0.7 ± 2.2 °C. Celle du mois d'août est de 15.2 ± 1.1 °C. Les précipitations moyennes annuelles sont de 670 mm (Environnement Canada 2017).

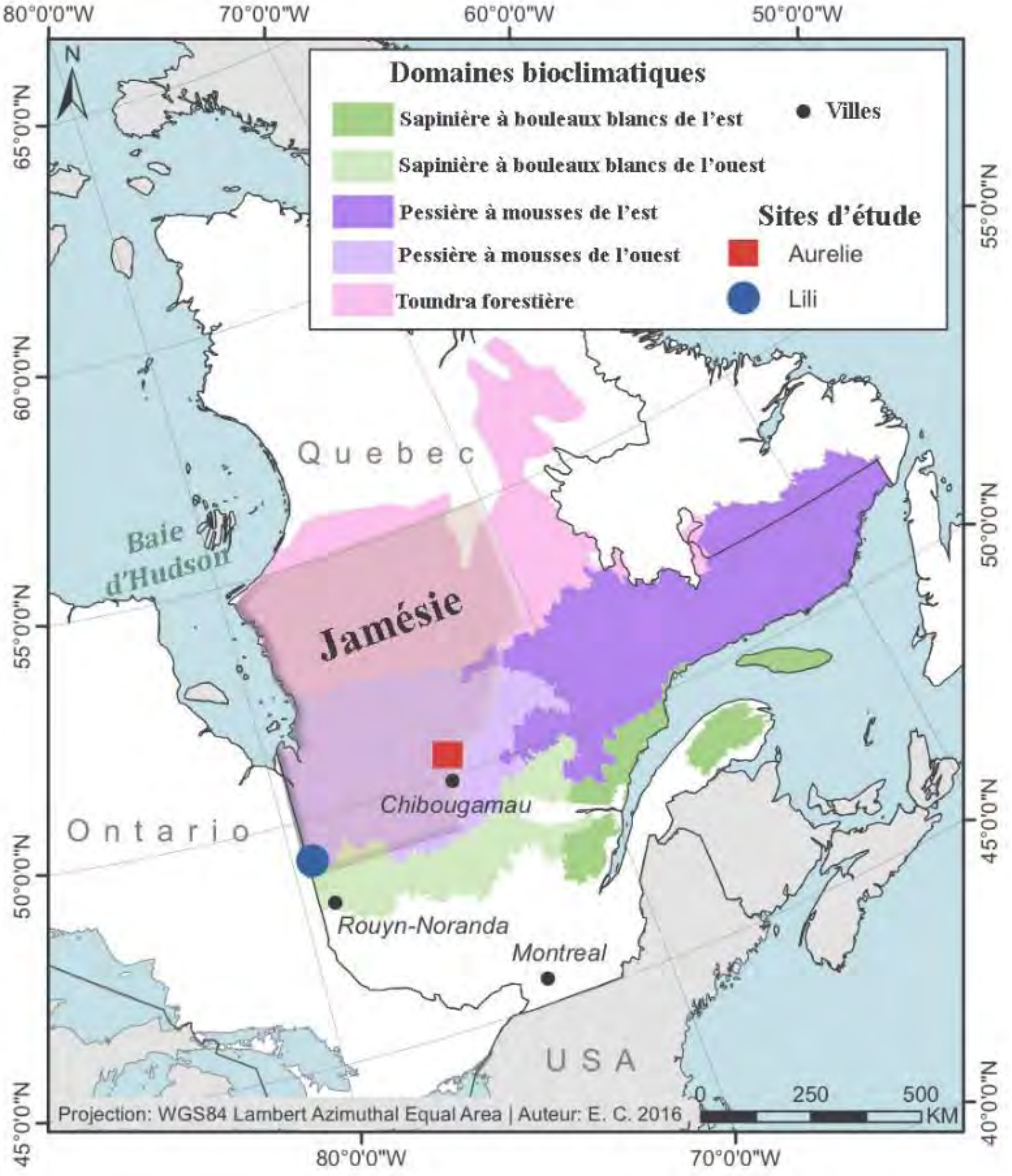

Figure 0.3Localisation des sites d'étude : *Lac Aurélie* et *Lac Lili* dans le domaine bioclimatique de la pessière à mousses de la Jamésie (région boréale de l'ouest du Québec).

CHAPITRE I

MAJOR POSTGLACIAL SUMMER TEMPERATURE CHANGES IN THE CENTRAL CONIFEROUS BOREAL FOREST OF QUEBEC (CANADA) INFERRED USING CHIRONOMID ASSEMBLAGES

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1.1 Abstract

Chironomid head capsules preserved in lake sediments were used to reconstruct 8200 years of summer temperatures in the boreal forest of northeastern Canada. Two training sets were used derived from Canadian and Eastern Canadian transfer functions. Both models reconstructed similar climate patterns, but the Canadian model provided temperatures generally 2-3 °C colder than the Eastern Canadian model. Three main thermal changes inferred by chironomids were: (i) the Holocene Thermal Maximum, which occurred between 8 and 5 k cal a BP, with inferences generally warmer than today's temperatures, maximum temperatures between 8–6.5 k cal a BP, and an average of +0.9 °C; (ii) the Medieval Climate Anomaly around 1.1–1.2 k cal a BP with an amplitude of +0.7 °C; and (iii) a colder period reconstructed between the 14th and 19th centuries, corresponding to the Little Ice Age, with summer temperatures on average -0.5 °C lower than the climate normal. For each of these three climatic events, the timing and the amplitude of changes were similar with other published regional, North American, and Northern Hemispheric records.

1.2 Résumé

Les capsules céphaliques des Chironomidae préservées dans les sédiments lacustres ont été utilisées pour reconstituer les températures estivales de la forêt boréale du Nord-Est canadien sur 8200 ans**.** Deux modèles (Canada et Est Canada) permettent de reconstituer les mêmes patrons climatiques mais le modèle canadien propose des températures généralement plus froides de 2-3 °C que le modèle Est canadien. Trois changements thermiques principaux sont mis en évidence par les Chironomidae : (i) le Maximum Thermique de l'Holocène, qui apparait entre 8000 et 5000 ans AA avec des inférences généralement plus chaudes que les températures actuelles, les températures maximales étant entre 8000 et 6500 ans AA avec une moyenne de +0,9 °C ; (ii) l'Anomalie Climatique Médiévale aux environs de 1100–1200 ans AA avec une amplitude de +0,7 °C ; and (iii) une période plus froide reconstituée entre le 14ème et le 19ème siècles, correspondant au Petit Âge Glaciaire, avec des températures estivales plus basses que les normales climatiques (-0,5 °C en moyenne). Pour chacun de ces trois événements climatiques, la période et l'amplitude des changements sont similaires avec des enregistrements régionaux, nord-américains et ceux de l'Hémisphère Nord disponibles.

1.3 Introduction

Paleoclimatic records covering the Northern Hemisphere are still too sparse to obtain a precise representation of past climate change (Naulier et al., 2015). For example, the amplitude and duration of the Medieval Climate Anomaly (hereafter MCA) are still under debate (Esper and Frank, 2009; Mann and Jones, 2003; Viau et al., 2006). The MCA has been characterized by notably warmer temperatures between ~950 and 1.2 k years AD over a large part of the North Atlantic, in Southern Greenland, the Eurasian Arctic, and parts of North America (Lamb, 1965). However, the amplitude, location, and its extent are still undefined for most parts of the Northern Hemisphere.

Another period of concern in North America is the Holocene Thermal Maximum (HTM). In Canada, the HTM seems to have varied between shorter (7 to 5 k cal a BP) and longer (10 to 3 k cal a BP) durations and its amplitude was different depending on the location (Renssen et al., 2012). Thus, it is impossible to strictly define these periods of interest in North America since quantitative long-term data are missing in several regions.

Climate models need quantitative data to be able to accurately predict future ecosystem functioning. Proxy-climate based reconstructions must be realistic and reliable, and if possible, they should be validated by independent climate reconstructions from other proxies (Birks, 2003). Climate (temperature, precipitation) records from biological proxies such as pollen and chironomids preserved in lacustrine deposits allow adequate long-term information to quantify past climatic variability (Heiri et al., 2015; Larocque-Tobler et al., 2012).

Chironomids (Insecta: Diptera: Chironomidae) have been shown to generate high-resolution independent air temperature records due to their capacity to respond rapidly to climatic fluctuation with their short generation time and the ability of winged adults to move readily from site to site (Larocque-Tobler et al., 2015; Walker and Mathewes, 1987). The head capsule of the chironomid larvae is made of chitin, a substance resistant to degradation, thus allowing the larval exoskeletons to be preserved for thousands of years. The distribution of chironomids has been shown to be influenced by air/water temperatures (Walker and Mathewes, 1987). In addition, with the help of transfer functions (Birks, 1998), they can record small amplitude summer temperature changes (Brooks, 2006; Larocque-Tobler et al., 2015). For example, when comparing instrumental data to chironomid-inferred temperatures, the differences were on average 0.75 °C in a Polish lake (Larocque-Tobler et al., 2015) and 0.65 °C in a Swiss lake (Larocque et al., 2009).

In the boreal region of northeastern Canada, Holocene quantitative reconstructions of past climate change are mostly based on pollen analysis using the modern analogue technique (Viau and Gajewski, 2009; Viau et al., 2012). Paleoclimatic data are available but with contradictory information. For instance, according to Viau and Gajewski (2009) and Viau et al. (2012), the MCA was cooler than the present-day (1961-1990 AD) while warmer conditions were reconstructed in other parts of the country (Naulier et al., 2015).

Thus, doubts persist regarding the recording of this climate anomaly in northeastern Canada, as well as for the other major climate changes, notably those of weak amplitude, such as the Little Ice Age (hereafter LIA). Consequently, it is important to increase our knowledge of millennial time-scale temperature fluctuations using proxies able to capture low amplitude climatic fluctuations. In this context, the main goal of this study is to present a new Holocene mean August air temperature reconstruction in the coniferous boreal forest of northwestern Quebec (Canada) based on subfossil chironomid assemblages, allowing a discussion of the duration and amplitude of the HTM, MCA, and LIA for this region.

1.4 Methods

1.4.1 Study area and site

The study site is located in central Quebec (Fig. 1.1), 66 km north of the town of Chibougamau. “*Lac Aurélie*” (unofficial name; 50°25’12” N; 74°13’47” W; 440 m a.s.l.) covers an area of 1 ha and its maximum water depth (10 m) is in the central part of the lake.

The lake is located in the black spruce – feather moss bioclimatic domain (Saucier *et al.*, 2009) dominated by black spruce (*Picea mariana* Mill.) and jack pine (*Pinus banksiana* Lamb). The mean annual temperature from the closest meteorological station [Chapais 2: 1971-2000, 49°47’N; 74°51’W] is 0.0 ± 1.3 °C with an August temperature average of 14.9 ± 1.4 °C. Annual and August precipitation averages are 961 and 105 mm, respectively (Environnement Canada, 2017). Further details about the study site characteristics can be found in El-Guellab *et al.* (2015).

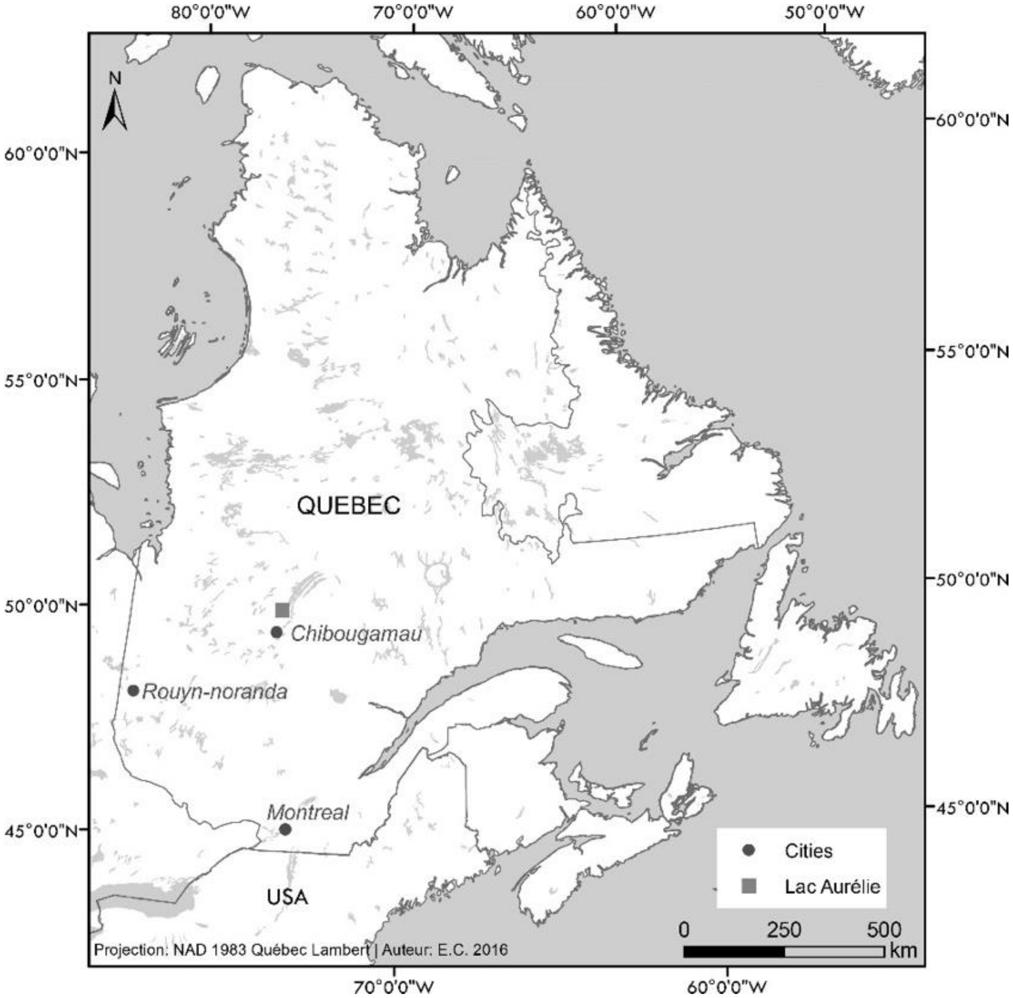


Figure 1.1 Location map of the study lake "*Lac Aurélie*" in central Quebec, Canada.

1.4.2 Coring, LOI analysis, and chronology

Two overlapping sediment cores (providing a continuous record) were taken in March 2010 on a frozen surface at the centre of the lake using a modified Livingstone-type square-rod piston corer (100 × 5 cm) (Wright *et al.*, 1984). Sediments were covered in polyurethane and aluminium foil for transportation to the laboratory and preserved at 4 °C before they were sliced for analyses. The water-sediment interface was collected using a Kajak-Brinkhurst (KB) gravity corer (Glew, 1991). Sub-samples (1 cm^3) were used for measuring the organic matter content by loss-on-ignition (LOI) at 550 °C for 4h (Heiri *et al.*, 2001). Radiocarbon dates (calibrated at 2 sigma ranges based on the Intcal13.14C data set (Reimer *et al.*, 2013)) and chronology have already been published by El-Guellab *et al.* (2015). A summary is presented in Table 1.1.

Table 1.1 Radiocarbon dates at different depths. Dates were obtained from terrestrial plant macroremains. Chronology (not show in this study) was obtained from accelerated mass spectrometry (AMS) and has already been published in El-Guellab *et al*. (2015).

Lab code	Depth (cm)	^{14}C age (a BP)	Calibrated ^{14}C age ranges (cal a BP; 2σ)	Materials
Poz-35983	43-44	2870 ± 30	3007 (2879-3136)	Plant macroremains
Poz-35984	111-112	3990 ± 35	4443 (4319-4568)	Plant macroremains
Poz-36014	163-164	4750 ± 35	5457 (5329-5586)	Plant macroremains
Poz-36016	220-221	6140 ± 40	7047 (6931-7163)	Plant macroremains
Poz-36017	236-237	6490 ± 40	7396 (7317-7476)	Plant macroremains
Poz-36018	326-327	7460 ± 50	8279 (8185-8373)	Plant macroremains

Poz, Poznan radiocarbon Laboratory.

1.4.3 Chironomid analysis

A total of 180 samples were analysed (see supplementary data) at a temporal resolution varying between ca. 5 and 165 years (ca. 45 years in average). Chironomid head capsules were extracted from 2 cm^3 subsamples by soaking the samples overnight in 10 % KOH. The subsamples were then water-rinsed through a sieve of 100 µm. The remnant was poured into a Bogorov tray and observed under a Leica stereomicroscope at 20× magnification. Individual subfossil head capsules were picked with fine forceps and mounted on a microscope slide in a drop of Hydromatrix.

Previous studies suggested that at least 50 head capsules should be mounted for temperature reconstructions (Heiri and Lotter, 2010; Larocque *et al.*, 2001), but samples larger than 30 head capsules can also provide inferences below the error of the model (RMSEP) (Larocque *et al.*, 2009; Larocque-Tobler *et al.*, 2016). Taxonomic identification was made using a Motic microscope at 400-1000× magnification following the taxonomic keys of Brooks *et al.* (2007); Larocque and Rolland (2006); Oliver and Roussel (1983); and Wiederholm (1983).

1.4.4 Statistical analysis, palaeoecological diagrams, and constrained zonation

A chironomid percentage diagram was drawn using C2 software (Juggins, 2003). Detrended correspondence analysis (DCA) was performed using ade4 and vegan packages from R v3.2.2 (Borcard *et al.*, 2011) on the n (number of samples) by p (number of taxa) chironomid matrix of percentages. Data were square-root transformed to stabilize the variance. Rare taxa (present in only one sample or with a relative abundance always < 2 %) were removed from the analysis. The length of the first DCA-axis determines whether the distribution of the data set along this axis is linear or unimodal (Borcard *et al.*, 2011). Here, a gradient of 1.95 standard deviation units (SD) was obtained, suggesting linear techniques such as PCA were appropriate on our data set.

A principal component analysis (PCA) was then performed using C2 on the same data matrix used for the DCA. This method was coupled with a constrained sum-of-squares cluster analysis (CONISS) using the program ZONE version 1.2 (Juggins, 1991) to highlight major changes in assemblage composition (Grimm, 1987). The optimal number of significant zones created was determined by a broken stick model (Bennett, 1996).

Percentage diagrams of warmer-than-today and colder-than-today taxa were made using the temperature optimum (Table 1.2) for each taxon obtained using the Eastern Canadian calibration set (see below). Percentages of eutrophic, oligo-mesotrophic, littoral, and profundal taxa were calculated using ecological descriptions from (Brooks *et al.*, 2007). To better understand changes in the lake's conditions, ratios using these percentages were calculated. A >1 eutrophic/oligo-mesotrophic ratio suggests a tendency towards eutrophic conditions, whereas a ratio <1 suggests a tendency towards oligo-mesotrophic conditions. A littoral/profundal ratio >1 indicates a dominance of littoral taxa and a dominance of profundal taxa if it is <1.

Table 1.2 Occurrence of taxa in the sediment of *Lac Aurélie* (total of 179 samples). Comparison of temperature optima obtained with WA for the three transfer functions: (a) Eastern Canadian transfer function. (b) Canadian transfer function (Fortin *et al.,* 2015) and temperature categories.

Taxa identified in sediment	Occurrence in sediment	Optima		Category	
		(a) Eastern Canada	(b) Canada	Colder than today (13.5 °C)	Warmer than today (13.5 °C)
Ablabesmyia spp	131	14.7	4.5		X
Allopsectrocladius spp	33	14.7	10.4		X
Brillia spp	2	14.3	9.2		X
Chaetocladius spp	34	13	9.2	X	
Chironomus spp			9.7		
Chironomus anthracinus-type	164	12.5	*merged into Chironomus*	X	
Chironomus plumosus-type	147	14	*merged into Chironomus*		X
Cladopelma lateralis-type	75	13.1		X	
Cladotanytarsus mancus-type	87	12.2	10.2	X	
Constempellina spp	34	14	9.3		X
Corynocera oliveri-type	45	10.4	11.2	X	
Corynoneura spp	43	8.7	8.3	X	
Cricotopus/ Orthocladius spp			7.9		
Cricotopus spp	96	11.6	*merged with Orthocladius*	X	
Cryptochironomus spp	48	14.7	*not in model*		X
Dicrotendipes nervosus-type	119	14	11.3		X
Einfeldia spp	11	12.9	10.0	X	
Endochironomus tendens-type	54	15.2	11.8		X
Glyptotendipes pallens-type	36	14.4	11.1		X

Suite

Heterotrissocladius spp			10.9		
H. grimshawi-type	17	12.1	7.7	X	
H. marcidus-type	17	11.8	*merged in Heterotrissocladius*	X	
H. subpilosus-type	6	8.3	*merged in Heterotrissocladius*	X	
Lauterborniella spp	60	19.8	13.9		X
Limnophyes spp	19	15.6	13.4		X
Mesocricotopus spp	8	10	8.6	X	
Micropsectra spp			6.2		
Micropsectra bidentata-type	19	13.8	*merged in Micropsectra*		X
Micropsectra insignilobus-type	44	13.5	*merged in Micropsectra*	X	
Micropsectra radialis-type	47	9.4	*merged in Micropsectra*	X	
Microtendipes pedellus-type	130	13.3	*not in model*	X	
Nanocladius spp	3	11.7	11.0	X	
Orthocladius spp	39	12.8	10.8	X	
Pagastiella spp	26	14.2			X
Parachaetocladius spp	2	14.5	11.2		X
Parachironomus varus-type	5	*not in model*	*not in model*		
Paracladius spp	1	7.5	10.4	X	
Paracladopelma spp	2	13.7	4.5		X
Paracricotopus spp	1	11.1		X	
Parakiefferiella spp	40	10.7	9.6	X	
Paratanytarsus spp	96	12.3	8.4	X	
Paratendipes nudisquama-type	13	*not in model*	*merged in Tanytarsina*		
Pentaneurini spp	83	14.4	11.9		X
Phaenopsectra spp	9	16.8	9.3		X

Suite

Polypedilum nubeculosum-type	101	17.1	11.0		X
Procladius spp	168	13.9	11.0		X
Psectrocladius septentrionalis-type	55	13.1	9.5	X	
Psectrocladius sordidellus-type	141	12.2	10.6	X	
Pseudochironomus spp	63	*not in model*	10.9		
Pseudosmittia spp	7	13.3	11.9	X	
Rheocricotopus spp	1	*not in model*	8.5		
Sergentia coracina-type	20	25.9	9.1		X
Smittia spp	5	11.6	7.1	X	
Stempelinella spp	21	15.8	*not in model*		X
Stenochironomus spp	2	*not in model*	10.6		
Stictochironomus spp	10	7.9	*not in model*	X	
Tanytarsina			8.3		
Tanytarsus lugens-type	145	13	*merged in Tanytarsina*	X	
Tanytarsus mendax-type	145	13.6	*merged in Tanytarsina*		X
Tanytarsus pallidicornis-type	74	13.7	*merged in Tanytarsina*		X
Tanytarsus spp	173	12.5	*merged in Tanytarsina*	X	
Tanytarsus glabrescens-type	95	14.6	*merged in Tanytarsina*		X
Tanytarsus with spur on antenna	44	14.3	*merged in Tanytarsina*		X
Thiennemaniella spp	16	9.9		X	
Thiennemanyia spp	3	*not in model*	9.9		

Suite

Zalutschia mucronata-type	49	13	*not in model*	X
Number of taxa not included in the training set		6	19	
Maximum temperature (°C)		25.9	13.9	
Minimum temperature (°C)		6.2	4.5	

1.4.5 Transfer functions

Two chironomid-based transfer functions were used to reconstruct mean August air temperature and evaluate their reliability in inferring past climate changes. The Eastern Canadian transfer function was first published by Larocque (2008) and was modified. Two lakes were added, and 11 lakes had their temperature measurements changed to mean August air temperature (Lakes A to H) as the earlier version of the calibration possessed only punctual measurements.

In the new Eastern Canadian model, the mean August temperature varied from 3 °C to 21 °C (instead of 27 °C) for a temperature gradient of 18 °C. The new data will be available on the NOAA website once the paper is published. The calibration set comprises 75 lakes and 79 taxa. The WAPLS 999-bootstrap transfer function with two components yielded a correlation coefficient (r^2_{boot}) of 0.85, a rooted mean-square error of prediction (RMSEP) of 1.67 °C, and a maximum bias of 3.05 °C.

The second transfer function combined data sets from Canada (Fortin *et al.*, 2015). It comprises 485 lakes and 78 taxa. The mean August temperatures varied from -0.3 to 15.7 °C (gradient = 16 °C). It contains 52 of the 75 lakes in the Eastern Canadian transfer function of (Larocque, 2008). The correlation coefficient (r^2_{boot}) is 0.73, the RMSEP is 1.8 °C, and the maximum bias is 2.9 °C (Fortin *et al.*, 2015).

To verify if the transfer functions could be applied to the fossil assemblages of *Lac Aurélie*, we estimated if fossil assemblages had modern analogues using the minimum distance to modern assemblages (Overpeck *et al.*, 1985). If the minimum distance was within the 1st to 5th percentiles, the assemblages were considered as having "good analogues". If the distance was above the 20th percentile, the samples were considered as having no analogues.

Furthermore, the goodness-of-fit was calculated by passively adding downcore samples of *Lac Aurélie* into a CCA analysis of the Eastern Canadian transfer function samples constrained by temperature (Heiri and Lotter, 2010), using the Canoco 4.5 program. If the distance between downcore and transfer function samples were above the 10th percentile, the downcore sample was characterized as not having a good fit to temperature (Andrén *et al.*, 2015).

Thirdly, a percentage of the fossil taxa present in the training set was calculated. A reconstruction should be considered adequate if samples have high percentages of fossil taxa present in the transfer function. Finally, to interpret and compare the chironomid-inferred temperature with other palaeoecological climate records, a LOESS regression (span= 0.2) was applied.

1.5 Results

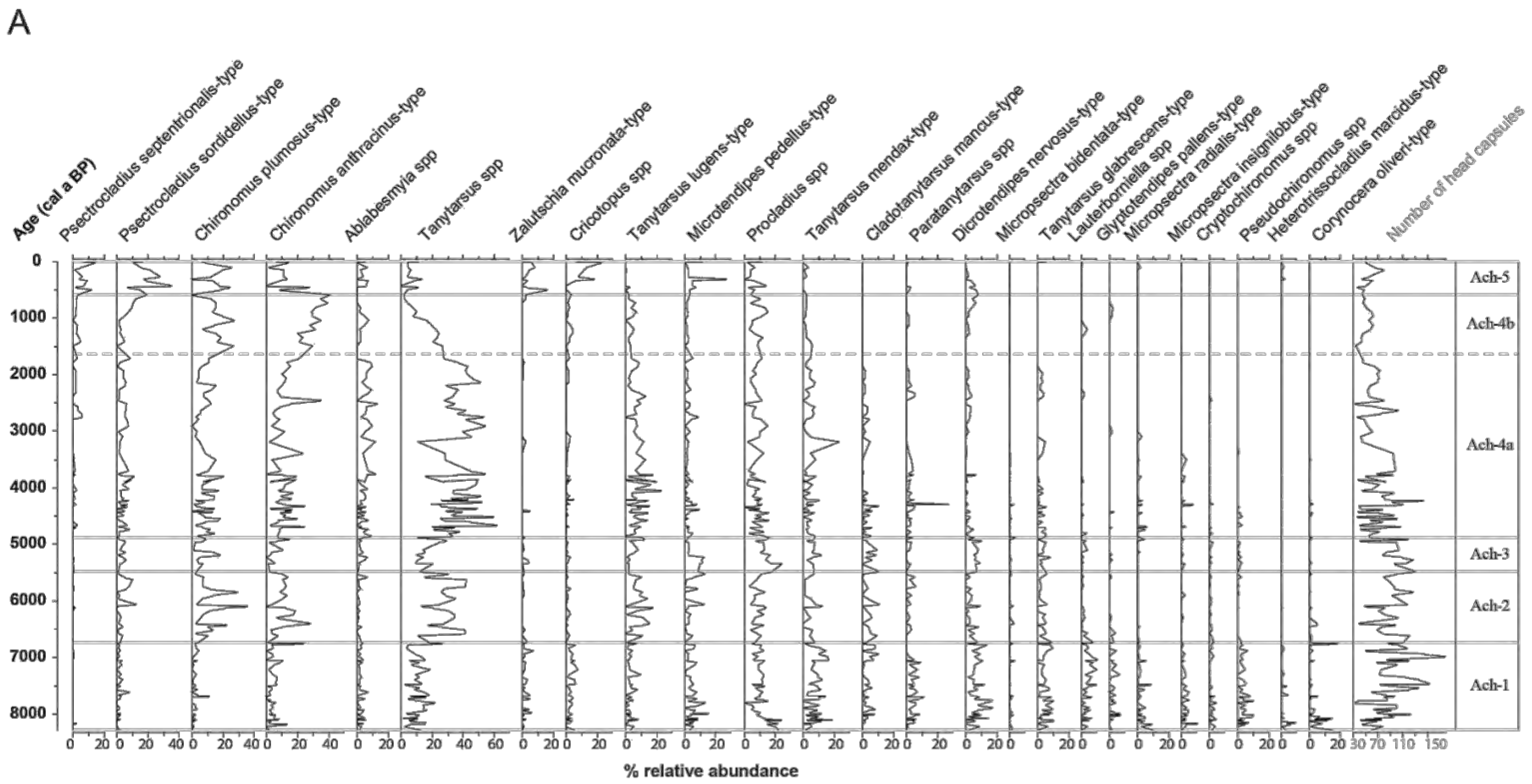
1.5.1 Organic matter content

The 335 cm long was composed entirely composed of gyttja. At the bottom of the core (326-327 cm), an age of ca. 8.2–8.4 k cal a BP (2 sigma range) was yielded (Table 1.1).

The uppermost 22 cm of the sediment was completely used for biological analysis, thus LOI analysis could not be performed for this section of the core. Before ca. 7.7 k cal a BP, the percentages of organic matter were below 60. Between ca. 7.7 and 7.8 k cal a BP, the percentages were very low (below 20 %) and the sediment was composed of a sandy layer.

1.5.2 Chironomid analysis

Of the 180 samples analyzed, one (48 cm) did not have any head capsules. Fifteen samples with less than 30 head capsules were merged for a total of 164 samples. Of those 164, 35 samples had head capsule numbers between 32 and 49.5, thus 80 % of the samples had more than 50 head capsules. In total, 63 taxa were identified to genus or species morphotypes. PCA axes 1 and 2 had eigenvalues of 0.25 and 0.11 respectively. The 25 most abundant taxa (percentages reaching at least 10 %) are shown in Fig. 1.2A.



A
Age (cal a BP)
Psectrocladius septentrionalis-type
Psectrocladius sordidellus-type
Chironomus plumosus-type
Chironomus anthracinus-type
Ablabesmyia spp
Tanytarsus spp
Zalutschia mucronata-type
Cricotopus spp
Tanytarsus lugens-type
Microtendipes pedellus-type
Procladius spp
Tanytarsus mendax-type
Cladotanytarsus mancus-type
Paratanytarsus spp
Dicrotendipes nervosus-type
Micropsectra bidentata-type
Tanytarsus glabrescens-type
Lauterborniella spp
Glyptotendipes pallens-type
Micropsectra radialis-type
Micropsectra insignilobus-type
Cryptochironomus spp
Pseudochironomus spp
Heterotrissocladius marcidus-type
Corynocera oliveri-type
Number of head capsules
0
1000
2000
3000
4000
5000
6000
7000
8000
Ach-5
Ach-4b
Ach-4a
Ach-3
Ach-2
Ach-1
0 20 0 20 40 0 20 40 0 20 40 0 20 0 20 40 60 0 20 0 20 0 20 0 20 0 20 0 20 0 20 0 20 0 20 0 0 20 0 0 0 20 0 0 0 20 0 0 20 30 70 110 150
% relative abundance

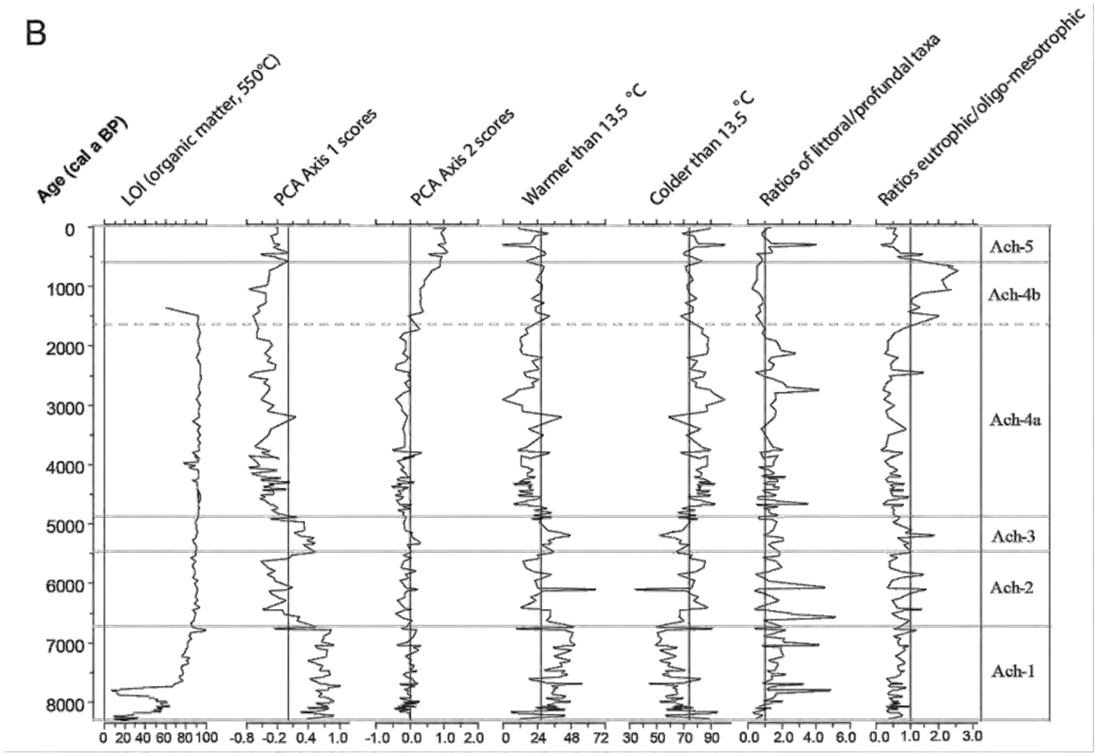


Figure 1.2**A.** Chironomid stratigraphy of the 26 most abundant taxa (percentages reaching at least 10 % in more than 4 samples) and the number of head capsules identified in each sample. **B.** Organic matter content (loss-on-ignition at 550 °C) is illustrated. PCA axis 1 and 2 are the sample scores of the first and second axis in a principal component analysis. The vertical line is the PCA 0 score. The warmer- and colder- than 13.5 °C taxa followed their sums of percentages in Table 1.2. Profundal and littoral taxa were defined using Brooks *et al.* (2007). Ratios littoral/profundal and eutrophic/oligo-mesotrophic taxa were calculated (see methods), the baselines are 1. Ratios >1 suggest oligo-mesotrophic conditions and a dominance of littoral over profundal taxa.

Five significant zones (Ach-1 to Ach-5) were numerically identified (Fig. 1.2A). In zone Ach-1 (ca. 8.3–6.7 k cal a BP), the PCA axis 1 scores were positive. This zone was dominated by taxa with temperature optima above 13.5 °C (Fig. 1.2B) such as *Dicrotendipes nervosus*-type, *Procladius* spp, *Tanytarsus mendax*-type, *Polypedilum nubeculosum*-type, and *Endochironomus tendens*-type. Colder-than-today taxa (Fig. 1.2B) had percentages reaching 90 at the very beginning of the record (8.2-8.0 k cal a BP) and many of the cold indicators such as *Corynocera oliveri*-type, *Micropsectra radialis*-type, and *Heterotrissocladius marcidus*-type (Fig. 1.2A) had their highest percentages of the record in the first few samples of this zone. The lake was possibly oligotrophic during this zone, as the ratio of eutrophic/oligo-mesotrophic taxa being was below 1 (Fig. 1.2B). Littoral taxa dominated after 8.1 k ca. a BP.

In zone Ach-2 (ca. 6.7–5.5 k cal a BP), PCA axis 1 scores were below 0 (Fig. 1.2B). Warm indicators had percentages generally below average except in one sample at ca. 6.2 k cal a BP. *Tanytarsus* spp dominated the assemblages with percentages around 40 %. *Chironomus plumosus*-type, *C. anthracinus*-type, *T. lugens*-type, and *Procladius* spp were also well represented in the assemblages. Unstable conditions were identified by oscillating eutrophic/oligo-mesotrophic and littoral/profundal ratios being recorded (Fig. 1.2B).

Zone Ach-3 (ca. 5.5–4.9 k cal a BP) was characterized by PCA axis 1 scores above 0. The percentages of warm taxa were above average, and the assemblages were dominated by *D. nervosus*-type, *T. mendax*-type, *Procladius* spp, *P. nubeculosum*-type, *C. mancus*-type, and *Pseudochironomus* spp. The ratios of eutro/oligo-mesotrophic taxa were slightly below 1, suggesting mesotrophic conditions. Littoral taxa dominated.

In zone Ach-4 (ca. 4.9 k cal a BP – 0.6 k cal a BP), PCA scores were all below 0. This zone was divided into two subzones based on changes in taxa percentages and PCA axis 2 scores, which were above 0 after ca. 1.5 k cal a BP.

In subzone Ach-4a (ca. 4.9–1.7 k cal a BP), the percentages of warm taxa decreased below average, suggesting conditions colder than today. The dominant taxon was *Tanytarsus* spp, a taxon which is considered as a colder-than-today indicator. The lake had a tendency towards oligo-mesotrophy with ratios generally below 1. Littoral taxa dominated.

In subzone Ach-4b (1.7 k cal a BP–600 cal a BP), changes in PCA axis 2 scores were observed and the number of head capsules was generally between 30 and 70. Both cold and warm taxa were at average values, suggesting a slight climatic amelioration to warmer conditions. The main changes in taxa were the strong decrease in *Tanytarsus* spp percentages and the increase in both *Chironomus* types. These increases in *Chironomus* types were linked to sharp increases in eutrophic/oligo-mesotrophic ratios and decreases in littoral/profundal taxa (Fig. 1.2B), *Chironomus* types are considered as eutrophic and profundal taxa (Brooks *et al.,* 2007).

During zone Ach-5 (ca. 600 cal a BP–present), PCA axis 1 scores remained below 0 and PCA axis 2 scores continued to increase. Cold taxa were above average while warm taxa were below average, suggesting colder conditions. *P. sordidellus*-type, *P. septentrionalis*-type, *Zalutschia mucronata*-type, and *Psectrocladius* spp. *Cricotopus* spp dominated for the first time. Trophic conditions had a tendency towards oligo-mesotrophy with ratios below 1 and littoral taxa were dominant.

1.5.3 Chironomid-inferred temperature reconstructions

The temperature reconstruction patterns obtained by the two transfer functions are similar (Fig. 1.3). However, the Canadian transfer function provided estimates which were 2-3 °C colder than those of the Eastern Canadian model. The temperature anomalies obtained from the Canadian model were mostly inferred as colder than today, which does not fit with known climate patterns. The Eastern Canadian reconstruction was thus used to look at details of climate change.

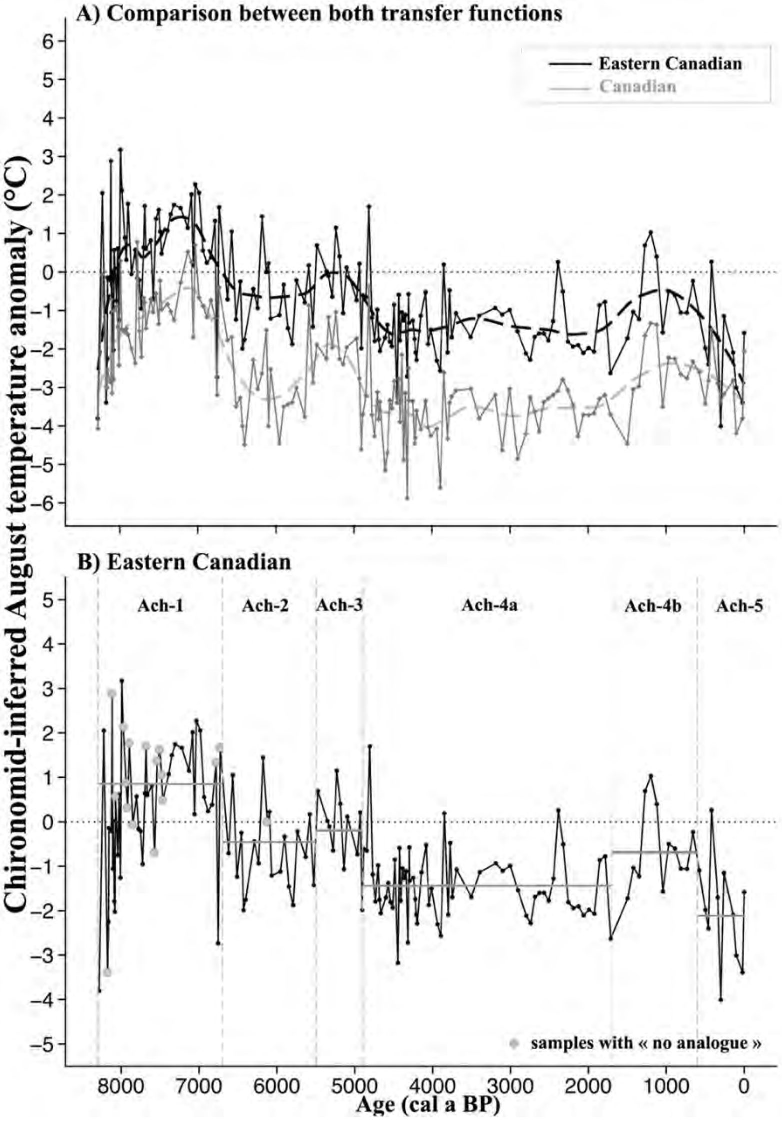


Figure 1.3 Chironomid-inferred August air temperature anomaly (°C) at *Lac Aurélie.* **A)** Comparison between the Eastern Canadian transfer function and the Canadian transfer function of Fortin *et al.* (2015). **B)** Details of the Eastern Canadian transfer function, which illustrate a more reliable record. The vertical lines indicate the zonation obtained from the chironomid stratigraphy (Fig. 1.2A). The horizontal bold lines indicate the average anomaly of the chironomid zones.

The PCA Axis 1 scores and inferred temperatures with the Eastern Canadian model had a significant correlation ($r_{Pearson}$= 0.62, $p<0.05$). Cold temperatures were recorded before 8 k cal a BP with an average anomaly of -0.8 °C (Fig. 1.3). Temperatures increased to reach a maximum around ca. 8 k cal a BP and remained warm until ca. 6.7 k cal a BP with an average anomaly of 0.9 °C.

During zone Ach-2 (ca. 6.7–5.5 k cal a BP), temperatures were generally colder than previously with an average anomaly of -0.5 °C. During zone Ach-3 (ca. 5.5–4.9 k cal a BP), the inferred temperatures were similar to today's temperature with average anomaly of -0.2 °C. In zone Ach-4, temperatures were colder today (-1.4 °C in average). Changes occurred at around 1.2–1.1 k cal a BP with an average anomaly of 0.7 °C, while the zone had colder than today temperature (-0.8 °C), in average. During zone Ach-5 (ca. 600 cal a BP–present) the average anomaly was -2.1 °C.

1.6 Discussion

1.6.1 Ecological interpretation

The first axis of the PCA could be interpreted as a climate gradient likely related to temperature; the correlation ($r_{Pearson}$) between PCA axis 1 scores and the temperature reconstruction was 0.62. Many taxa had higher temperature optima in the Eastern Canadian than those modelled with the Canadian transfer function (Table 1.2). Most of the colder than today indicators are similarly characterized in (Brooks *et al.*, 2007).

Changes in PCA axis 2 scores starting at ca. 1.5 k cal a BP with PCA axis 1 scores remaining below 0 suggest that temperature is not the only factor influencing the changes in chironomid assemblages through time. In our core, PCA axis 2 scores were correlated with the ratios of oligo-meso/eutrophic taxa and to the ratio of littoral/profundal taxa. The effects of nutrients and water depth on chironomids has been previously shown (Larocque *et al.*, 2006; Lotter *et al.*, 1997) and models to reconstruct both parameters were developed (Engels *et al.*, 2012; Langdon *et al.*, 2006). Most members of the *Tanytarsini* tribe being both littoral (except *T. lugens*-type) and eutrophic, their decrease starting at ca. 1.5 k cal a BP identify trophic levels and water depth as two of the main drivers of the observed ratios.

In zone 4b (1.5 k cal a BP), profundal taxa dominated (as suggested by ratios above 1), probably due to the increase in both types of *Chironomus*. These taxa have haemoglobin (Walshe, 1950), allowing them to survive short periods of oxygen depletion (Brooks *et al.*, 2007), suggesting that oxygen availability might have changed during this period. Percentages of *Polypedilum nubeculoseum*-type, associated with macrophytes, also increased during this time. Presence of macrophytes has been shown to influence chironomids (Langdon *et al.*, 2008) and lower oxygen levels have been recorded in lakes with a developed macrophyte community (Rose and Crumpton, 1996).

In zone 5, represented by a further increase in PCA axis 2 scores, the percentages of both *Psectrocladius* types and *Cricotopus* spp largely increased with *Pentaneurini* spp and *Ablabesmyia* spp. *Psectrocladius* is often associated with macrophytes (Brodersen *et al.*, 2001; Langdon *et al.*, 2008) and is acidophilic (Pinder and Morley, 1995), as pH is another factor affecting chironomids (Orendt, 1999). *Cricotopus, Ablabesmyia,* and *Zalutschia* spp are associated with vegetation (Brooks *et al.*, 2007), while *Zalutschia* spp and *Ablabesmyia* occurs in acidified lakes (Brooks *et al.*, 2007).

Based on the changes in the chironomid communities, macrophytes, changes in oxygen and pH might have influenced the chironomid assemblages since ca. 1.5 k cal a BP. However, low variability climate changes, such as the LIA, have also been reconstructed from our assemblages (see below), which suggests that, although other factors influenced the assemblages, the pattern of chironomid-inferred-temperature changes was still adequately reconstructed. Luoto and Nevalainen (2017) have shown that chironomids can reconstruct climate effectively even under the influence of eutrophication and pollution.

1.6.2 Reliability of the chironomid inferred temperature reconstructions

The Canadian transfer function of Fortin *et al.* (2015) has a very large number of lakes (435) and would, at first, be considered as the most suitable to reconstruct climate in a lake in the boreal forest of Quebec. However, only a few of these lakes have August temperatures above 14 °C and the residuals (Figure 4 in Fortin *et al.* (2015)) suggest that warmer temperatures will be underestimated. As *Lac Aurélie's* current August temperature is 15 °C, which is located at the end of the gradient of the Canadian transfer function, its present day temperature should possibly be underestimated with the model of Fortin *et al.* (2015).

If the temperatures were warmer in the past, the inferences would also be colder than expected. Furthermore, because the temperature gradient is relatively small (-0.3 to 15.7 °C) and contains mostly lakes with cold temperatures, the optimum for each taxon are relatively low (4.5 to 13.9 °C; Table 1.2), which explains why the reconstruction is 2-3 °C colder than the one obtained with the other training set. In addition, Fortin *et al.* (2015) merged certain taxa to a lower taxonomic level, as identified in some of the calibration sets. Consequently, this grouping could induce less realistic inferred temperature reconstructions. However, it should be remembered that the pattern of changes is very similar between each transfer function.

The Eastern Canadian transfer function (Larocque, 2008) is an extended version of the 52 lakes from Larocque *et al.* (2006) that was used in the Canadian model of Fortin *et al.* (2015). It contains a few lakes north (3 °C) and south (21 °C), thus increasing the temperature gradient (3-21 °C). Although it comprises fewer lakes (75) than the

Canadian transfer function, the increased gradient might provide more accurate optima. The temperature optima in the Eastern Canadian model vary between 7.5 and 20.5 °C (Table 1.2).

However, this training set does not include any lakes with August temperatures between 16.8 and 19 °C, temperatures which might have been experienced at *Lac Aurélie* in the past, thus many of the fossil samples did not resemble those found in the training set. To obtain the best coverage (larger gradient and lakes evenly distributed along the gradient) of possibly experienced temperatures, lakes with temperatures between 16 and 19 °C should be added. Unfortunately, this data was not available as lakes were not yet sampled within this range.

We assume that the inferences were possibly colder than they should be. However, as Weighted Average Partial Least Squares is based on temperature optima for each taxon found in the fossil record, it is important to include the most fossil taxa possible in the training set. This is the case in the fossil record of *Lac Aurélie*, with all samples having more than 83 % of their taxa found in the training set lakes, and 133 of 179 samples (74 %) having fossil taxa represented in the training set above 95 %.

A problem, which needs to be considered in evaluating the accuracy of a model is the absence of modern analogues. Seventeen of the 164 samples had no modern analogues (Fig. 1.3). These samples were mainly in the lower portion of the sedimentary core (<6.7 cal a BP). Nevertheless, WA-PLS methods perform well in non-analogue situations because the estimates are based on modelled taxon temperature optima assuming unimodal responses to temperature (Birks, 1998). This allows the model to infer temperatures outside the range of the calibration set. In these cases, comparison with other regional paleoclimate records is essential to evaluate the reliability of the temperature reconstruction.

The applicability of the Eastern Canadian transfer function to the *Lac Aurélie* samples was further assessed using goodness-of-fit to temperature. None of the *Lac Aurélie* samples was above the 10th percentile, thus we assume that all downcore samples had good fit to temperature.

1.6.3 8.2 cal a BP cold event and Holocene Thermal Maximum (HTM)

After the retreat of the last remnant of the glacier (Dyke, 2004), the chironomids in *Lac Aurélie* inferred temperatures 2-3 °C colder than today in three samples around ca. 8.2 k cal a BP (8282 to 8175 cal a BP). This might represent the so-called 8.2 k cal a BP event (Alley *et al.*, 1997). The Greenland ice core record indicated that temperatures cooled by ca. -3.3 °C and lasted 150 cal. years (Kobashi *et al.*, 2007; Thomas *et al.*, 2007). Our results correspond to the ice core record in both timing (ca. 110 years, limited by our sampling technique) and amplitude of change (-3 °C).

The HTM lasted between 11 to 5 k cal a BP in the northern Hemisphere, but with many regional variations (Renssen *et al.*, 2009). Based on pollen data from sites in northwestern Quebec, Viau and Gajewski (2009) highlighted warm temperatures between 6 and 2 k cal a BP. Our results show higher than or similar to today summer temperatures between ca. 8.3 and 4.9 k cal a BP, but with a sharp decline around ca. 6.5 k cal a BP. Our reconstruction corresponds to paleoclimate records obtained from the Arctic (GISP2 ice core; (Kobashi *et al.*, 2010), from pollen across northeastern America (Viau *et al.*, 2006), and from a chironomid record on Baffin Island (Axford *et al.*, 2009) (Fig. 1.4A).

The increase in temperature (+2-3 °C in 3 samples at the beginning of the record) was similarly recorded in the ice core (+3 °C) and from Baffin Island (+4 °C) (Fig. 1.4A). However, the combined records of pollen registered an increase in temperature of about only 1 °C (Viau *et al.*, 2006). This could be due to the merging of various fossil records across northeastern Canada. Stacking of records of different amplitudes at many locations, as per Viau *et al.* (2006), decreases the average variation. Another reason for differences in amplitude is the use of different models to infer climate.

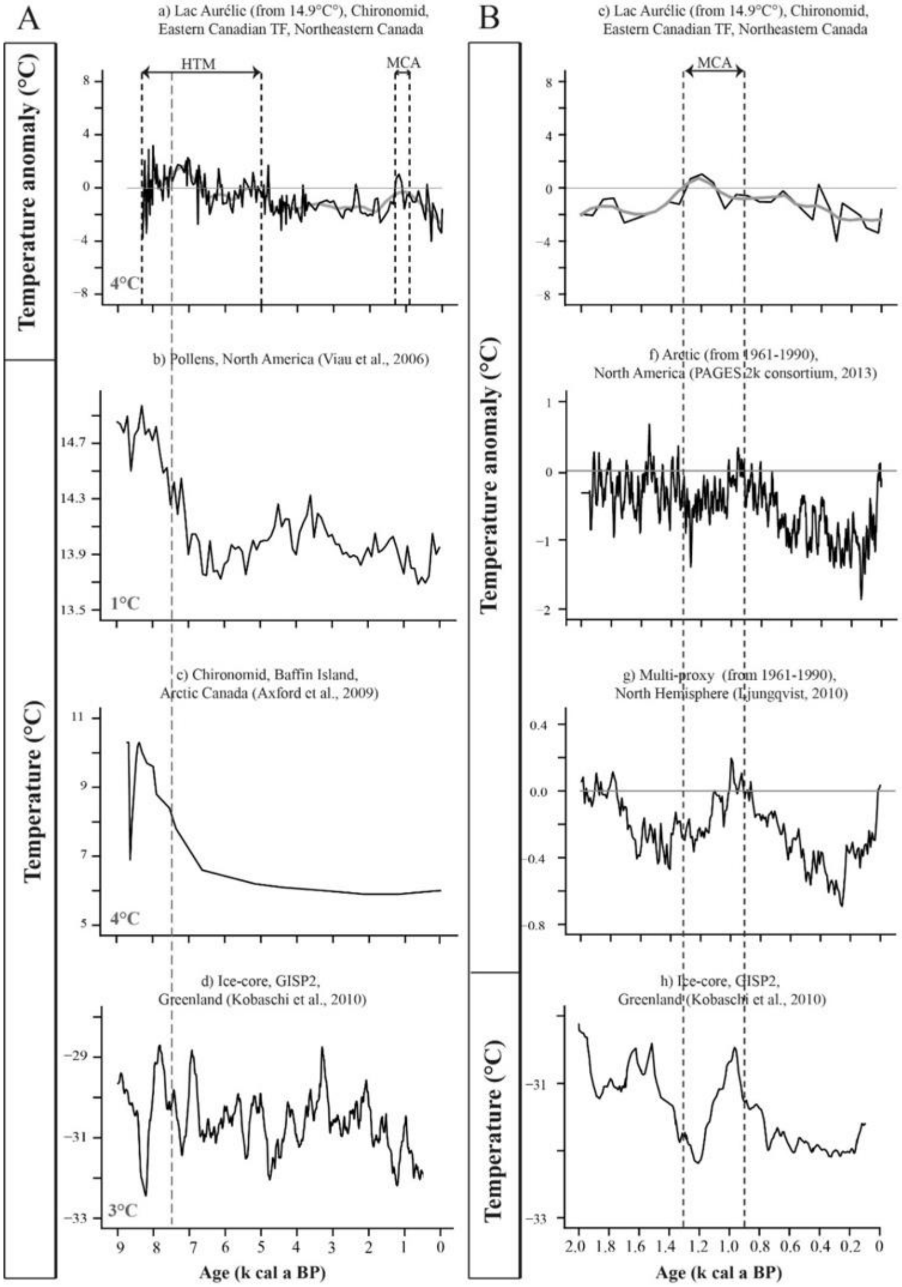


Figure 1.4A Comparison of various temperature reconstructions during the past 9 k cal BP. The data were obtained from the National Oceanic and Atmospheric Administration (NOAA) World Data Center for Paleoclimatology. (a) Chironomid-inferred August mean temperature anomaly, span of 0.2 (black line) and 95 % confidence interval (light grey shading) at *Lac Aurélie* for the past 8.5 k cal a BP related to today's study area temperature (15.0 °C) (this study). (b) Pollen-inferred North-American mean July temperatures for the past 9 k cal a BP (Viau *et al.*, 2006). (c) Chironomid-inferred July temperatures at Lake CF8 (Baffin Island, Canada) for the past 9 k cal a BP (Axford *et al.,* 2009). (d) GISP2, Ice-core inferred Greenland temperatures for the past 9 k cal a BP (Kobashi *et al.,* 2010)

1.4B Comparison of different temperature reconstructions during the past 2 cal a BP. (e) Chironomid-inferred August mean temperature anomaly, span of 0.2 (black line) and 95 % confidence interval (light grey shading) at *Lac Aurélie* related to today's temperature of at Chibougamau (15.0 °C) (this study). (f) North Hemisphere Arctic temperatures from 1961–1990 (PAGES 2k Consortium, 2013). (g) Multi-proxy inferred extra-tropical Northern Hemisphere (90–30°N) decadal mean temperature anomaly (dark line) related to 1996–1990 with 2 standard deviation error bars (light grey shading) (Ljungqvist, 2010). (h) GISP2, Ice-core inferred Greenland temperature (Kobashi *et al.*, 2010).

The Modern Analogue Technique generally provide changes of much lower amplitude than the Weighted Average Method used here (Birks, 2003). The amplitude of change has been shown to attain 5 °C at the highest latitudes, between 2.5–5 °C in our study region, and smaller amplitudes at lower latitudes (Renssen et al., 2012).

Thus, the amplitude of change reconstructed by chironomids at *Lac Aurélie* seems to be plausible. Furthermore, the decrease in temperature from the late Holocene (4.5–1.5 k cal a BP) could be the result of the cold and wet Neoglacial period (Viau and Gajewski, 2009).

1.6.4 Medieval Climate Anomaly (MCA)

Chironomid assemblages showed an increase in temperature (+0.7 °C) around 1.1–1.2 k cal a BP (Figs. 1.3 and 1.4) likely corresponding to the MCA recorded by various proxies in the Northern Hemisphere (Mann *et al.*, 2009). The pollen data results of Viau *et al.* (2006) recorded across North America are in agreement with ours. Viau and Gajewski (2009) also recorded this warming period in northern Quebec.

Rolland *et al.* (2009) inferred a warming period between 1160 and 1360 AD on Southampton Island (Nunavut, Canada) based on chironomid assemblages. In the central Northwest Territories (Canada), chironomid-inferred temperature reconstructions have shown a warming which occurred between 1 k–0.7 cal a BP (Upiter *et al.*, 2014). Arseneault and Payette (1997) also observed a warming trend based on tree rings at the treeline in northwestern Quebec.

When comparing our record to other proxy records (Fig. 1.4A), the period around ca. 1.5–1 k cal a BP is clearly identified as warmer than today with a concomitant timing (PAGES 2k Consortium, 2013). Using chironomids, Millet *et al.* (2009) reconstructed a warming of 1.3 °C in the French Alps. Larocque-Tobler *et al.*, 2012 showed increased temperatures (1–2 °C) during the MCA in two Swiss lakes and the composite records composed of tree-rings and diatoms inferred an increase of 0.5 °C (Trachsel *et al.*, 2012), exemplifying that combining different fossil proxies/sites smooths the record.

During this period, PCA axis 2 scores suggested that factors other than climate (macrophytes, oxygen, and pH) affected the chironomid assemblages at *Lac Aurélie*. However, because the MCA seems to have been plausibly reconstructed, it appears that it did not completely affect the relationship with temperature.

1.6.5 Little Ice Age (LIA)

The Little Ice Age (LIA) is a colder-than-today period which occurred between 1300 and 1850 AD (Matthews and Briffa, 2005) and is defined in northeastern Canada between the late 1500s to the late 1800s (Payette and Delwaide, 2004). During the LIA, the cooling with the largest amplitude occurred in northern Quebec (Viau and Gajewski, 2009). The temporal resolution of our record decreases during this period (about 40-80 years).

The main features of this period are recognized with the start of the cooling being recorded at around 1390 AD and punctuated by a short warming period. Three colder periods are generally seen in high-resolution records at around 1650, 1779, and 1850 AD (Mann *et al.*, 2008; Mann and Jones, 2003). At *Lac Aurélie*, the two coldest-inferred temperatures were temporally close to these high-resolution records at ca. 1663 and 1900 AD.

However, the colder-than-today temperatures of 1 °C (average 0.5 °C) were inferred in only three samples and should be considered with caution. This amplitude is consistent with high-resolution chironomid records from Switzerland (*i.e.* Larocque-Tobler *et al.*

(2012), but larger than dendrochronological records in northern Europe (Moberg *et al.*, 2005) and combined proxy records from Switzerland (Trachsel *et al.*, 2010).

In conclusion, despite methodological limits of the transfer function, good correspondences between our climate reconstruction and those obtained at other sites and from diverse proxies suggests that chironomids are useful to detect temperature changes at this site. Main climate events such as the HTM, the Neoglacial period, the MCA, and the LIA have been recorded by chironomids at *Lac Aurélie*. Hence, further high-resolution regional studies, based on chironomids analyses, should be conducted to improve our understanding of past natural climate changes in boreal forest ecosystems.

1.7 Acknowledgments

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CHAPITRE II

A CHIRONOMID-INFERRED HOLOCENE TEMPERATURE FROM A SHALLOW BOREAL LAKE: POTENTIALS AND PITFALLS

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2.1 Abstract

The biodiversity of shallow (z_{max} <5–7 m) lakes is sensitive to water-level and climate changes, but few such aquatic ecosystems have been studied in the context of quantitative climate reconstruction. Lac Lili (unofficial name) is located in the boreal forest of western Quebec, Canada, and was chosen for its shallowness (z_{max} = 1.40 m) to assess if chironomid assemblages in the sediments could be used to reconstruct Holocene temperature fluctuations quantitatively. Inferred temperatures displayed a decreasing trend from a maximum value ca. 8000–3500 cal year BP, slight warming between ca. 3500 and 3000 cal year BP, followed by cooling to the present. Although chironomid assemblages were influenced by factors other than climate, primarily water depth and changes in macrophyte richness, the reconstructed Holocene temperature pattern was very similar to the known regional climate history. Temperature inferences derived from the chironomid assemblages were, however, warmer than the two reference periods. This deviation was likely a consequence of three factors: (1) shallowness of the lake, which favoured littoral taxa with warmer-than-today temperature optima, (2) the low number of lakes warmer than 16 °C in the training set, and (3) the absence of shallow lakes in the training set.

2.2 Résumé

La biodiversité des lacs peu profonds est sensible aux variations du niveau d'eau et aux changements climatiques, mais seulement peu de ces écosystèmes ont été étudiés dans le contexte d'une reconstitution climatique quantitative. Le Lac Lili (nom non-officiel), situé dans la forêt boréale de l'Ouest du Québec (Canada), a été choisi pour sa profondeur (hauteur d'eau : 1,40 m) dans le but d'évaluer si les assemblages Chironomidae peuvent être utilisés pour reconstituer quantitativement les fluctuations thermiques de l'Holocène. Nos résultats indiquent une tendance à la diminution des températures maximales entre 8000 et 3500 ans AA, un léger réchauffement entre 3500 et 3000 ans AA et enfin une chute abrupte des températures vers le présent. Bien que les assemblages de Chironomidae soient influencés par des facteurs autres que le climat, principalement la hauteur d'eau et les changements dans la richesse des macrophytes, ils permettent de reconstituer des patrons de températures cohérents avec l'histoire connue du climat régional. Cependant, les inférences obtenues par les assemblages de Chironomidae sont plus chaudes que les deux périodes de référence. Cette différence est probablement due à trois facteurs : (1) la profondeur du lac, favorisant des espèces littorales avec des optima thermiques plus chauds que ceux d'aujourd'hui, (2) le faible nombre de lacs aux températures moyennes supérieures à 16 °C et (3) l'absence de lacs peu profonds dans la base de données modernes.

2.3 Introduction

Ponds and shallow lakes [z_{max} <5-7 m, and with light penetration to the bottom (Wetzel 2001)] are the most abundant water bodies in the world (Meerhoff and Jeppesen 2009) and they are particularly sensitive to water-level fluctuations and climate changes (Jeppesen et al. 2014; Smol 2016).

Water level fluctuations between extreme highs and lows may cause shifts between turbid and clear-water, macrophyte-dominated states (Coops et al. 2003), thus affecting the biota and the lake's ecological functions. Submerged macrophytes play an important role in these lakes, as they influence oxygen conditions and inhibit the resuspension of sediments, which may possibly reduce phytoplankton biomass (Blindow et al. 2002).

Shallow eutrophic lakes can develop in two states of equilibria: a clear-water state characterized by high water transparency and abundant submerged vegetation, and a turbid state characterized by high phytoplankton densities and low transparency. A shift from one state to the other can result from water-level changes (Blindow et al. 2002; Scheffer and van Nes 2007; Tarkowska-Kukuryk and Kornijów 2008).

Climate projections for the eastern Canada Boreal Shield display an increase in annual mean temperature by 2100, ranging up to 5 °C in summer, as well as an increase of 13 % in annual precipitation, mainly in winter and spring. with less in summer (Price et al. 2013). Consequently, Mooij et al. (2007) suggested that this change in climate will enhance external nutrient loading, possibly causing a shift from a clear to a turbid state in lacustrine ecosystems. These predictions, however, lack long-term data to study the dynamics among climate (temperature and precipitation) changes, water-level fluctuations, and biotic changes, notably in shallow lakes.

Long-term relationships between shallow lake ecological functions and climate can be obtained from chironomids preserved in lake sediments (Smol 2016). Chironomid (non-biting midges) head capsules are made of chitin that can be preserved for up to 200,000 years (Axford et al. 2009), and have been used to reconstruct air temperature quantitatively in many areas of the world (Brooks and Birks 2001; Walker and Cwynar 2006; Heiri et al. 2007; Millet et al. 2012), sometimes with high accuracy (difference between instrumental and inferred data = 0.8 °C on average) (Larocque and Hall 2003; Larocque et al. 2009; Larocque-Tobler et al. 2016; Luoto and Ojala 2017; Zhang et al. 2017). Although the technique can provide accurate results, most of the studied lakes were deep. To our knowledge, quantitative temperature reconstructions using chironomid head capsules have never been conducted in shallow lakes in Eastern Canada and were attempted in only one shallow (depth <5 m) lake in Western Canada (Upiter et al. 2014).

In shallow [<5–7 m (Wetzel 2001)] lakes, chironomid assemblages are composed mainly of littoral taxa influenced primarily by water-level changes (Engels and Cwynar 2011; Engels et al. 2012), turbidity (Greffard et al. 2012), macrophyte species richness (Langdon et al. 2010), and total phosphorus (Brodersen and Lindegaard 1997). Temperature is also an important factor that influences chironomid communities in shallow lakes, but as such communities are composed of littoral taxa, which tend to have warm optima (Korhola et al. 2002), reconstructions based on these assemblages might yield warmer inferences than would otherwise be expected. Nevertheless, because shallow lakes are very sensitive to temperature and precipitation, climate reconstructions from these ecosystems might be valuable.

Our study site is located in western Quebec (Fig. 1), 110 km north of the town of Rouyn-Noranda. "*Lac Lili*" (Unofficial name: 49°10'25.501"N; 79°22'26.931"O, 320 m a.s.l.) is a shallow lake (z_{max} = 1.40 m) that covers an area of 10 ha and lacks both inlets and outlets. It is located in the black spruce-feather moss bioclimatic domain

(Saucier et al. 2009). Forest cover is dominated by trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana* Mill.). and jack pine (*Pinus banksiana* Lamb) (Blouin and Berger 2005). The mean annual temperature recorded at the closest meteorological station [La Sarre: 1961–1990] is 0.8 °C, with August temperature averages of 15.0 °C (1961–1990) and 15.4 °C (1981–2010). Mean annual precipitation is 640 mm, of which 250 mm falls as snow (Environnement Canada 2016).

Lac Lili is located 395 km from *Lac Aurélie* (49°10'25.501"N; 79°22'26.931"W; black spruce-feather moss bioclimatic domain; 320 m a.s.l; 1 ha. 10 m deep) (Fig. 2.1), where a chironomid-inferred temperature reconstruction was carried out and was similar to regional and hemispheric temperature records (Bajolle et al. 2018).

Multi-site comparison [*Lac Lili versus Lac Aurélie* (Bajolle et al. 2018)] will place the climate reconstruction within a regional context. If the patterns are similar at both sites, it will provide support for regional climate change having been reconstructed accurately, whereas if they diverge. the differences might be a consequence of local effects (e.g. water-level fluctuations. fire regime). The goal of this study was to assess if chironomid assemblages from a shallow lake can be used to infer air temperature quantitatively and reconstruct the general pattern of climate change in this region.

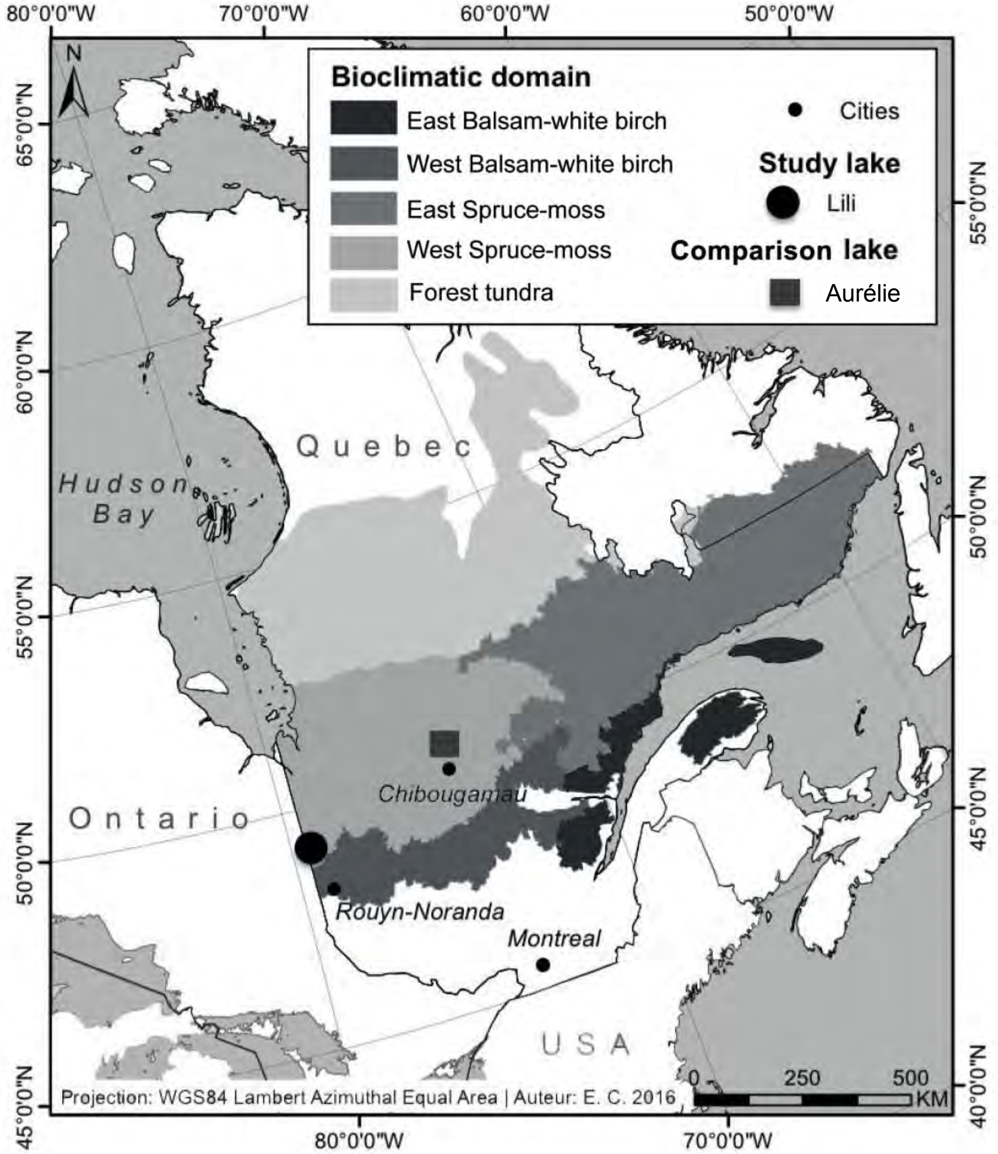

Figure 2.1 Map of Quebec (Canada) showing the location of study sites and the bioclimatic domains.

2.4 Materials and methods

2.4.1 Coring, stratigraphy, chronology

Two overlapping sediment cores were taken in March 2014 through the frozen surface at the centre of *Lac Lili* using a modified Livingstone-type square-rod piston corer (100 × 5 cm). The water-sediment interface was collected using a Kajak-Brinkhurst (KB) gravity corer (Glew 1991). The extruded cores (310 and 306 cm long) were sectioned into 0.5-cm intervals to achieve a high-scale temporal resolution. Terrestrial plant macrofossils (seed, needle and bark) were retrieved from seven samples for AMS radiocarbon dating (Table 2.1).

Table 2.1 Radiocarbon dates from terrestrial plant macroremains.

Laboratory code	Depth (cm)	^{14}C age (yr BP)	Calibrated ^{14}C age ranges (cal yr BP; 2σ-ranges) [a]	Material dated
Beta-427033	23-27	410 ± 30	**430-519 (0.83)**	Plant macroremains
			331-358 (0.12)	Plant macroremains
Beta-427032	48-50	1150 ± 30	**978-1145 (0.90)**	Plant macroremains
			1158-1170 (0.05)	Plant macroremains
Beta-427031	118-120	2730 ± 30	**2762-2876 (0.95)**	Plant macroremains
			2915-2915 (0.01)	Plant macroremains
Beta-427030	178-182	3180 ± 30	**3358-3453 (0.95)**	Plant macroremains
Beta-427029	228-232	4780 ± 30	**5468-5589 (0.95)**	Plant macroremains
Beta-427028	278-282	6150 ± 30	**6966-7159 (0.94)**	Plant macroremains
			6960-6963 (0.01)	Plant macroremains
Beta-427027	304-306	7670 ± 30	**8407-8522 (0.90)**	Plant macroremains
			8528-8538 (0.05)	Plant macroremains

[a] Calibrated ages: the means of the 2σ-ranges with highest probabilities (bold).

The ^{14}C dates were calibrated at 2σ ranges using the Clam package (Blaauw 2010) of R software version 3.0.1 (R Core Team 2016) based on the non-marine (IntCal13) radiocarbon calibration curve (Hua et al. 2013; Reimer et al. 2013). The age-depth model (Fig. 2.2) was obtained using a 'classical' age-depth model with a smoothing spline function (Blaauw 2010). All dates are expressed in calibrated years before present (hereafter cal year BP).

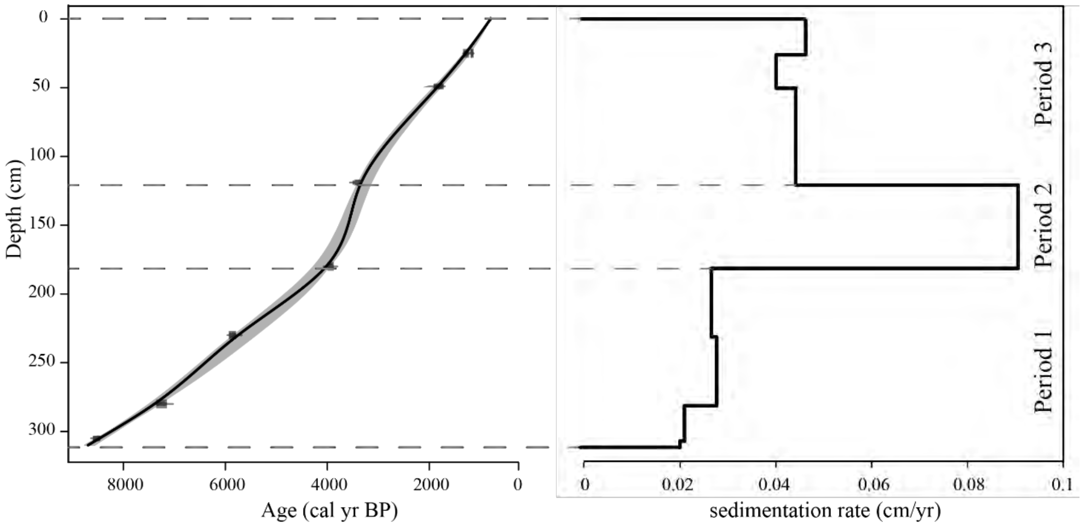

Figure. 2.2 Age-depth model and sediment accumulation rates for the *Lac Lili* core.

2.4.2 Chironomid analyses

Sediment slices of 0.5 cm were sampled at intervals varying between 4, 2, and 1 cm for a total of 116 samples. Samples were soaked overnight in 10 %, KOH and then rinsed with water and filtered through a 100 µm-mesh. The remnants were poured into a counting tray and observed under a stereomicroscope at a 10× magnification. Each head capsule (whole and half mentum) was individually picked with fine tweezers and mounted on a microscope slide in a drop of glycerine. Slides were observed under a light microscope at 400–1000× of magnification following the taxonomic guide of Brooks et al. (2007). A minimum of 50 head capsules is needed for temperature reconstructions (Larocque 2001; Heiri and Lotter 2010). All samples in this study contained at least 92 head capsules.

A chironomid stratigraphy (percentage of each taxon in each sample) was constructed using C2 software (Juggins 2003). Only taxa present in more than six samples are shown in Fig. 3. A detrended correspondence analysis (DCA) was performed on a matrix of square-root-transformed percentages using ade4 and vegan packages from the R v3.2.2 software package (Borcard et al. 2011). The length of the DCA-axis shows whether or not the distribution of the data set along the axis is linear or unimodal (Borcard et al. 2011).

A PCA calculated with C2 software was used to study the changes in chironomid assemblages through time on a dispersion matrix of square-root-transformed percentages into which rare taxa with abundances <1 % in fewer than two samples were removed.

A constrained sum-of-squares cluster analysis (CONISS; Grimm 1987) was used to identify zones in the stratigraphy. with the significance of each zone tested with the broken stick model (Bennett 1996) using the Rioja R package (Juggins et al. 2015). Percentages of littoral and eutrophic taxa were determined (Table 2.2) based on Brooks et al. (2007).

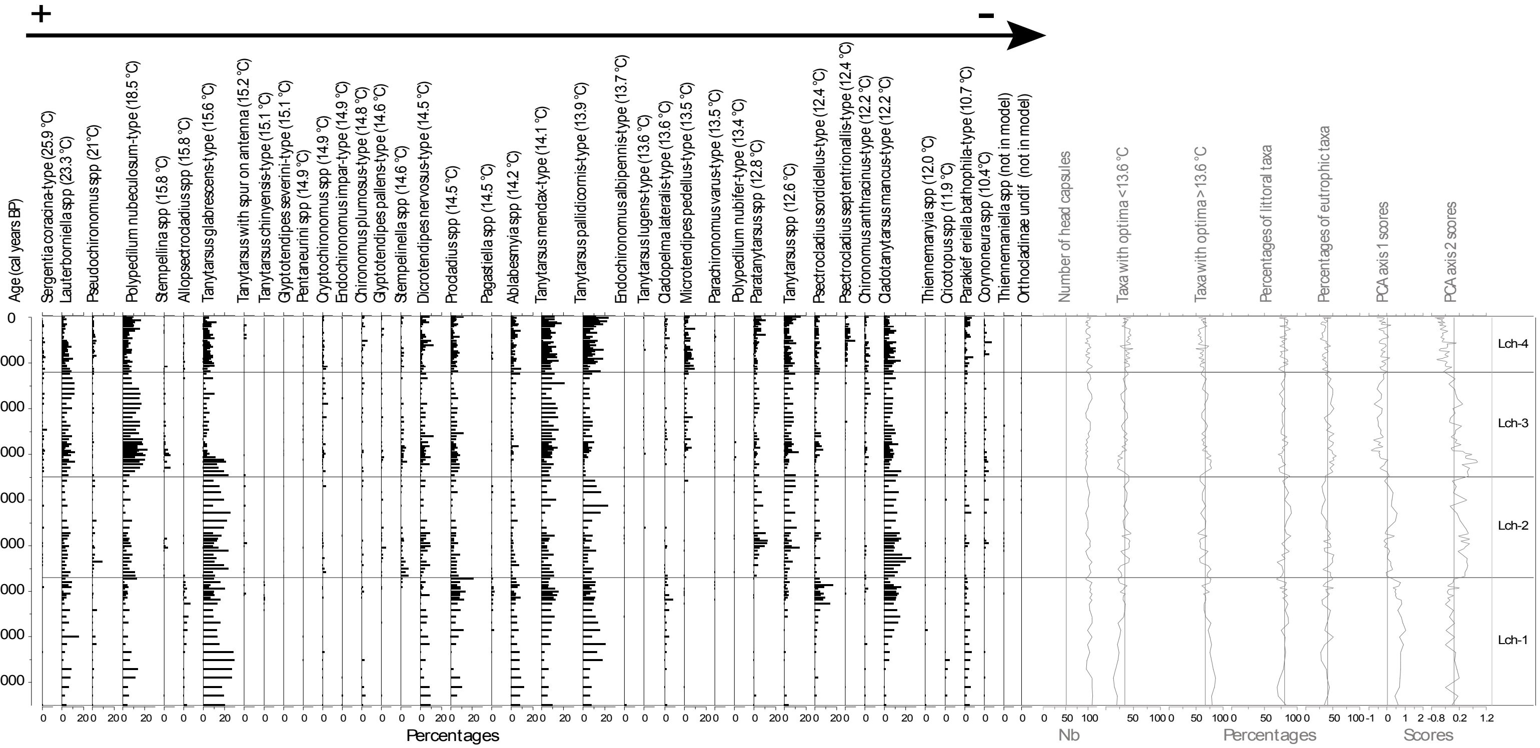

Figure 2.3 Chironomid stratigraphy of *Lac Lili*. Chironomid percentage changes for the taxa present in more than six samples, the number of head capsules per samples, percentage of littoral taxa (based on Brooks et al. 2007), percentage of eutrophic taxa (based on Brooks et al. 2007), and the percentage of colder-than-today taxa (based on the East Canadian temperature optima). PCA axis 1 and 2 are the scores of the principal component analysis made on the percentages of chironomid taxa with percentages >1 %. Vertical lines displayed in the percentage of littoral taxa and the percentage of colder-than-today taxa are the Holocene average. The vertical lines in the PCA axis 1 and 2 scores are the 0 score. The horizontal lines represent four significant zones identified using CONISS and the broken stick method. The chironomid taxa are ordered by their temperature optima in the training set. The black arrow identified the 27 taxa with temperature optima equal to or warmer than 13.6 °C.

Table 2.2 Occurrence and maximum percentages of taxa in the sediment of *Lac Lili* (total of 116 samples), littoral and eutrophic taxa (Brooks et al 2007), temperature optima yielded by WA from the East Canadian transfer function (Larocque 2008, *modified*), and temperature categories in relation to optima

Lac Lili	Occurrence	Maximum percentages	Not included in Fig. 3	Littoral taxa	Eutrophic taxa	Optima	Category	
Taxa identified in sediment core						East Canadian	Colder than today (13.6 °C)	Warmer than today (13.6 °C)
Ablabesmyia spp.	110	12.8				14.2		X
Allopsectrocladius spp.	44	6.9		X		15.8		X
Chironomus anthracinus-type	82	6.1			X	12.2	X	
Chironomus plumosus-type	63	6.0			X	14.8		X
Cladopelma lateralis-type	70	8.3		X		13.6		
Cladotanytarsus mancus-type-1	115	25.7		X	X	12.2	X	
Corynoneura spp.	58	7.5				10.4	X	
Cricotopus spp.	33	5.2		X		11.9	X	
Cryptochironomus spp.	81	5.9				14.9		X
Dicrotendipes nervosus-type	114	12.7		X	X	14.5		X
Einfeldia spp.	4	1.0	X	X		12.8	X	
Endochironomus albipennis-type	11	2.8		X	X	13.7		X
Endochironomus impar-type	8	1.9		X	X	14.9		X
Endochironomus tendens-type	1	1.0	X	X	X	15.8		X
Gymnometriocnemus-Bryophaenocladius spp.	1	1.0	X			*not in model*		
Glyptotendipes pallens-type	47	5.0		X	X	14.6		X
Glyptotendipes severini-type	15	1.1		X	X	15.1		X

Suite

Heterotrissocladius maeri-type	1	1.1	X			9.6	X	
Hyporygma spp.	2	1.0	X			*not in model*		
Lauterborniella spp.	115	16.5		X	X	23.3		X
Mesocricotopus spp.	1	1.0	X			9.9	X	
Microtendipes pedellus-type	75	10.3		X		13.5	X	
Nanocladius spp.	2	1.0	X			12.5	X	
Omisus spp.	1	1.0	X			15.2		X
Orthocladinae spp.	10	1.1				*not in model*		
Orthocladius spp.	2	1.0	X			13.6		
Pagastiella spp.	34	3.8		X		14.5		X
Parachironomus varus-type	27	1.9		X		13.5	X	
Parakiefferiella spp.	92	8.7		X	X	10.7	X	
Paraphaenocladius spp.	1	1.9	X			*not in model*		
Paratanytarsus spp.	95	13.3		X		12.8	X	
Paratendipes nudisquama-type	5	1.0	X	X		*not in model*		
Pentaneurini spp.	16	1.9				14.9		X
Polypedilum nubifer-type	116	23.2		X	X	13.4	X	
Polypedilum nubeculosum-type	10	2.1		X	X	18.5		X
Procladius spp.	114	22.1			X	14.5		X
Psectrocladius septentrionalis-type	49	10.0		X		12.2	X	
Psectrocladius sordidellus-type	111	18.1		X		12.4	X	
Pseudorthocladius spp.	1	1.0	X			22.6		X
Sergentia coracina-type	57	4.8				25.9		X

Suite

Stempellina spp.	72	7.9			15.8		X
Stempelinella spp.	43	6.5			14.6		X
Stenochironomus spp.	1	1.0	X		*not in model*		
Stictochironomus spp.	2	1.0	X		7.9	X	
Tanytarsus spp.	110	15.6		X	12.6	X	
Tanytarsus chinyensis-type	8	1.9		X	15.1		X
Tanytarsus glabrescens-type	114	29.9		X	15.6		X
Tanytarsus lugens-type	14	2.1			13.6		
Tanytarsus mendax-type	116	21.4		X	14.1		X
Tanytarsus pallidicornis-type	116	24.3		X	13.9		X
Tanytarsus with spur on antenna	21	3.9		X	15.2		X
Thiennemaniella spp.	13	1.9			*not in model*		
Thiennemanyia spp.	10	3.1			12	X	
Zalutschia mucronata-type	1	0.9	X		13	X	
Zalutschia zalutschicola-type	4	1.1	X		14.7		X
Number of taxa not included in the training set					**7**		
Maximum temperature (°C)					**20.5**		
Minimum temperature (°C)					**7.9**		

2.4.3 Temperature reconstruction

A new Eastern Canadian model modified from Larocque et al (2006) and Larocque (2008); and utilized for climate reconstruction at *Lac Aurélie* (Bajolle et al. 2018) was used. The training set lake comprises 75 lakes (no outlier) and 79 taxa with abundances of >1 % in more than two lakes. Mean August temperature varied from 3 to 21˚C for a temperature gradient of 18˚C. WAPLS 999-bootstrap with two components yielded a correlation coefficient (r^2_{boot}) of 0.85, an RMSEP of 1.67˚C and a maximum bias of 3.05˚C. Occurrence of taxa and temperature optima can be found in Bajolle et al. (2018) and in Table 2.2. Sample specific errors (eSEP) were calculated.

To validate the use of the transfer function. an evaluation of modern analogues for each sample was performed using the minimum distance of the fossil sample to the training set assemblages (Overpeck et al. 1985). Fossil samples with a distance above the 20th percentile were considered as having "no analogues", and those above the 10th were considered to be "poor analogues" (Overpeck et al. 1985).

Percentages of taxa colder or warmer than 13.6 °C (average of temperature optima of taxa found in *Lac Lili*) were calculated using the temperature optima obtained from the transfer function (Table 2.2). This site-specific cut-off is not far from the average temperature optima of the 79 taxa found in the training set (13.2 °C). The difference between average temperature inferences and reference values (climate normals: 1961–1990 and 1981–2010) was performed using a t-test.

2.5 Results

2.5.1 Chronology and sedimentation rates

The core was 310 cm long and composed entirely of gyttja. An age of ca. 8407–8522 cal year BP (2 sigma range) was obtained at the bottom of the core (304–306 cm) (Table 2.1). Three periods were identified with respect to sedimentation rates, based on the age-depth model (Fig. 2.2). Period 1 (ca. 8600–3500 cal year BP; 310–180 cm) showed a low sedimentation rate (mean: 0.04 cm/yr). During Period 2 (ca. 3500–2700 cal year BP; 180–120 cm), the average sedimentation rate increased quickly to 0.09 cm/yr. Period 3 (ca. 2700 cal year BP to Present; 120–0 cm) was characterized by a decrease in sedimentation rate (mean: 0.02 cm/year).

2.5.2 Chironomid stratigraphy

In total, 116 samples were analysed. with a total of 11,693 head capsules (hereafter HC) identified. All samples had more than 92 HC, with an average of 100 HC per sample (Fig. 2.3). Fifty-eight taxa were identified and 42 of them are presented in Fig. 3. The 16 taxa not illustrated occurred in <6 samples at percentages <1.9 %, thus did not contribute much to the temperature reconstruction (Table 2.2).

The chironomid stratigraphy was divided into four statistically significant zones (Lch-1 to Lch-4; Fig. 3). In general, both littoral and warmer-than-13.6 °C taxa dominated the chironomid community throughout the core, with average percentages of 80 % and 66 %. Respectively, whereas colder-than-13.6 °C taxa had percentages that ranged between 13 and 50 % (average: 34 %). DCA yielded a gradient of 1.6 SD, suggesting that linear regression such as PCA was appropriate. PCA Axis 1 and had eigenvalues of 0.18 and 0.12, respectively.

During zone Lch-1 (ca. 8500–5700 cal year BP; 310–240 cm), littoral taxa were below average and increased after 6300 cal year BP. Eutrophic taxa oscillated around the average. PCA Axis 1 scores were above 0, whereas PCA Axis 2 scores were generally below 0. The dominant taxa were *Tanytarsus glabrescens*-type, *Procladius* spp., *Ablabesmyia* spp., *Polypedilum nubeculosum*-type, *Tanytarsus pallidicornis*-type, *Lauterborniella* spp., *Dicrotendipes nervosus*-type and *Tanytarsus mendax*-type. *Cladotanytarsus mancus*-type and *Psectrocladius sordidellus*-type percentages increased towards the end of the zone. *Pagastiella* spp. and *Allopsectrocladius* spp. had their highest percentages of the record. Taxa with warmer-than-13.6 °C optima dominated the assemblages, with percentages >68 %.

In zone Lch-2 (ca. 5700–3500 cal year BP; 240–180 cm), percentages of colder-than-13.6 °C taxa increased above average (32 %), while warmer-than-13.6 °C taxa decreased below average. but always remained higher than 48 %. PCA Axis 1 scores decreased compared to the previous zone, but remained slightly above 0, whereas PCA Axis 2 scores were mainly above 0. Eutrophic taxa percentages were above average until ca. 5000 cal year BP, then decreased below average until the end of the zone. Percentages of littoral taxa started below average until ca. 5000 cal year BP but increased until the end of the zone. The dominant taxa were the same as in the previous zone, however *Paratanytarsus* spp. started to be recorded consistently and *Tanytarsus* spp. increased towards the end of the zone. *Stempellinella* had higher percentages at the beginning of the zone than in the previous section. but it decreased and occasionally disappeared after ca. 5000 cal yr BP.

In zone Lch-3 (ca. 3500–1200 cal year BP; 180–55 cm), the percentages of littoral taxa fluctuated around the average. Eutrophic taxa percentages started well above average. decreased. and then finally increased again after 2000 cal year BP. PCA Axis 1 scores decreased below 0 and PCA Axis 2 scores remained above 0, with a tendency to decrease to the end of the zone. *T. glabrescens*-type percentages decreased sharply compared to zone Lch-2. *Microtendipes pedellus*-type, *Chironomus anthracinus*-type and *Guttipelopia* spp. were recorded consistently. *Stempellinella* spp. and *Stempellina* spp. had higher percentages at the beginning of the zone and then decreased thereafter. Warmer-than-13.6 °C and colder-than-13.6 °C taxa percentages oscillated around their averages.

Zone Lch-4 (ca. 1200 cal year BP to present; 55–0 cm) had increases in the percentages of *P. septentrionalis*-type, *P. sordidellus*-type, *M. pedellus*-type, *Paratanytarsus* spp., *T. pallidicornis*-type, *T. mendax*-type and a slight increase in *T. glabrescens*-type. *Ablabesmyia* spp. was also recorded more regularly. PCA Axis 1 and Axis 2 scores were below 0. The percentages of eutrophic taxa decreased below average while littoral taxa oscillated. Percentages of colder-than-today taxa were above average (32-50 %) whereas warmer-than-13.6 °C were below average, but percentages remained higher than 48.

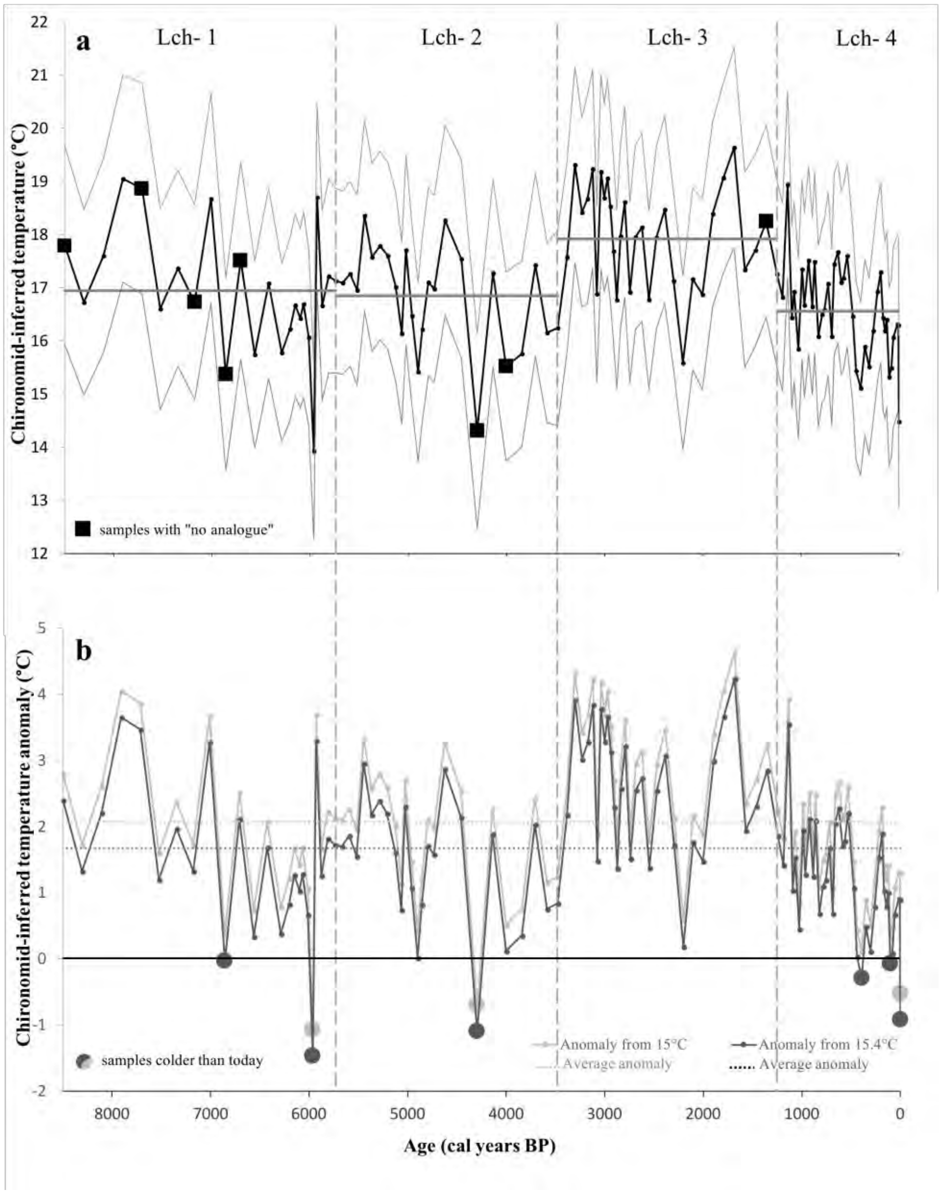

Figure 2.4 **a** Temperature reconstruction using chironomids preserved in the sediment of *Lac Lili*. The black line is the temperature reconstruction and the grey dots are the sample specific errors. The vertical doted lines are the zones identified in the chironomid stratigraphy. The horizontal grey lines are the average inferred temperatures within the zones. The black squares identify the eight samples with no analogues. **b** Chironomid-inferred temperature anomaly (°C) in relation to 15 °C (1961–1990) and 15.4 °C (1981–2010). Inferences colder than reference periods are illustrated by large circles. The horizontal dotted bars are the mean anomaly compared to 15 and 15.4 °C.

2.5.3 Temperature reconstructions

Eight of the 116 fossil samples had no modern analogues (Fig. 2.4a) and 85 samples had poor analogues compared to the training set samples. During zone Lch-1 (8500–5800 cal year BP). the average reconstructed temperature was 16.9 °C, with a decrease from 19 °C (maximum) to 17 °C at the end of the zone. In zone Lch-2 (ca. 5700–3500 cal year BP), temperatures had an average of 16.8 °C, with a decrease from 17.8 °C around 5200 cal year BP to 16.2 °C at 3400 cal year BP. Zone Lch-3 (ca. 3500–1200 cal year BP) started with inferences for high temperatures (19.3–18.5 °C), followed by a decrease to 16.8 °C between ca. 3000 and 2500 cal year BP. An increase (18.3 and 19.6 °C) was inferred for the period between 1800 and 1500 cal year BP. The average chironomid-inferred temperature during Zone 3 was 17.9 °C. In the last zone (Lch-4), the temperatures decreased from ca. 17.5 °C at the beginning of the zone to 14.8 °C at the end of the zone. The average during this zone was 16.5 °C.

The temperature anomalies show that throughout the whole record. only six of the inferences were colder than the climate normal of 15.4 °C and three were colder than today. with the climate normal of 15 °C (Fig. 2.4b). The average anomaly from 15 °C (2.10 °C) and from 15.4 °C (1.70 °C) for the whole record showed that the temperature inferences were generally and significantly ($p < 2.2\ 10^{-16}$), warmer than today.

2.6 Discussion

2.6.1 Chironomid assemblages

As expected for a shallow lake, the chironomid assemblages were dominated by littoral and eutrophic taxa, which tend to have warmer optima (Table 2.2) and are generally influenced by water levels (Engels and Cwynar 2011; Engels et al. 2012), turbidity (Greffard et al. 2012), macrophyte species richness and abundance (Langdon et al. 2010), and total phosphorus (Brodersen and Lindegaard 1997).

In *Lac Lili*, when the PCA Axis 1 scores decreased below 0, the sum of Chironomini increased (Fig. 2.5). Korhola et al. (2002) also observed that chironomids with warm temperature optima dominated assemblages in a shallow lake in Finland, and high sums of Chironomini have been linked to water levels and macrophyte species richness and abundance (Langdon et al. 2010). Thus, water levels and macrophytes were possibly the main factors that drove chironomid assemblages in *Lac Lili*.

The main changes occurred ca. 3500 cal year BP when PCA axis 1 scores changed from positive to negative. Before ca. 3500 cal year BP, the assemblages were dominated by *Tanytarsus glabrescens*-type and were replaced by *Polypedilum nubeculosum*-type and *Microtendipes pedellus*-type, which are often associated with floating-leaved plants and other macrophytes (Learner et al. 1989; Tarkowska-Kukuryk and Kornijów 2008). Synchronously, Tanytarsini-dominated communities shifted to Chironomini-dominated assemblages (Fig. 2.5), possibly with a change in water level (shallowing) and macrophyte species richness and abundance (Langdon et al. 2010), as illustrated by the strong increase in *Nuphar* (a floating-leaved plant) pollen in *Lac Lili* (Fig. 2.5).

The timing of this major change in the chironomid assemblages coincides with the start of the Neoglacial, when climate became wetter in this region (Garralla and Gajewski 1992; Viau and Gajewski 2009; Hély et al. 2010; Ali et al. 2012; El-Guellab et al. 2015).

After 1500 cal year BP, the percentages of both *Psectrocladius* types and *Cricotopus* spp. largely increased along with Pentaneurini spp. and *Ablabesmyia* spp. *Psectrocladius* is often associated with macrophytes (Brodersen et al. 2001; Langdon et al. 2008). *Cricotopus*. *Ablabesmyia* and *Zalutschia* spp. are associated with vegetation (Brooks et al. 2007). Although Chironomini still dominated, they started to decrease, while Tanytarsini started to increase. This change suggests the onset of a new state, perhaps as a response to colder conditions, as suggested by the decrease in taxa with optima warmer than 13.6 °C.

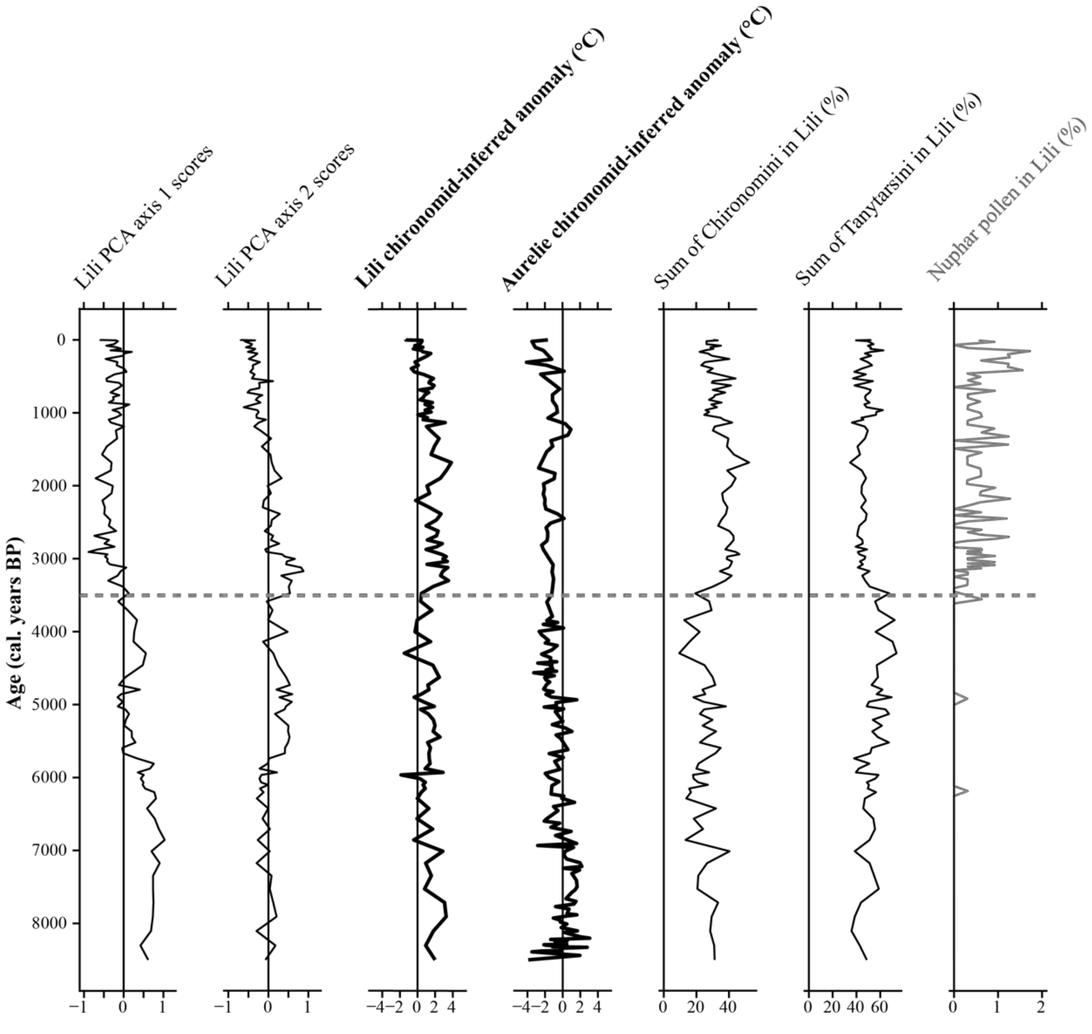

Figure 2.5 Summary of changes in *Lac Lili* and *Lac Aurélie*.

2.6.2 Comparison with other regional climate records

PCA axis 1 seems to be related with warmer-than-13.6 °C taxa, but not directly to inferred temperature, suggesting that confounding factors (eutrophication, water-level changes and macrophytes) impacted the chironomid assemblages more than temperature.

Nevertheless, the general pattern of temperature changes (i.e. warm middle Holocene to ca. 3500 cal year BP, with a decreasing trend to the present) reconstructed using the chironomids follows the quantitative paleoclimatic reconstructions based on the chironomid record of *Lac Aurélie* (Fig. 2.5) and pollen from the Province of Quebec (Viau et al. 2006). A Neoglacial period with cooler conditions started at 3500 cal year BP in this region (Garralla and Gajewski 1992; Viau and Gajewski 2009; Ali et al. 2009; Hély et al. 2010).

The PCA axis 2 scores showed their main changes between ca. 3500 and 3000 cal year BP when chironomid-inferred temperatures were warmer and eutrophic percentages increased. The sedimentation rates during that period also increased (Period 2; Fig. 2.2). Major changes in sedimentation rates at that time were also recorded by Ali et al. (2008) in western Québec and were interpreted as having been caused by a major flood in the watershed between ca. 3600 and 1900 cal year BP, causing a rapid rise in lake level. Consequently, the increase in sedimentation rate is possibly associated with an increase in precipitation, as suggested by the changes in the chironomid assemblages that show highest percentages of eutrophic taxa.

A similar warming (~1 °C) period was also reconstructed using chironomids at *Lac Aurélie* (Fig. 2.5) and in the pollen record of Viau and Gajewski (2009), but at lower amplitude. The agreement between our results and other regional records suggests that although temperature was not the only factor that affected chironomid assemblages, patterns of climate change could still be adequately reconstructed.

2.6.3 Quantitative temperature reconstruction in a shallow boreal lake

The temperature pattern through the Holocene was similar to that in other regional records. The goal of using quantitative methods to reconstruct climate, however, is to obtain accurate inferences, not only a pattern of change. Reconstruction of climate from chironomid assemblages in a shallow study lake may compromise its accuracy. For instance. most inferences were warmer by 1.7 to 2 °C than the climate normals (1981–2010, 15.4 °C: 1961–1990, 15 °C) (Fig. 2.4).

This was not the case for the chironomid-inferred reconstruction in Lac Aurélie or in pollen records of the region (Viau and Gajewski 2009). which all show periods with colder-than-the-climate normal inferences. Twenty-seven of the taxa have temperature optima warmer-than-13.6 °C and nine of fourteen taxa with percentages reaching 20 % or higher have warmer-than-13.6 °C optima (Fig. 2.3). Thirteen taxa have temperature optima between 14.9 and 25.3 °C. Three of them have percentages of 20 % or more and temperature optima between 15.8 and 25.3 °C. When using WAPLS. these taxa contribute more to the temperature inference and thus lead to temperature inferences well above the climate normal.

This lower accuracy can potentially be explained by a few factors: (1) littoral taxa dominate the assemblages (average = 80 %), (2) warm-optimum taxa also dominate (average = 66 %), (3) the training set has only 11 lakes with mean August temperature above 15.8 °C (the actual temperature at *Lac Lili*) and only five lakes between 15 and 16 °C, and (4) the training set function is perhaps inappropriate for shallow lakes. Shallow-water taxa tend to have warmer-than-today temperature optima (Korhola et al. 2002). Thus. it is not surprising that inferences were generally too warm. Lacking a cool hypolimnion, the lake can only support taxa that prefer warmer conditions. This could explain why colder-than-today percentages were always low (average of 32 %) in *Lac Lili*.

The training set mainly comprises lakes with water depths greater than 5 m. To increase the accuracy of the chironomid inferences, a larger number of shallow lakes should be added, or preferably, a new transfer function, composed only of shallow lakes. could be developed. Absence of modern analogues in eight samples and poor analogues in 85 samples suggest that fossil samples were dissimilar to the training set, possibly because of the high percentages of littoral taxa in the fossil assemblages.

This situation was also observed in a shallow lake used for reconstructing climate in western Canada (Upiter et al. 2014), and the authors concluded that although the pattern of temperature changes was similar to those of the studied region, all inferences were within the error of the model and thus should be viewed with caution.

The training set used in this study also possesses few lakes with mean-August temperatures similar to *Lac Lili*, and no lakes between 16.8 °C and 18.9 °C. Inferences above 15 °C are thus generally under-estimated (Fig. S2.1). More lakes with mean-August temperatures above 15 °C should be sampled to improve the accuracy of the model.

2.7 Conclusion

It has been shown that shallow lakes are impacted by climate change and temperature reconstructions from chironomids, along with other variables in sediments such as diatoms, zooplankton, and pollen, could help decipher the effects that temperature had on lake communities throughout the Holocene.

Lac Lili provided an opportunity to determine if shallow lakes could be used to obtain reasonable temperature inferences, which are typically derived from deeper lakes around the world. Our results showed that although chironomids were effective for reconstructing the general pattern of climate change, their ability to provide accurate inferences was compromised and most were above the climate normal.

Better accuracy in shallow lakes could be attained if appropriate transfer functions were used; either by increasing the number of shallow lakes in an existing training set, or by developing a transfer function with data exclusively from shallow lakes. In our opinion, the first option is preferable, as lakes that are presently shallow might have been deeper in the past, and if no deep lakes are included in the transfer function, temperature might not be accurately reconstructed, as samples from such lake will have poor analogues. Furthermore, lakes with temperatures between 16 and 19 °C should be added to the existing transfer function to increase temperature coverage within the overall range.

2.8 Acknowledgments

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2.9 Supplementary material

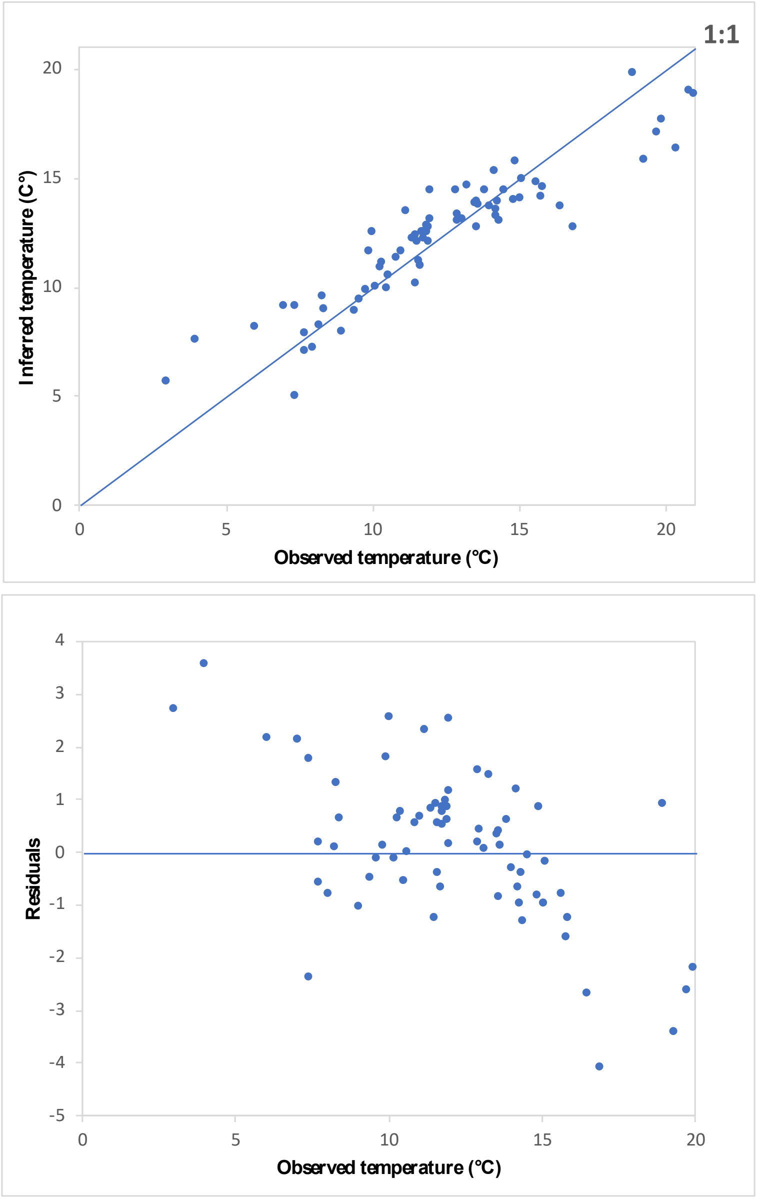

Figure S2.1 Results of the transfer function. Upper panel: observed versus inferred temperatures of the lakes in the training set. Lower panel: observed temperature versus residuals. Residuals are the differences between observed and reconstructed temperature while the 1 :1 shows the relationship between observed and inferred temperature. From the 1 :1 relationship we can see which samples are over or underestimated, from the residuals we can see by how much degrees. The lakes warmer than 15 °C are generally under-estimated and there are no lakes between 16.8 and 18.9 °C.

CHAPITRE III

AUGUST TEMPERATURE VARIABILITY OVER THE PAST 8000 YEARS IN THE WESTERN QUÉBEC BOREAL FOREST (CANADA): A COMBINED APPROACH BASED ON CHIRONOMIDS AND POLLEN DATA

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3.1 Abstract

This study presents the first combined quantitative August temperature reconstruction (CATR) from two lacustrine sites located in the western Québec boreal forest (Canada) and covering the last 8500 years. The reconstruction was based on a multi-proxies approach including pollen (Modern Analogue Technique) and chironomids (Weighted Average Partial Least Square) data. Three main periods were recorded: (i) 8500-4500 cal BP, identified as the Holocene Thermal Maximum, in which August temperatures were warmer than today (maximal mean value of *ca.* +2.6 °C); (ii) 4500-1000 cal BP, marked by the onset of the cold Neoglacial period, where temperatures oscillated around modern values; and (iii) 1000 cal BP to present, characterized by a general decrease of temperature. Several shorter climate events have also been identified in each period: (i) the 8200 cold event (sharp drop of about 2 °C); (ii) the 4200 cal BP warm event (*ca.* +0.5 °C); (iii) the Roman Warm Period (*ca*. 1900-1700 cal BP, *ca.* +1.0 °C); (iv) the Dark Ages Cold Period (*ca.* 1700-1500 cal BP, anomaly close to 0 °C); (v) the Medieval Climate Anomaly (*ca.* 1100 cal BP, *ca.* +1.3 °C); and (vi) the Little Ice Age (*ca.* 500-250 cal BP, *ca.*-1.2 °C). A series of colder events were also observed at *ca.* 5900, 4300, 2800 and 400 cal BP referring probably to the "Bond events". The duration and amplitude of observed climate events were similar with other regional, North American, and Northern Hemisphere records.

3.2 Résumé

Cette étude présente la première reconstitution combinée (pollen et Chironomidae) des températures d'août (RCTA) des 8500 dernières années pour deux sites lacustres localisés dans la forêt boréale occidentale du Québec (Canada). Cette reconstitution est basée sur une approche multi-indicateurs incluant des données polliniques (Technique d'Analogues Modernes) et Chironomidae (fonction de transfert). Trois périodes principales sont enregistrées : (i) 8500-4500 ans AA, identifiée comme le Maximum Thermique de l'Holocène (HTM), durant laquelle les températures d'août sont plus chaudes que les températures actuelles (température maximale moyenne : +2,6 °C) ; (ii) 4500-1000 ans AA, marquée par le début de la période Néoglaciaire froide où les températures oscillent autour des valeurs actuelles et (iii) les derniers 1000 ans AA, caractérisés par une diminution générale des températures. Plusieurs événements climatiques courts ont également été identifiés pour chaque période : (i) l'évènement froid de 8200 ans AA (chute d'environ 2 °C) ; (ii) l'évènement chaud de 4200 ans AA (+0,5 °C) ; (iii) la période chaude Romaine (RWP, 1900-1700 ans AA, +1,0 °C) ; (iv) la période froide de l'Âge Sombre (DACP, 1700-1500 ans AA, anomalie proche de 0 °C) ; (v) l'Anomalie Climatique Médiévale (MCA, 1100 ans AA, +1,3 °C) et (vi) le Petit Âge Glaciaire (LIA, 500-250 ans AA, -1,2 °C). Une série d'événements plus froids est également observée à 5900, 4300, 2800 et 400 ans AA, se référant probablement aux évènements « Bond ». La durée et l'amplitude observées des événements climatiques sont similaires avec les enregistrements régionaux, nord-américains et de l'ensemble de l'Hémisphère Nord disponibles.

3.3 Introduction

Because of their significant carbon reservoirs, boreal ecosystems play a fundamental role in the climatic balance of the Earth (Harden et al. 1997). As of today, gaps remain in our understanding of the influence of past and recent climatic variability on the boreal forest, which is mainly structured by frequent disturbances such as climatically-driven fire (Flannigan et al. 2009; Remy et al. 2017a). More frequent and intense fires are expected, under a simulated warmer climate (IPCC 2013), which could represent a potential threat to boreal ecosystems (Flannigan et al. 2009; Ali et al. 2012).

While we understand both the postglacial vegetation dynamics and fire regime changes rather well in eastern Canada (Ali et al. 2009; Hély et al. 2010; El-Guellab et al. 2015; Remy et al. 2017a), relatively few high resolution paleoclimatic records have been developed, thereby limiting inferences that can be made about long-term fire, vegetation and climate couplings.

Holocene pollen-inferred summer temperature reconstructions have been provided for North America (Viau et al. 2006, 2012; Gajewski and Viau 2011; Ladd et al. 2015; Shuman and Marsicek 2016; Kaufman et al. 2016; Izumi and Bartlein 2016; Commerford et al. 2017) and across the Canada, Canadian subarctic, arctic and Greenland (e.g. Kerwin et al. 2004; Fréchette et al. 2008; Viau and Gajewski 2009; Fréchette and de Vernal 2013; O'Reilly et al. 2014; Gajewski 2015; Keizer et al. 2015). In Québec-Labrador, Holocene quantitative summer temperature reconstructions based on pollen are just starting to emerge (e.g. Muller et al. 2003; Lavoie et al. 2013; Paquette and Gajewski 2013; Lafontaine-Boyer and Gajewski 2014; Richerol et al. 2016; Fréchette et al. 2018).

As pollen data, chironomids assemblages are a source of long-term information to quantify past climatic variability, particularly to estimate the summer temperature

(Heiri et al. 2015). Holocene chironomid-inferred summer temperature reconstructions have been yielded for North America (e.g. Lotter et al. 1999; Porinchu et al. 2002; Walker and Cwynar 2006; Fortin et al. 2015; Medeiros et al. 2015), across Canada (e.g. Rosenberg et al. 2004; Chase et al. 2008; Upiter et al. 2014), for Canadian arctic (e.g. Porinchu et al. 2009; Rolland et al. 2009; Fortin and Gajewski 2016) and for arctic and southern Québec (e.g. Axford et al., 2009; Fallu et al., 2005; Hausmann et al., 2011; Saulnier-Talbot et al., 2015). However, the boreal forest of western Québec is almost depleted of chironomid quantitative climate reconstructions, although it contains numerous lakes with sediment preserving chironomids to quantify past climatic variability at high temporal resolution as showed by Bajolle et al. (2018a, 2018b).

This study presents the results of a paleoclimatic reconstruction based on two biotic indicators (pollen and chironomid) for two sites in the boreal forest of western Québec (Canada). Pollen analysis is often used to reconstruct vegetation dynamics and/or climatic fluctuations (temperature and precipitation) (Viau and Gajewski 2009; Richerol et al. 2016; Ladd et al. 2017). The August temperature can be reconstructed using different methods such as transfer functions (Birks 1998), or assemblages approach such as the Modern Analogue Technique (MAT: Guiot 1990). Chironomids have been shown to generate high-resolution independent air temperature records due to their capacity to respond rapidly to climatic fluctuation with their short generation time and the ability of winged adults to move readily from site to site (Walker and Mathewes 1987; Larocque-Tobler et al. 2015). Today, it is recognized that chironomids can record small amplitude Holocene temperature changes (Brooks 2006; Larocque et al. 2009; Larocque-Tobler et al. 2011, 2015).

However, the combination of pollen and chironomids to infer past climate changes has the advantage of providing a direct validation of climate reconstructions from two independent (aquatic and terrestrial) (Peyron et al. 2005; Birks et al. 2014; Engels et al. 2014; Veski et al. 2015). The first two chironomid-inferred temperature reconstructions in the coniferous boreal forest of western Québec have been investigated recently (Bajolle et al. 2018a, 2018b).

Major climatic changes were identified such as the Holocene Thermal Maximum (HTM, a warm and dry period) between *ca.* 8300 and 3500 cal BP and the cold and wet Neoglacial period (<3500 cal BP), the latter having been interrupted by the Medieval Climate Anomaly (MCA, a less warm than HTM and wet event) around *ca.* 1000 cal BP. The changes in timing and duration of these climatic periods and events were similar with other regional, North American and Northern Hemisphere records based on different proxies (Kaufman 2004; Viau et al. 2006; Axford et al. 2009; Ljungqvist 2010; Kobashi et al. 2010; PAGES 2k Consortium 2013).

If the temperature records inferred by chironomids and pollen assemblages present the same pattern, it can be concluded that the reconstructed climate history is more solid and to be valid, while discrepancies can be used to better decipher the impact of local environmental factors during taphonomical processes on each proxy production and sequestration in lake sediments.

In this context, the aims of the present paper were to: (i) reconstruct Holocene vegetation and August temperature changes using pollen at two sites of the boreal forest of western Québec; (ii) cross-compare pollen and chironomids-inferred temperature values in order to highlight a potential similar pattern in August temperature changes; and (iii) establish a high resolution and robust reconstruction of temperature changes during the Holocene period in western Québec boreal forest.

3.4 Materials and methods

3.4.1 Study sites

Lac Lili (unofficial name; 49° 10' 25.501"N; 79° 22' 26.931"O, 320 m a.s.l) and *Lac Aurélie* (unofficial name; 50°25’12” N; 74°13’47” W; 440 m a.s.l) are located 395 km from each other (Fig. 3.1). In western Québec, *Lac Lili* covers an area of 10 ha and has a maximum water depth of about 1.40 m. *Lac Aurélie*, located in central Québec, covers an area of 0.5 ha, has a maximum depth of about 10 m. Both regions deglaciated around ca. 9000 cal BP (Dyke 2004). However, they were submerged by the proglacial Lake Ojibway. The final draining of Lake Ojibway occurred 8470 years ago and has left a thick clayey glaciolacustrine deposit (Vincent and Hardy 1977).

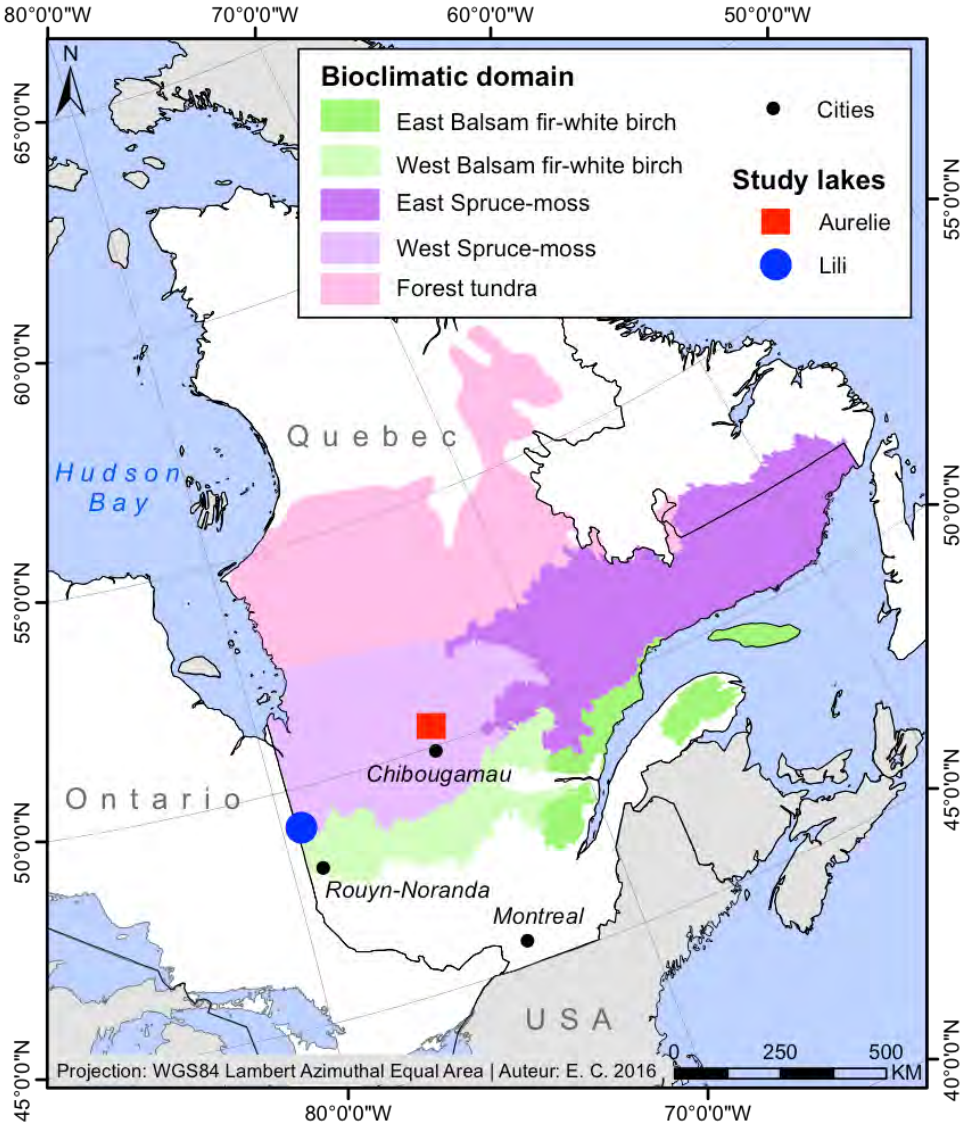

Figure 3.1 Location map of study sites: *Lac Lili* and *Lac Aurélie* (black spruce – feather moss bioclimatic domain).

The study sites belong to the black spruce-moss bioclimatic domain (Fig. 3.1). The forest cover around *Lac Lili* is dominated by mixed populations of *Picea mariana* Mill., *Pinus banksiana* Lamb. and *Populus tremuloides* Michx, while *Lac Aurélie* is mainly dominated by coniferous especially *P. mariana* and *P. banksiana.* (Blouin and Berger

2005). Mean annual temperature from the closest meteorological stations (*Lac Lili*, La Sarre: 1961-1990) and (*Lac Aurélie,* Chapais 2: 1961-1990) are 0.8 °C and -0.1 °C, respectively. Mean august temperatures are 15 °C at *Lac Lili* and 14.5 °C at *Lac Aurélie*. Mean Annual precipitations are 640 mm, of which 250 cm falling as snow at *Lac Lili*, and 648 mm of which 270 cm falling as snow at *Lac Aurélie* (Environnement Canada 2017).

3.4.2 Coring stratigraphy and chronology

For each lake, two overlapping sediment cores were taken in March 2010 (*Lac Aurélie*) and March 2014 (*Lac Lili*) on a frozen surface at the centre of the lake using a modified Livingstone-type square-rod piston corer (100 × 5 cm) in 10 m and 1.40 m of water, respectively. The water-sediment interface was collected using a Kajak-Brinkhurst (KB) gravity corer (Glew 1991). All the extracted cores were sampled into 0.5 cm intervals to obtain a high-scale temporal resolution.

Terrestrial plant macrofossils were retrieved from seven (*Lac Lili*) and six (*Lac Aurélie*) samples for AMS radiocarbon dating (Table 3.1). The chronology of *Lac Lili* has already been described in Bajolle et al. (2018a) and that of *Lac Aurélie* in El-Guellab et al. (2015). The ^{14}C dates were calibrated at 2σ-ranges using the Clam R package based on the IntCal13.14C data set (Hua et al. 2013; Reimer et al. 2013). Age-depth models were obtained using a Bayesian method (Parnell et al. 2008). All dates are expressed in calibrated years before present and rounding to the nearest hundredth (hereafter cal BP).

Table 3.1 Radiocarbon and calibrated ages, *Lac Lili* and *Lac Aurélie*.

Laboratory code	Depth (cm)	^{14}C age (cal BP)	Calibrated ^{14}C age ranges (cal BP; 2σ-ranges)	Materials
Lac Lili				
Beta-427033	23-27	410 ± 30	**430-519 (0.83)**	Plant macroremains
			331-358 (0.12)	Plant macroremains
Beta-427032	48-50	1150 ± 30	**978-1145 (0.90)**	Plant macroremains
			1158-117à (0.05)	Plant macroremains
Beta-427031	118-120	2730 ± 30	**2762-2876 (0.95)**	Plant macroremains
			2915-2915 (0.01)	Plant macroremains
Beta-427030	178-182	3180 ± 30	**3358-3453 (0.95)**	Plant macroremains
Beta-427029	228-232	4780 ± 30	**5468-5589 (0.95)**	Plant macroremains
Beta-427028	278-282	6150 ± 30	**6966-7159 (0.94)**	Plant macroremains
			6960-6963 (0.01)	Plant macroremains
Beta-427027	304-306	7670 ± 30	**8407-8522 (0.90)**	Plant macroremains
			8528-8538 (0.05)	Plant macroremains

Suite

Lac Aurélie				
Poz-35983	43-44	2870 ± 30	**2916-3076 (0.93)**	Plant macroremains
			2879-2913 (0.06)	Plant macroremains
Poz-35984	111-112	3990 ± 35	**4404-4535 (0.98)**	Plant macroremains
			4556-4567 (0.01)	Plant macroremains
Poz-36014	163-164	4750 ± 35	**5451-5586 (0.83)**	Plant macroremains
			5329-5377 (0.16)	Plant macroremains
Poz-36016	220-221	6140 ± 40	**6930-7163 (1.0)**	Plant macroremains
Poz-36017	236-237	6490 ± 40	**7317-7474 (1.0)**	Plant macroremains
Poz-36018	326-327	7460 ± 50	**8186-8373 (1.0)**	Plant macroremains

*Beta: Beta Analytic Laboratory, Poz: Poznan radiocarbon Laboratory. Calibrated ages the means of the 2σ-ranges with highest probabilities (bold). The ^{14}C dates were calibrated using the Clam R package based on the IntCal13.14C data set (Reimer 2013)

3.4.3 Pollen analyses

Subsamples (1 cm^3) were collected at intervals of 2-cm (*Lac Lili*), providing temporal resolution between *ca*. 20 and 100 years, and at 4-cm (*Lac Aurélie*) with temporal resolution between *ca.* 40 and 300 years. *Lycopodium* marker tablets (Stockmarr 1971) were added to each subsample for estimation of the pollen concentration (CP: grains cm^{-3}). Pollen grains and spores were extracted following Faegri et al. (1989) in which successive suspensions in 40 % HF, 10 % HCl and acetolysis were used to remove silicates, carbonates and cellulose respectively. Ten percent KOH was used to deflocculate the sediments in preparation for staining with fuchsine.

The pollen grains and spores were counted under a light microscope at 400× magnification. Identification followed using McAndrews et al. (1973) and Richard (1970) supplemented by the modern pollen collection of the *Institut des Sciences de l'Évolution de Montpellier (ISEM, Université de Montpellier, France)*. At least 300 pollen grains of terrestrial vascular plants were counted per subsample (pollen sum). Pollen percentages, concentrations and accumulation rates (PAR: grains cm^{-2} yr^{-1}) were calculated based on the pollen sum. Pollen diagrams were constructed using the C2 software (Juggins 2013). *Juniperus communis* and *Thuja occidentalis* were combined into *Juniperus/Thuja*, *Ostrya* sp. and *Carpinus* sp. into *Ostrya/Capinus*, and *Pinus banksiana* and *Pinus resinosa* into *Pinus banksiana/resinosa*_type owing to their morphological similarity almost indistinguishable (McAndrews et al. 1973). *Picea mariana* and *Picea glauca* pollen grains were differentiated according to saccus shape, attachment reticulum, and saccus area/corpus area (McAndrews et al. 1973; Hansen and Engstrom 1985). However, with a *Picea glauca* percentage <1 % per sample identified, *P. glauca* and *P. mariana* pollen grains were combined into *Picea mariana*_type. Only pollen taxa reaching at least 1 % in at least one sample were illustrated in the pollen diagrams. All herb species were grouped.

A constrained sum-of-squares cluster analysis (CONISS; Grimm 1987) was used to identify pollen assemblage zones, and the significance of each zone was tested with the broken stick model (Bennett et al. 1986) using the 'rioja' R package (Juggins et al. 2015).

3.4.4 Pollen chironomid inferred August temperature reconstructions

3.4.4.1 Pollen inferred reconstruction

For the MAT, a comparison between fossil and modern assemblages is performed through the calculation of a dissimilarity index based on the squared chord distance (SCD, Overpeck et al. 1985). The temperature estimate of each fossil assemblage is calculated as the weighted average of the climate values corresponding to the best modern assemblages selected (with the lowest distance). Here, we used 5 analogues, which limit the risk of excessive heterogeneity within the modern analogue retained for reconstruction. The modern pollen database comprises 1010 sites and 52 taxa, extracted from the North American and Greenland pollen database (Whitmore et al. 2005) but restricted to cover eastern Canada (forest tundra, boreal and mixed forests above 44°N and east of 100°W). Further methodological details (sites and modern climate data) can be found in Fréchette et al. (2018).

The pollen-inferred August temperature reconstructions via MAT model were performed with the "bioindic" package (Guiot and Gally, 2014) built on the R program. In order to validate tests and error calculations, we split off the data set and followed methods as described by de Vernal et al. (2013). The correlation coefficient and the error of prediction were established at r2=0.89 and RMSE=1.13 °C, respectively.

3.4.4.2 Chironomids inferred reconstruction

The chironomid-inferred August temperature reconstructions were performed with the Eastern Canadian WAPLS transfer function published by Larocque (2008) and modified by Bajolle et al. (2018b). Two lakes were added and 11 lakes had their temperature measurements changed to mean August air temperatures (Lakes A to H) as the earlier version of the calibration was based on punctual measurements. In the new Eastern Canadian transfer function, mean August temperatures varied from 3 °C to 21 °C (instead of 27 °C) for a temperature gradient of 18 °C. The calibration set comprises 75 lakes and 79 taxa. The WAPLS 999-bootstrap transfer function with two components yielded a correlation coefficient (r^2_{boot}) of 0.85, a rooted mean-square error of prediction (RMSEP) of 1.67 °C, and a maximum bias of 3.05 °C. To validate the use of the transfer function, an evaluation of modern analogues for each sample was performed by the CANOCO 4.5 program using the minimum distance of the fossil sample to the training set assemblages (Overpeck et al. 1985). Fossil samples with a distance above the 20th percentile were considered as having “no analogues” (Overpeck et al. 1985).

At *Lac Aurélie,* none of the 180 fossil samples (at temporal resolution varying between *ca.* 5 and 165 years) was above the 10th percentile, thus all downcore samples had a good fit to temperature. At *Lac Lili,* eight of the 116 fossil samples (at temporal resolution varying between *ca.* 20 and 100 years) had no modern analogues compared to the training set samples. More details are given in Bajolle et al. (2018a, 2018b).
Correlations between the pollen- and chironomid-inferred August temperature reconstructions were computed using Pearson’s correlation coefficients with a 95 % confidence interval computed using a bootstrapping technique accounting for serial persistence in data (Mudelsee 2003).

3.4.5 Combined inferred August temperature reconstruction

To interpret and compare the temperature reconstructions from the two proxies, a LOESS regression (span = 0.2) has been applied using the R software. Each August temperature reconstruction relative to the 1961-1990 reference period was interpolated to an annual resolution using spline estimation. A combined annually-resolved August temperature reconstruction was then created by bootstrapping (resampling the polled means 999 times) of these individual reconstructions and collecting the 2.5th, 50th, and 97.5th percentiles of the bootstrapped distributions.

Correlation between the combined temperature reconstruction and the multi-proxy (based on tree-rings and ice core data essentially) North hemisphere Arctic annual temperature reconstruction (relative to 1961-1990 reference period) (PAGES 2k Consortium 2013) was computed during the past two millennia, using Pearson's correlation coefficients with a 95 % confidence interval computed using a bootstrapping technique accounting for serial persistence in data (Mudelsee 2003). Further, this combined August temperature record (hereafter, CATR) allowed a comparison with other climate reconstructions of the duration and amplitude of the major climate periods and events occurred during the Holocene.

3.5 Results and interpretations

3.5.1 Vegetation history

At *Lac Lili,* 49 taxa (39 woody plants and 10 herbs) were identified in the 154 samples analysed. Four main zones (Lpo-1 to Lpo-4) as well as subzones were numerically defined (Fig. 3.2) to describe the observed changes in the main pollen assemblages. The description of each (sub-)zone is summarized in Table 3.2.

At *Lac Aurélie,* 61 taxa (37 wood plants and 24 herbs) were identified in the 79 samples analysed. Four zones (Apo-1 to Apo-4) as well as subzones were numerically defined (Fig. 3.3). The description of each (sub-) zone is summarized the Table 3.3.

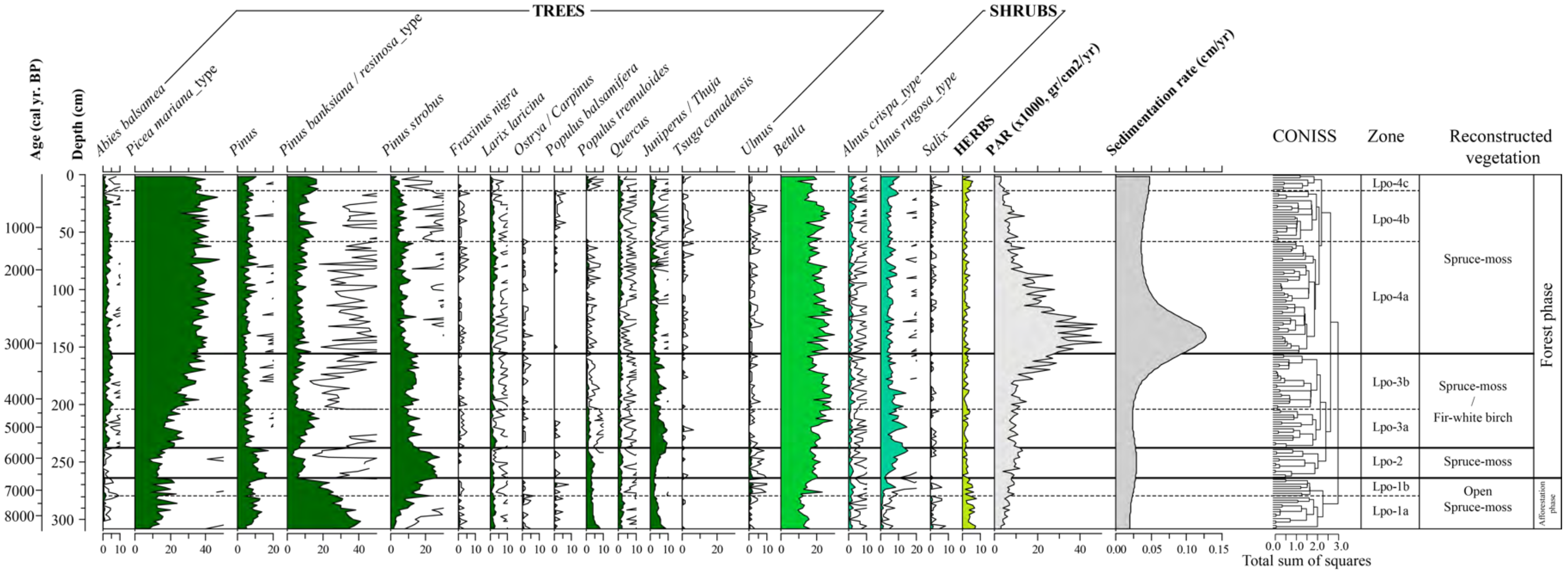

Figure 3.2 Pollen percentage stratigraphy of *Lac Lili*. The 19 most abundant taxa with a value ≥ 1 % in at least one sample are shown. Pollen accumulation rate concentration (PAR, grains cm^{-2}.yr^{-1}) and sedimentation rate (cm^{-1}yr^{-1}) are represented. CONISS identified four significant zones (horizontal solid line) but two (horizontal dashed lines) further separations were used to describe the observed changes in the main pollen assemblages. Reconstructed vegetation history is identified.

Table 3.2 The zone descriptions of *Lac Lili*'s pollen diagram. For each zone, the age (cal BP) and depth (cm) are yielded. Species present in each are illustrated by their average percentages, taxa in bold represent those that dominate the zone, key species, and reconstructed vegetation history are identified. Pollen Accumulation Rate (PAR, grains cm^{-2} yr^{-1}) is yielded. The afforestation (dark gray) and forest (light gray) phases are also indicated.

Zone Age (cal BP) Depth (cm)	**Species (Taxa in bold dominate the zone) ↗ increase and ↘ decrease in pollen percentages**	**Key species**	**Reconstructed vegetation**	**PAR** (grains cm^{-2}yr^{-1})
Lpo-4c *ca.* 240-0 14-0	- ***P. banksiana/resinosa*-type (15 %)** and *A. rugosa*-type (8 %) ↗ - ***P. mariana*-type (35 %), *Betula* sp. (17 %)** and *P. strobus* (3 %) slighty ↘ - *P. tremuloides* reappears (1 %) - Herbs slighty ↗ (4 %)	***Picea mariana*-type** ***Betula* sp.** ***Pinus* sp.** ***Abies balsamea***	**Spruce-moss**	↘ lowest values *ca.* 5200
Lpo-4b *ca.* 1300-240 14-60	- ***P. mariana*-type (still high, 37 %),** *P. banksiana/resinosa*-type (20 %) and *A. balsamea* (>3 %) slighty ↗ - *P. strobus* (6 %) ↘ - No pollen grains of *P. tremuloides* - ***Betula* sp. (20 %)** ↗ then ↘ towards the end			↘ *ca.* 7700
Lpo-4a *ca.* 3100-1300 60-160	- ***P. mariana*-type (37 %) and *Betula* sp. (>23 %)** ↗ to their maximum, - *P. strobus* (10 %), *Juniperus/Thuja* (3 %) and *A. balsamea* (3 %) ↘ - *L. laricina* (2 %) ↗			Rapidly ↗ from 3700 cal BP Between 3700-2500 cal BP *ca.* 29 600 **average maximum**
Lpo-3b *ca.* 4300-3100 160-200	- ***Betula* (23 %, maximum), *P. mariana*-type (30 %)** - *P. strobus* (>12 %), *A. balsamea* (highest values 4 %), *Juniperus/Thuja* (5 %) and *A. rugosa*-type (7 %)	***Betula* sp.** ***Picea mariana*-type** ***Pinus strobus*** ***Abies balsamea***	**Spruce-moss** / **Fir-white birch**	
Lpo-3a *ca.* 5800-4300	- *P. strobus* (10 %) and *Pinus* spp (6 %) ↘ - *P. banksiana/resinosa*-type (11 %), ***Betula* sp. (21 %)** and ***P. mariana*-type (21 %)**↗	***Picea mariana*-type** ***Pinus* sp.**		↘

(suite)

200-240	- *Juniperus/Thuja* (highest percentages, 7 %), *Abies balsamea* (2 %)	***Thuja***		*ca.* 15 100
Lpo-2 *ca.* 6600-5800 240-260	**- *P. strobus* (24 %, highest values)** - *P. banksiana/resinosa*-type (7 %) and **_P. mariana_-type (13 %)** ↘ - *Junipers/Thuja* (5 %) ↗ towards the end **- _Betula_ sp. (19 %)** and *A. rugosa*-type (8 %) ↗ - Herbs (2 %) ↘	***Pinus strobus*** **_Betula_ sp.** **_Picea mariana_-type**	**Spruce-moss**	↗ *ca.* 23 000
Lpo-1b *ca.* 7200-6600 260-280	**- *P. strobus* (17 %)** ↗ **- _P. banksiana/resinosa-type_ (22 %),** *Pinus* (8 %) and *Junipers/Thuja* (2 %)↘ - *Ulmus* (<1 %), **_Betula_ sp. (15 %)** and **_P. mariana_-type (17 %)** ↗ - *Alnus rugosa*-type ↗ to 10 % - Herbs still relatively high (4 %)	***Pinus banksiana/resinosa-type*** **_Picea mariana_-type** **_Betula_ sp.** **_Populus_ sp.**	**Open** **Spruce-moss**	↗ *ca.* 6700
Lpo-1a *ca.* 8500-7200 380-310	**- _P. banksiana/resinosa-type_ (highest values, 34 %), _P. mariana_-type (14 %), _Betula_ sp. (13 %) dominate** - *P. strobus* (6 %) ↗ - *Populus tremuloides* and *Juniperus/Thuja* (5 %) ↘ towards the end - Herbs (highest percentages, 5 %) - *Larix laricina* and *Quercus* (5 %) - *Abies balsamea, Fraxinus nigra*-type, *Populus balsamifera* and *Ostrya/Carpinus, Alnus* spp and *Salix* sporadically recorded			low values *ca.* 3400 in average

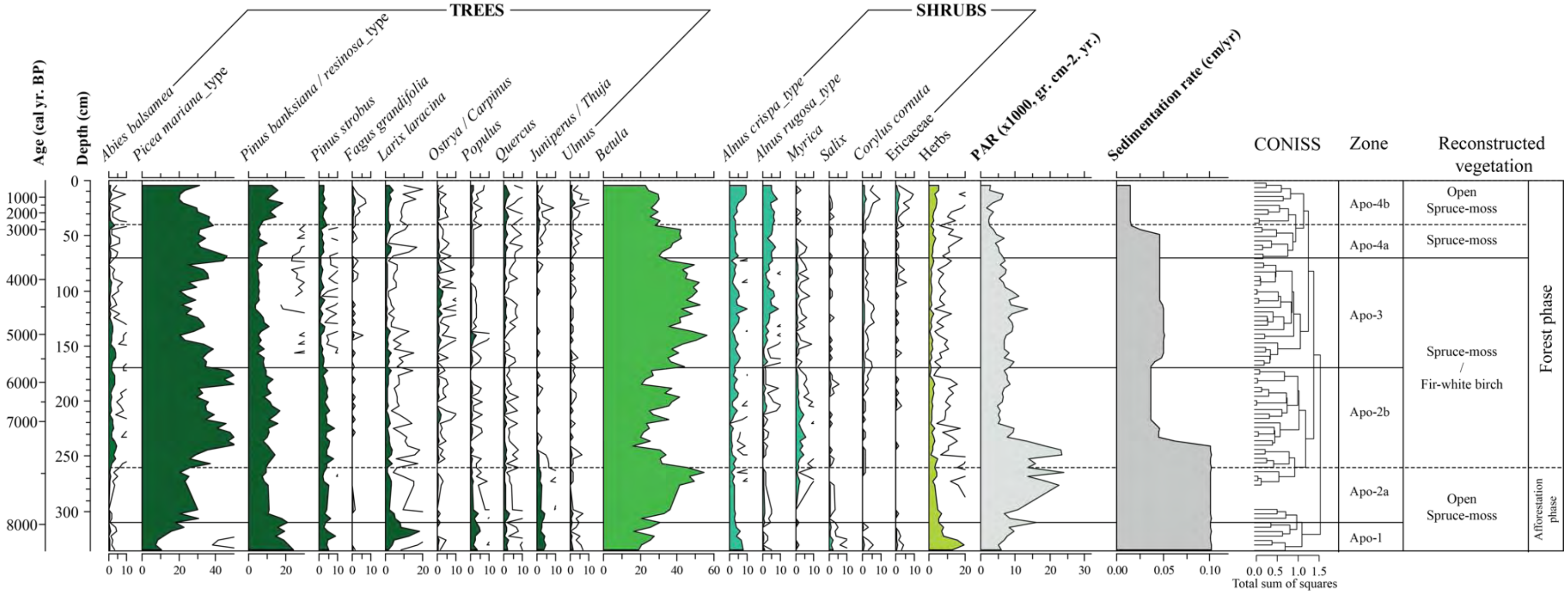

Figure 3.3 Pollen percentage stratigraphy of *Lac Aurélie*. The 19 most abundant taxa with a value ≥ 1 % in at least one sample are illustrated. Pollen Accumulation Rate concentration (PAR, gr.cm^{-2}.yr^{-1}) and sedimentation rate (cm^{-1}yr^{-1}) are represented. CONISS identified four significant zones (horizontal solid line) but four (horizontal dashed lines) further separations were used based on the ecological knowledge to describe the observed changes in the main pollen assemblages. Reconstructed vegetation history is identified.

Table 3.3 The zone descriptions of *Lac Aurélie*'s pollen diagram. For each zone, the Age (cal BP) and depth (cm) are yielded. Species present in each are illustrated by their average percentages, taxa in bold represent those that dominate the zone, key species and reconstructed vegetation history are identified. Pollen Accumulation Rate (PAR, grains cm^{-2} yr^{-1}) is yielded. The afforestation (dark gray) and forest (light gray) phases are also indicated.

Zone Age (cal BP) Depth (cm)	**Species** **(Taxa in bold dominate the zone)** **↗ increase and ↘ decrease in pollen percentages**	**Key species**	**Reconstructed vegetation**	**PAR** (grains cm^{-2}yr^{-1})
Apo-4b *ca.* 2800-0 40-0	- ***P. mariana*-type (30 %) and *Betula* (27 %)** ↘ - ***P. banksiana/resinosa*-type (13 %)** and *A. crispa*-type (6 %)↗ - *A. balsamea, Fagus grandifolia, Populus, Juniperus/Thuja*, *Ulmus, Corylus cornuta* (1 %) and Ericaceae slightly ↗ to 1 % and to 2 % for *L. laricina* and *Quercus.* - *A. rugosa*-type (6 %) and Herbs (4 %) slightly ↗	***Picea mariana*-type** ***Betula*** ***Pinus banksiana/resinosa*-type**	**Open Spruce-moss**	↘ *ca.* 3400 lowest values
Apo-4a *ca.* 3600-2800 72-40	- ***P. mariana*-type (36 %),** *L. laricina* (>1 %), *Quercus* (>1 %), *A. rugosa*-type (5 %) and Herbs (3 %) ↗ - ***Betula* sp. (37 %)**, *A. crispa*-type (3 %) and *A. balsamea* (<1 %) ↘	***Picea mariana*-type** ***Betula***	**Spruce-moss**	↘ *ca.* 5400
Apo-3 *ca.* 5600-3600 168-72	- ***P. mariana*-type (30 %)** ↘ while *Betula* sp. (45 %)↗ - *A. rugosa-type (3 %) and A. crispa-type (4 %)* ↗ - *P. banksiana/resinosa*-type (6 %), *P. strobus* (2 %) and *A. balsamea* (<2 %) ↘	***Betula* sp.** ***Picea mariana*-type**	**Spruce-moss** **/** **Fir-white birch**	↘ *ca.* 8100

(suite)

Apo-2b *ca.* 7500-5600 260-168	***P. mariana*-type (highest values 40 %)** ↘ fluctuating between 30 and 50 %, - ***Betula* sp. (30 %)** ↘ fluctuating between 15 and 40 % - *A. balsamea* and *Myrica* (their highest values, >2 %) ↗ - *P. banksiana/resinosa*-type (>12 %), *P. strobus* (5 %) and *Alnus* spp ↗ - *L. laricina* and Herbs (2 %) ↘	***Picea mariana*-type** ***Betula* sp.** ***Pinus* sp.**		↘ *ca.* 10 000
Apo-2a *ca.* 8000-7500 310-260	- ***Betula* sp. (40 %)** and ***P. mariana*- type (24 %)** ↗ - *P. banksiana/resinosa*-type (12 %), *P. strobus* (4 %), *L. laricina* (4 %), *Populus* (>1 %), *Quercus* (>1 %), *Juniperus/Thuja* (3 %), *A. crispa*-type (3 %) and Herbs (5 %) ↘	***Betula* sp.** ***Pinus* sp.** ***Picea mariana*-type**	**Open** **Spruce-moss**	↗ *ca.* 15 000 highest values
Apo-1 *ca.* 8400-8000 335-310	***Betula* sp. (23 %, on average), *P. banksiana/resinosa*-type *(highest values, 20 %),*** *P. mariana*-type (17 %) and Herbs (highest values, 12 %) *P. strobus* (5 %), *Larix laricina* (8 %), *Populus* (4 %), *Juniperus/Thuja (4 %), A. crispa*-type (6 %) and *Quercus* (2 %) with their highest percentages			*ca.* 7200 in average

In general, pollen assemblages of both sites were characteristic of the black spruce-feather moss of western Québec, dominated by *Picea mariana*-type, *Betula* and *Pinus banksiana/resinosa*_type.

From 8500 to 7500-6600 cal BP, low PAR values and the high representation of herbs in the pollen assemblages suggest an open boreal forest cover dominated by *P. mariana*_type and *P. banksiana/resinosa*_type, corresponding to an afforestation phase (*Lac Lili*: Zone Lpo-1; *Lac Aurélie*: Zone Apo-1). At both sites, subsequent pollen zones (*Lac Lili:* Zones Lpo-2 to Lpo-4; *Lac Aurélie*: Zones Apo-2 to Apo-4) correspond to the forest phase. *P. mariana*_type and *Betula* dominate pollen assemblages of the forest phase, but *Abies balsamea*, a low pollen producer (Richard, 1993), was also abundant, especially in the pollen diagram of *Lac Lili*.

3.5.2 Quantitative August temperature reconstructions

Both proxies in *Lac Lili* (Fig. 3.4A and 3.4B) and *Lac Aurélie* (Fig. 3.4C-D) showed similar patterns of temperature. However, correlations between the four individual reconstructions (Table 3.4) are not statistically significant except to between the chironomid- and pollen-inferred temperature reconstructions at *Lac Lili* and *Lac Aurélie,* respectively, which showed a low significant correlation (0.22; 95 % confidence intervals [0.03; 0.39]). The low temperature variations from data and uncertainty in chronologies could partly explains this lack of statistical significance. Chironomid-inferred August temperature reconstructions show generally larger amplitude changes. From *ca.* 8500 to *ca.* 4000-5000 cal BP, proxies-inferred individual reconstructions recorded a decreasing trend of 1 to 2 °C. Then, relatively stable values are reconstructed from *ca.* 4000-5000 to *ca*. 1000 cal BP (Fig. 4B-D). Finally, a cooling (about 1 °C) is recorded during the last millennium for all records. The reconstruction inferred from pollen and chironomids matched well except the chironomids values reconstructed for *Lac Lili* from *ca.* 4000-5000 to *ca.* 1000 cal BP where temperatures increase (Fig. 3.4A).

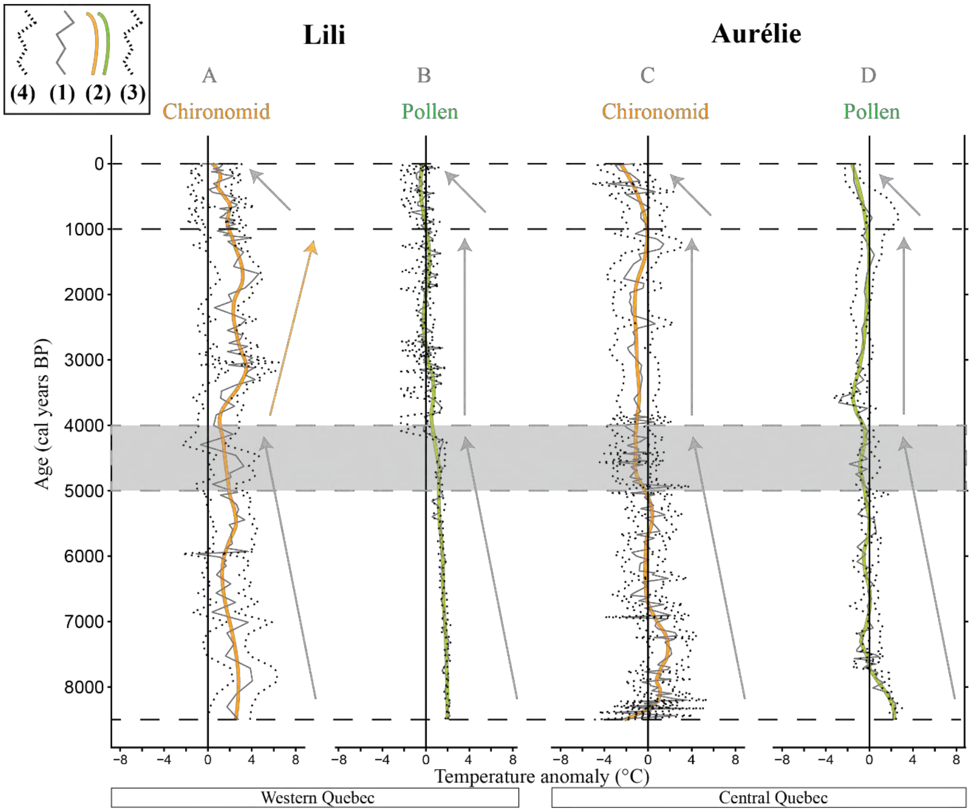

Figure 3.4 August temperature reconstructions, in anomalies relative to the 1961-1990 reference period (°C). (A) Chironomid-inferred August temperature anomaly at *Lac Lili* (Bajolle et al. 2018a), (B) pollen-inferred August temperature anomaly at *Lac Lili*, (C) chironomid-inferred August temperature anomaly at *Lac Aurélie* (Bajolle et al, 2018b) and (D) Pollen-inferred August temperature anomaly at *Aurélie*. The curves reconstructed from the weighted-averaging partial least squares regression (WAPLS) for chironomid-proxy and the modern analogue technique (MAT) for pollen-proxy show (1, chironomid) the mean value calculated over the temperature optima for each taxon performed using weighted average (Larocque-Tobler et al, 2015 and Bajolle et al, 2018a, 2018b), (1, pollen) the mean value calculated over the 5 best analogues, (2) the smoothed mean value using a LOESS regression (span=0.2), (3) the mean minimum and (4) the mean maximum values. The horizontal dotted lines indicate the three main chronological periods identified with their temperature trend illustrates by grey arrows. The transition 4000-5000 is illustrated by the grey band. Compared to all reconstructions only the chironomid-inferred temperature reconstruction at *Lac Lili* show a different temperature trend between 4000 and 100 cal BP indicate by an orange arrow.

Table 3.4 Pearson’s correlation coefficients

Inferred August temperature anomaly (°C)	Lili chironomid	Lili pollen	Aurélie chironomid	Aurélie pollen	**PAGE 2k consortium, 2013**
Lili chironomid	1.00				
Lili pollen	0.03 [-0.19; 0.24]	1.00			
Aurélie chironomid	0.14 [-0.11; 0.37]	0.42 [-0.10; 0.77]	1.00		
Aurélie pollen	**0.22** ** **[0.03; 0.39]**	0.36 [-0.06; 0.67]	0.28 [-0.03; 0.54]	1.00	
CATR					**0.38**** **[0.21, 0.53]**

Significant correlation coefficients are in boldface type with *P* values reported as follow: ***P*<0.05

The combined August temperature reconstruction (CATR) (Fig. 3.5) showed the same pattern than those obtained from the individual reconstructions, i.e. a gradual long-term decreasing trend and three main periods identified:

1) *ca.* 8500-4500 cal yr. BP: temperature anomalies were warmer than today with a decreasing trend (mean of +1.0 °C) marked by a cold peak at *ca.* 5900 cal BP;

2) *ca.* 4500-1000 cal yr. BP: temperature anomalies continued to decline toward relatively stable values oscillating around the current one (mean of *ca.* +0.3 °C) punctuated by several warmer periods at *ca.* 4200-4100, 3900-3700, 3400-3000, 2700-2300, 1900-1700 and 1400-1100 cal BP interrupted by several colder peaks or periods at *ca.* 4300, 4000, 3600, 2200 and 1700-1500 cal BP;

3) *ca*. 1000 cal BP to present-day: the temperature anomalies increased compared to previous periods (mean of *ca.* -0.1 °C) with some abrupt cold peaks at *ca.* 400, 300 and 50 cal BP.

During the past two millennia, a significant correlation between time series (combined and Arctic annual temperature reconstructions) is 0.38 with the 95 % confidence intervals [0.21, 0.52] (Table 3.4, Fig. 3.6).

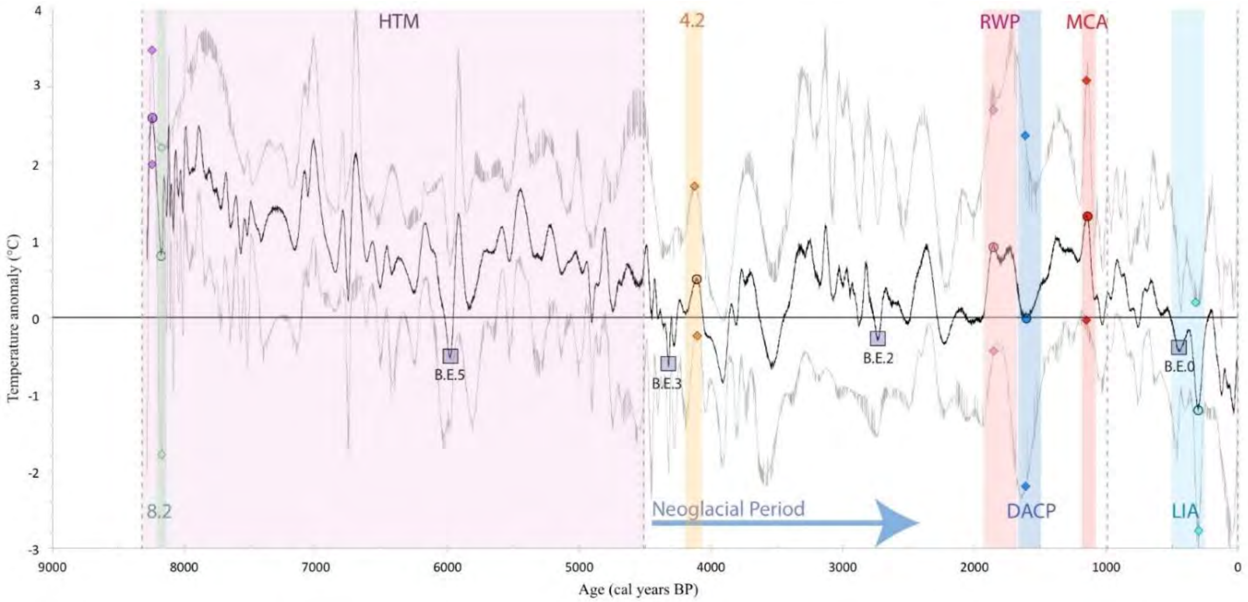

Figure 3.5 The combined August temperature reconstruction (CATR) relative to 1961-1990 reference period. The vertical dotted lines illustrate the three main chronological period identified: (i) 8500-4500 cal BP characterized as the Holocene Thermal Maximum (HTM), in which August temperatures were always warmer than today (maximal mean value of *ca.* +2.6 °C); (ii) 4500-1000 cal BP, marked by the onset of the cool and wet Neoglacial period, where August temperatures oscillating around modern values; and 1000 cal BP to present, characterized by a relevant decrease of temperature. Particular climate events have been identified into each period and characterized by their thermal anomaly from the modern temperature: (i) the 8200 cold event (sharp drop in temperature, about 2 °C); (ii) the 4200 cal BP warm event (*ca.* +0.5 °C); (iii) the Roman Warm Period (*ca.* 1900-1700 cal BP, *ca.* +1.0 °C); (iv) the Dark Ages Cold Period (*ca.* 1700-1500 cal BP, anomaly close to 0 °C); (v) the Medieval Climate Anomaly (around *ca.* 1100 cal BP, *ca.* +1.3 °C); and (vi) the Little Age Ice (*ca.* 250-500 cal BP, *ca.*-1.2 °C). A series of rapid cold peaks were also observed at 5900, 4300, 2800 and 400 cal BP referring probably to the “Bond events”.

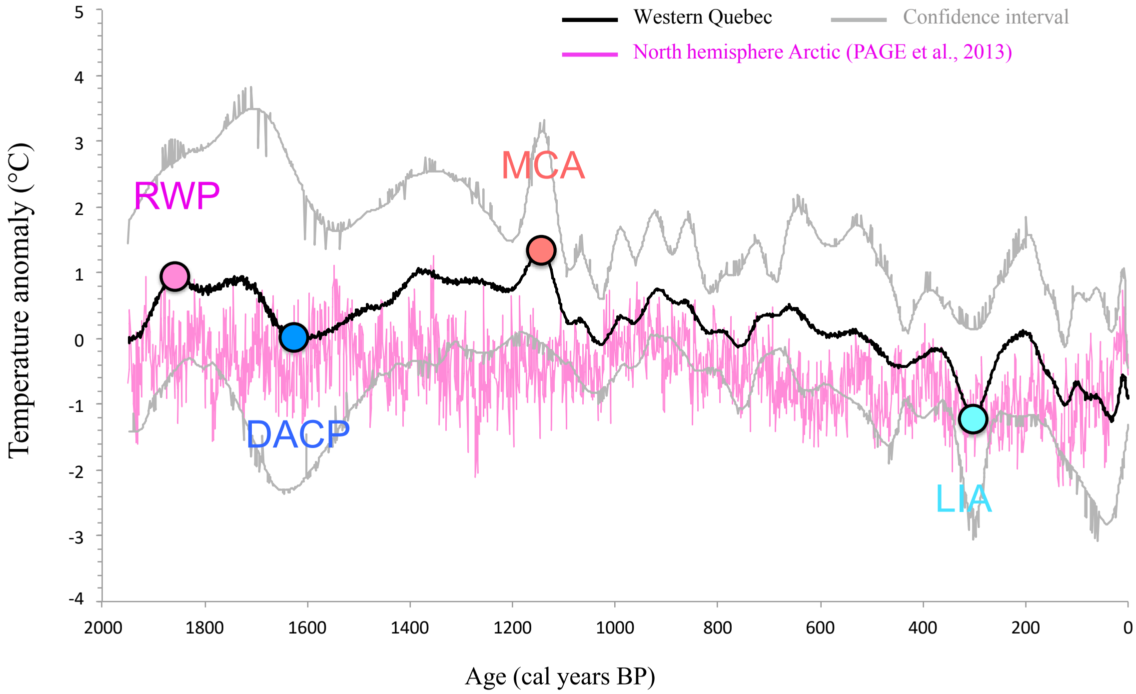

Figure 3.6 Comparison of our western Québec reconstruction (CATR) with the North Hemisphere Arctic temperature based on tree rings and diatoms (PAGES 2k Consortium (2013) from 1961-1990 during the past 2000 years. A significant correlation r between time series (combined and Arctic temperature reconstructions) is 0.38 with the 95 % confidence intervals [0.21, 0.52].

3.6 Discussion

3.6.1 Combined approach

Pollen data has the capacity to give information about temperature and precipitation because plant distributions respond to bioclimatic parameters such as winter temperature, growing degree days and moisture balance (Peyron et al. 2005). Nevertheless, the vegetation dynamic can be also influenced by other factors such as edaphic conditions, fire regime and their interactions during the Holocene (Bremond et al. 2010; Genries et al. 2012; Blarquez et al. 2015; Remy et al. 2017b), that may yield biases in climatic reconstruction (Peyron et al. 2005). Consequently, to confirm the accuracy of the pollen-based temperature reconstruction, it is essential to compare the results with at least one independent temperature proxy (Birks 2003) such as chironomid (Peyron et al. 2005; Samartin et al. 2017) or molecular biomarkers (Watson et al. 2018).

Our results showed that the pollen- and chironomid-inferred individual reconstructions yielded similar patterns in temperature variability over the past 8000 years (Fig. 3.4), suggesting that both proxies probably responded to climate forcings. As follows, we assumed that the combined approach (chironomid-pollen) performed here provided a robust regional reconstruction of temperatures during the Holocene for western Québec.

The relevant correspondence between our results and the North Hemisphere Arctic temperature reconstruction based on tree-rings and ice core data essentially (PAGES 2k Consortium 2013) on the past two millennia strengthened this hypothesis. Between 8000 and 2000 cal BP, our reconstruction indicated a cooling trend about 2.5 °C, while based on hydrogen isotope record in the north-eastern United States Gao et al. (2017) demonstrated a cooling trend about 3.4 °C. Moreover, our reconstruction is able to infer rapid temperature changes, probably thanks to the capacity of chironomids to record smaller amplitude temperature changes (Brooks 2006; Larocque et al. 2009; Larocque-Tobler et al. 2015).

In fact, vegetation response in western Québec to abrupt temperature events seems too slow to well record the rapid and low amplitude variations. This is probably due to probably a large range of physiological thermal acclimation (photosynthetic and respiration) of plants to climate changes (Dillaway and Kruger 2010). These acclimation processes and subsequent large ecological valence of plants regarding temperatures, could also justify weaker amplitude in the pollen-inferred temperatures than those inferred by chironomids. It is also noteworthy that a remarkable similar trend highlighting the same small amplitude temperature changes was also observed in the hydrogen isotope record in the north-eastern United States for the past 8000 years (Gao et al. 2017). In this way, our results should enhance the temporal resolution of the available temperature reconstructions from both central (Viau and Gajewski 2009) and western Québec (Ali et al. 2012) based on pollen and model outputs (UGAMP model) respectively.

3.6.2 Regional Holocene climate history

3.6.2.1 8500-4500 cal BP

Our results showed warmer than today temperatures (Fig. 3.5), which could be interpreted as the Holocene Thermal Maximum period (HTM) (Kaufman 2004). Maximal mean value of *ca.* +2.6 °C bounded by a 95 % confidence interval (*ca.* +0.8 °C; *ca.* +3.5 °C) was obtained.

These results are in agreement with others pollen-inferred temperature reconstructions from central Canada (Viau and Gajewski 2009) and north-eastern America (Viau et al. 2006) that recorded warmer than today temperatures between 8000 and 5500 cal BP. However, in these studies, the range of temperature changes only about +1 °C warmer than today, may be due to the used of only pollen proxy.

Furthermore, our results match well with paleoclimate records yielded from the GISP2 Arctic ice core (+3 °C; Kobashi et al. 2010), from a chironomid record on Baffin Island (+4 °C; Axford et al. 2009) and from hydrogen isotope record of behenic acid in the northeastern United States (+2 °C; Gao et al. 2017).

In the Canadian arctic and Greenland, the highest temperatures based on the pollen and chironomid records were found between *ca.* 8200 and 5000 cal BP (Gajewski 2015; Fortin and Gajewski 2016). Regional mean temperatures (derived from pollen and alkenones) in mid-latitude North America pointed also to a maximum warmth combined with drought conditions between *ca.* 8000 and 5000 cal BP (Shuman and Marsicek 2016).

Our results are also consistent with pollen-inferred temperatures in Fennoscandia and the Baltic region (Heikkilä and Seppa 2010). This study highlighted the warm and dry HTM period from ca. 8000 and 4000 cal BP, with highest temperatures (*ca*. 2.5-3.5 °C) than the modern value and greatest anomalies (+3.0-3.7 °C) taking place between *ca.* 7500 and 5000 cal BP.

Furthermore, our reconstruction revealed a cold peak at *ca.* 5900 cal BP followed by warmer conditions between *ca.* 5600 and *ca.* 4600 cal BP. This warm period has also been found in the north-eastern United States (Newby et al. 2014; Gao et al. 2017). According to several studies, the HTM timing occurs during a maximum insolation induced by the variability in the atmospheric circulation (Kaufman 2004; Renssen et al. 2012; Ali et al. 2012; Fréchette et al. 2018).

A sharp drop of about 2 °C was recorded in our reconstruction around *ca.* 8170 cal yr. BP and lasted *ca.* 80 years. This could represent the so-called 8200 cal BP event (Alley et al. 1997). Based on the Greenland ice core record (Kobashi et al. 2007), the event began around *ca.* 8175 cal BP and lasted *ca.* 150 years with a magnitude cooling of *ca.* 3.3 ± 1.1 °C. In the north-eastern United States, hydrogen isotope record of behenic acid confirms also this 8200 cal BP event (Gao et al. 2017). In Fennoscandia, pollen-based summer temperatures reported this event around *ca.* (8350-8250) and 8150 cal yr. BP with a drop temperature of *ca.* -2.0 °C (Veski et al. 2004; Heikkilä and Seppa 2010). This event appears to be as a result of the increase in freshwater flux (inducing by final drainage of lakes Agassik and Objibway) which reduced sea surface salinity and altered ocean circulation (Barber et al. 1999).

3.6.2.2 4500-1000 cal BP

This period (Fig. 3.5) is marked by temperatures fluctuating around modern value with some distinct decreases (about 1 °C) throughout the first millennium of this period (*ca.* 4500-3500 cal BP). This thermal change, around 4500 cal BP, also observed in central Canada (Viau and Gajewski 2009), could be the consequence of the cool and wet Neoglacial period (Ali et al. 2012; Blarquez et al. 2015). This general cooling trend observed for 4500 years has already been recorded by several temperature-proxies in northern high-latitude regions. This cooling has been established as the result of orbital variations producing declining summer insolation in the North Hemisphere (Ali et al. 2012; Wanner et al. 2015; Gao et al. 2017).

Based on chironomid and pollen records, this transition is related to a major reorganization in the climate of the Canadian Arctic (Gajewski 2015; Fortin and Gajewski 2016). In mid-latitude North America, pollen-and alkenone-inferred temperatures recorded lower temperature between *ca.* 5500 and ca. 4800 cal BP (Shuman and Marsicek 2016). Our results pointed also to a series of rapid climate changes (Fig. 3.5 and 3.6) at *ca*. 4200-4100, 3900-3700, 3400-3000, 2700-2300, 1900-1700, 1700-1500 and 1400-1100 cal BP. Some of these changes can be attributed to well-known events.

The 4200 cal BP warm event (*ca.* +0.5 °C warmer than today [95 % confidence interval: *ca*. -0.3 °C, +1.7 °C]) has already been identified by several studies in North

America and characterized by drought conditions (Booth et al. 2005). This event was also recorded in north-eastern Unites States (Gao et al. 2017). The warmer event between *ca.* 1900 and *ca.*1700 cal BP (about +1 °C, [95 % confidence interval: *ca.* -0.6 °C, +3.0 °C]) could be corresponds to the Roman Warm Period (RWP) recorded in Eurasia (Hass 1996; Wang et al. 2012; Yan et al. 2015; Jach et al. 2018) and Greenland (Seidenkrantz et al. 2007; Perner et al. 2015).

Our results match well with multi-proxy-inferred temperatures of Ljungqvist (2010) in the extra-tropical Northern Hemisphere (90-30°N), which identified also the RWP (about +1 °C) between *ca.* 1900 and 1700 cal BP. In North America, several studies derived by different proxies reported warmer and wetter climate during the RWP: from a pollen-inferred reconstruction of total annual precipitation across North America (RWP; *ca.* 1900-1800 cal BP; Ladd et al. 2017), from isotope sclerochronology in archaeological shells and otoliths (southwest Florida: RWP; *ca.* 1650-1400 cal BP; Wang et al. 2013) and from a testate amoebae-inferred palaeohydrological reconstruction (Hudson Bay Lowlands in Canada: RWP; *ca.* 2500-1600 cal BP; Holmquist et al. 2016). In Hudson Bay Lowlands O'Reilly et al. (2014) also indicated warmer conditions during the RWP. A recent north American hydroclimate synthesis (NAHS) established by Rodysill et al. (2018) highlighted the RWP between *ca.* 1900 and 1700 cal BP.

A sharp drop in temperatures was recorded in our reconstruction until values close to modern ones (Fig. 3.5 and 3.6) followed the "RWP" warming, between *ca.* 1700-1500 cal BP. This cooling might correspond to the Dark Age Cold Period (DACP) characterized in Europe being "generally rather colder and more disturbed climate" (Lamb 1985). Nevertheless, the timing of the DACP is not well established, since the

DACP can be recorded over the Northern Hemisphere at various location between 1550 and 1185 cal BP (Helama et al. 2017).

For example, the DACP occurred between 1550 and 1270 BP in the chironomid-inferred reconstruction from Northern Alps by Millet et al. (2009), while Ladd et al. (2017) detected this event between 1600 and 1300 cal BP in North America. Our results are consistent with the recent NAHS established by Rodysill et al. (2018) and the multi-proxy temperature reconstruction in the extra-tropical Northern Hemisphere (Ljungqvist 2010). All these studies pointed to the DACP between *ca.* 1600 and 1200 cal BP. According to Helama et al. (2017), this event could be interpreted in the context of the North Atlantic event if ice-rafting debris (IRD) at about 1400 years ago (Bond et al. 1997) during which cooler surface waters were transported southward and/or as the result of ocean-atmospheric interactions involving the North Atlantic Oscillation.

Around *ca.* 1100 cal BP, our CATR shows a temperature increase with a maximal mean value of *ca.* +1.3 °C [95 % confidence interval: *ca.* -0.1 °C, +3.3 °C] that could be interpreted as the Medieval Climate Anomaly (MCA) (Fig. 3.5 and 3.6). Across North America, Viau et al. (2012) identified this warm event (+0.6 °C) between 1150 and 750 cal BP based on pollen data. Recent Hydroclimate syntheses in North America (Shuman et al. 2017; Rodysill et al. 2018) identified the MCA between *ca.* 1150 and 650 cal BP. According to Karst-Riddoch et al. (2005), striking changes in diatom communities in Bristish Columbia highlight the MCA at *ca.* 1200 cal BP. Furthermore, Holmquist et al. (2016) identified the MCA warm event between 1000 and 700 cal BP with wet conditions in northeastern Ontario. Some studies have also recorded the MCA with minor amplitudes anomalies (< +0,5 °C) based on: varved proglacial lake sediments in Alaska (Loso 2009) and; tree-rings/diatoms (Trachsel et al. 2012) and chironomids (Luoto et al. 2017) in Europe. Other studies highlighted it with higher anomalies (about 1-2 °C) in central Canada based on pollen data (Viau and Gajewski 2009) and in Europe based on chironomids (Millet et al. 2009; Larocque-Tobler et al. 2012). According to Goosse et al. (2012) the MCA has been established as a result a simple thermodynamical response of the climate system to relatively weak shifts in radiative forcing coupled with ocean and atmospheric circulation changes. In addition, according to Trouet et al. (2009), MCA identified across North America can be interpreted as an northward expansion of the summer Subtropical High Pressure system in the North Atlantic.

3.6.2.3 1000 cal BP to present

During this period (Fig. 3.5 and 3.6), our data showed a drastic fall in temperature reaching a minimal mean value of ca. -1.2 °C colder than today [95 % confidence interval: *ca*. -3.1 °C, +0.1 °C] around ca. 300 cal BP. Dated between 500-250 cal BP in our record, this period could be related to the Little Ice Age (LIA). This LIA has already been identified across the northern Québec by Viau and Gajewski 2009 around *ca.* 500 cal BP. The recent hydroclimate synthesis by Rodysill et al. (2018) highlighting the LIA between *ca.* 650 and 100 cal BP and the one by Shuman et al. (2017) indicating it between *ca.* 500 and 50 cal BP. Across North America, Viau et al. (2012) identified LIA between *ca.* 500 and 100 cal BP. In the north-eastern Canada, the LIA ranges from ca. 650 to 100 cal BP (Payette and Delwaide 2004; Matthews and Briffa 2005).

Our results are in agreement with the both chironomid and pollen-inferred temperatures in Canadian Arctic (Fortin and Gajewski 2016), which indicated the LIA occurred between 460 and 360 cal BP. Beside, temperatures for the past century are cooler than those inferred prior to *ca.* 4500 cal BP, up to 3 °C cooler, which is consistent with results revealed by Fortin and Gajewski (2016) from chironomid record.

Our results match well with the testate amoebae-inferred palaeohydrological reconstruction in peatlands in the Boreal Shield and James Bay Lowland regions of Ontario (Holmquist et al. 2016), which identified the LIA between *ca.* 550 and 250 cal BP. Camill et al. (2009) estimated also the LIA between 650-150 cal BP in the western Canada. Furthermore, our reconstruction indicates *ca.* 2.5 °C anomaly between MCA and LIA, while Mann et al. (2009) highlighted 1.8 °C between the both events in the Northern Hemisphere. The LIA might be influenced by a combination of: low orbital induced insolation; maximal volcanic activity and complex ocean-atmosphere interactions (Booth et al. 2005; Wanner et al. 2008; PAGES 2k Consortium 2013).

3.6.2.4 Bond events

The existence of pervasive Holocene cycles with a period of 1500 cal BP has been postulated by Bond et al. (1997). Nine Bond cycles are identified around 400, 1400, 2800, 4300, 5900, 8100, 9400, 10300 cal BP. The existence of these events has been noted in Eurasia, North and South America and Africa (Wanner et al. 2015). From our reconstruction, the negative temperature peaks seem to be detectable that could correspond to the Bond events 0 (400 cal BP), 2 (2800 cal BP), 3(4300 cal BP) and 5(5900 around 6000 cal BP).

According to Bond (2001), these events are the result of the influence of variations in solar output on the surface winds and the ocean hydrography. For Wanner et al. (2015), these Bond events were the result of the advection of southward and eastward drifting surface water from the Nordic and Labrador Seas, which gave rise to century-scale cold relapses in the North Atlantic and European regions.

Wanner et al. (2015) revealed several responsible processes to the formation of the cycles, including orbitally-driven solar insolation, solar irradiance changes, large volcanic eruptions, southern overturning ocean circulation or internal climate system variability. The possible causes such as tidal forcing, atmospheric processes or modifications of the geomagnetic field are also indicated by Debret et al. (2007).

3.7 Conclusions

The present study has shown the effectiveness of an innovative combined (pollen-chironomid) approach to reconstruct quantitatively temperature changes through the last 8500 years. It is the first climate reconstruction at high temporal resolution in the eastern Canadian boreal forest. Three main chronological periods have been identified associated to at least six rapid climatic events.

The HTM between 8500-4500 cal BP that was interrupted by the 8200 cal BP cooling event. The second period between 4500-1000 cal BP was characterized by fluctuating trend around today temperature. It resulted of the onset of the cool and wet Neoglacial period. Three abrupt climate events have been recorded: the 4200 cal BP warm event, the RWP warming between 1900-1700 cal BP, the DACP cooling between 1700-1500 cal BP and the MCA around 1100 cal BP. The third period from 1000 cal BP to present was characterized by a drastic fall in August temperatures, which marks the LIA cooling. This event ranged from 500 to 250 cal BP. Furthermore, the Bond events 0 (400), 2 (2800), 3(4300) and 5(5900 around 6000) cal BP seem to be identified by our reconstruction.

The evolution of regional August temperatures in eastern Canada is probably integrated into a more global climate system, may be influenced by complex interactions between both external orbital forcings (such as solar irradiance) and internal modes of variability in the ocean-atmosphere system, where punctual events (such as explosive volcanisms) can also interact.

According to previous studies, fire regime variations (fire frequency and size, biomass burning) are mainly influenced by climate changes. With our robust reconstruction, further investigations must be performed in order to be compared with available regional paleofire history and particularly to obtain better understanding the paleotemperature influence on the fire regime. From this combined climate approach, focusing on related fire activity in forested landscapes during the warmer periods of past millennia would allow to better prediction of future impacts of the ongoing warming on the boreal forest.

3.8 Acknowledgments

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CHAPITRE IV

CONCLUSION GÉNÉRALE

Ce doctorat a permis d'établir une approche croisée de reconstitution paléoclimatique basée sur deux bio-indicateurs (Chironomidae et grains de pollen) préservés dans les sédiments lacustres de deux sites. Cette approche constitue une première pour la région d'étude située au sein de la pessière à mousses de l'ouest du Québec, et plus largement pour l'ensemble du Québec.

Cette recherche avait pour objectif d'évaluer l'efficacité de ces bio-indicateurs ainsi que leur méthode de reconstitution quantitative des paléotempératures holocènes. Leur association a permis de renforcer la reconstitution de l'évolution des paléotempératures.

Dans cette conclusion, une discussion autour d'un premier volet méthodologique sera menée avec une attention particulière sur l'utilisation en milieu lacustre des Chironomidae comme indicateurs thermiques et de leur association avec les grains de pollen fossiles. Cette approche croisée sera appelée ici *reconstitution combinée des températures du mois d'août (RCTA).*

Ensuite, un second volet sur l'histoire paléoclimatique régionale sera présenté *via* cette RCTA, avec une insistance particulière sur les périodes et évènements importants survenus au cours des 8500 dernières années. Il s'agira également de montrer les relations entre les trois compartiments climat-végétation-feu afin de mettre en évidence les incidences éventuelles entre compartiments et surtout de répondre à une question essentielle : *La température estivale est-elle le facteur premier qui contrôle les changements dans les régimes de feu de la région d'étude ?* Enfin, dans une troisième partie, seront proposées les limites et les perspectives méthodologiques de ce travail de recherche.

4.1 Reconstitutions des paléotempératures holocènes basées sur des assemblages des indicateurs Chironomidae-pollen puis de leur approche croisée.

Le premier chapitre de cette thèse avait pour objectif de proposer une reconstitution quantitative des températures estivales holocènes à haute résolution temporelle, basée sur les assemblages de Chironomidae du *Lac Aurélie* dans la pessière à mousses de l'ouest du Québec. Pour cela, deux fonctions de transfert (FT) ont été appliquées afin de déterminer les forces et les faiblesses de chacune.

Le deuxième chapitre visait à mesurer la pertinence des assemblages de Chironomidae dans un lac peu profond comme indicateurs des changements des paléotempératures. Pour ce faire, la région de la plaine de Matagami de la pessière à mousses de l'ouest du Québec a été sélectionnée. Le *Lac Lili* dont la profondeur d'eau n'excède pas 1,40 m a été tout d'abord analysé, puis les résultats furent comparés à ceux obtenus pour le *Lac Aurélie* (Chapitre 1) dont la profondeur est nettement supérieure (10 m).

Le troisième chapitre visait à établir une reconstitution combinée (Chironomidae-pollen) des températures du mois d'août (RCTA) à partir des deux sites d'études précédents. Les reconstitutions des paléotempératures inférées par les assemblages polliniques ont été réalisées à haute résolution à l'aide de la Technique des Analogues

Modernes (MAT) dans le but d'être combinée avec les reconstitutions inférées par les Chironomidae (Chapitres 1 et 2).

Les résultats obtenus pour le *Lac Aurélie* (Chapitre 1) ont montré que la FT Est canadienne (Bajolle et al. 2018) donne une meilleure reconstitution quantitative des paléotempératures estivales par rapport à la FT canadienne (Fortin et al. 2015). Portant sur un grand nombre de lacs (435), la FT canadienne était attendue comme la plus adaptée pour reconstituer les paléotempératures à partir d'un lac en forêt boréale québécoise.

Toutefois, seulement quelques-uns des lacs du référentiel actuel de la FT canadienne possèdent des températures estivales au-dessus de 14 °C. Même en comprenant 52 des 72 lacs du jeu de données modernes de la FT Est canadienne réalisée par Larocque et al. (2006), le gradient des températures n'excède pas 15.7 °C (Chapitre 1). De ce fait, la FT canadienne a tendance à sous-estimer les températures supérieures à 15 °C, ce qui est limitatif pour le *Lac Aurélie*. En effet, même si la température actuelle à cet endroit est de 15 °C, les températures ont pu éventuellement par le passé dépasser cette valeur, notamment lors du Maximum Thermique de l'Holocène (HTM).

Par ailleurs, la FT canadienne prend en compte une majorité de lacs aux températures froides, favorisant l'obtention d'optimums thermiques relativement faibles entre 4.5 et 13.9 °C. De surcroît, comme cela est discuté dans le Chapitre 1, l'identification taxonomique est insuffisante dans le jeu de données modernes de la FT canadienne, étant donné que les auteurs ont dû regrouper de nombreux taxons pour s'adapter à la taxonomie des anciens jeux de données. Heiri and Lotter (2010) ont déjà démontré que les niveaux d'identification taxonomiques faibles réduisent les performances statistiques de fonctions de transfert et diminuent le réalisme des optimums.

En définitif, les patrons des changements de températures entre les deux FT ont certes montré des similarités, mais les estimations fournies par la FT canadienne sont constamment de 2 à 3 °C plus froides que la température actuelle de la région (15 °C).

La FT Est canadienne modifiée de Larocque (2008) est une extension de la version réalisée par Larocque et al. (2006). Le jeu de données modernes présente une amplitude thermique plus large (3–2 °C). Ainsi, même en comprenant moins de lacs (72) que la FT canadienne, les optimums sont plus réalistes variant de 7.3 à 22.6 °C, ce qui conduit à une meilleure reconstitution des températures. Cependant, le jeu de données modernes de la FT Est canadienne pourrait encore être amélioré en comblant la partie déficitaire entre 16.8 et 19 °C afin d'augmenter l'homogénéité du jeu de données.

Comme attendu pour un lac peu profond, compte tenu des informations concordantes déjà disponibles (Brodersen and Lindegaard 1997; Korhola et al. 2002; Langdon et al. 2010; Greffard et al. 2012), les résultats portant sur le *Lac Lili* (Chapitre 2) ont montré que les assemblages de Chironomidae étaient dominés par des taxons littoraux et eutrophes, livrant pour la plupart par des optimums de températures plus « chauds » que 13.6 °C (moyenne des optimums de température des taxons identifiés dans le *Lac Lili*). Par conséquent, les anomalies de paléotempératures reconstituées (par rapport à la période de référence 1981-2010 : 15.8 °C) ont révélé que seulement huit des inférences totales étaient plus froides qu'aujourd'hui, ce qui engendre donc une reconstitution globale plus chaude. Toutefois, la tendance des changements de température s'est avérée similaire à l'enregistrement Chironomidae du *Lac Aurélie* (Chapitre 1) et à ceux obtenus via les assemblages polliniques des sites de la Province de Québec (Viau et al. 2006). D'autres facteurs tels que l'eutrophisation, les changements du niveau de la colonne d'eau et les macrophytes ont davantage interféré sur ce site avec la température.

Les résultats obtenus pour les deux sites d'étude (Chapitre 3) ont révélé dans les reconstitutions individuelles (par site et par indicateur) des tendances similaires de changements de température mais avec des amplitudes différentes. La reconstitution combinée des températures du mois d'août (RCTA) a permis de mettre en lumière des changements rapides, probablement grâce à la capacité des Chironomidae de réagir rapidement aux changements de températures de faibles amplitudes.

Ceci nous amène à formuler l'hypothèse, avec toutes les réserves nécessaires, que la réponse de la végétation face aux changements climatiques serait trop lente pour enregistrer des variations thermiques rapides et de faible amplitude. Les espèces végétales seraient ainsi capables par des processus de photosynthèse et de respiration de générer une acclimatation thermique physiologique (Dillaway and Kruger 2010). Dans ce cas, nous pouvons penser que ces processus ont probablement donné aux plantes une valence écologique plus large au regard des températures, ce qui pourrait justifier l'amplitude plus faible des reconstitutions des températures inférées par les assemblages polliniques par rapport à celles basées sur les assemblages de Chironomidae.

Par conséquent, nos résultats démontrent l'intérêt majeur de combiner les reconstitutions basées sur les assemblages polliniques avec celles inférées par un indicateur indépendant tel que les assemblages de Chironomidae. Enfin, la concomitance entre la RCTA et la reconstitution des températures arctiques de PAGES 2k Consortium (2013) sur les deux derniers millénaires renforce l'hypothèse de la robustesse de cette approche combinée.

L'ensemble de cette discussion autorise les conclusions suivantes :

(i) En raison des différences taxonomiques entre les bases de données modernes utilisées par chacune des deux fonctions de transfert, la FT Est canadienne (Larocque, 2008) et la FT canadienne (Fortin et al. 2015) ont donné des reconstitutions des températures différentes pour ce qui est de l'amplitude thermique. La FT Est canadienne a été retenue pour être la plus appropriée à notre région d'étude (Chapitre 1).

(ii) Dans un lac peu profond, la surestimation des inférences basées sur les assemblages de Chironomidae peut être expliquée par la domination des taxons littoraux (généralement caractérisés par des optimums les plus chauds) et une fonction de transfert (FT Est canadienne) avec un jeu de données modernes déficitaire en lacs peu profonds (Chapitre 2).

(iii) L'approche combinée (RCTA) fournit une reconstitution quantitative robuste des températures régionales pour les 8500 dernières années. Elle améliore la résolution temporelle des reconstitutions des paléotempératures déjà disponibles pour les régions centrales (Viau and Gajewski 2009) et orientales du Canada (Ali et al. 2012), en révélant des périodes et évènements climatiques majeurs survenus au cours de l'Holocène (Chapitre 3).

4.2 Climat-végétation-feu, y a- t-il un impact direct des températures estivales sur le régime de feux ?

Dans cette section, nous mettons en évidence les relations entre le trio climat-végétation-feu à l'échelle des 8500 dernières années pour la forêt boréale de l'ouest du Québec. Pour le climat et le feu, des variables ont étaient sélectionnées afin d'évaluer si les changements de température estivale jouent un rôle particulier dans l'évolution du régime de feu (Fig. 4.1).

4.2.1 Les variables climatiques et feu

Le climat

Nous retiendrons comme variables climatiques :
(i) la température du mois d'août *i.e.* notre RCTA (°C) produite dans le Chapitre 3 ;
(ii) les précipitations annuelles PANN (mm) tirées de Fréchette et al. (2018) ;
(iii) l'ensoleillement estival (juin, juillet et aout) SJJA (%) également tiré de Fréchette et al. (2018). La reconstitution de l'ensoleillement documente les changements de la nébulosité directement liés aux variations de circulation atmosphérique de l'Amérique du Nord. En effet, d'après Fréchette et al. (2018), la circulation cyclonique (sens antihoraire) dans l'hémisphère Nord favorise le mouvement ascendant des masses d'air, la formation des nuages et des vents d'ouest (*westerlies*) faibles. En revanche, la circulation anticyclonique (sens horaire) entraine un mouvement descendant des masses d'air, une nébulosité faible, un air sec et des vents d'ouest forts.
Enfin (iv) ; l'indice de sécheresse (DC) estivale est tiré de Ali et al. (2012). Il peut être utilisée pour caractériser les changements de la durée de la saison des feux. En effet, la durée de la saison des feux repose sur le nombre de jours simulés durant une période donnée (ici estivale) où l'indice de sécheresse DC dépasse la valeur seuil 80. Au-delà de ce seuil, il existe un risque modéré de feu dans la région (Ali et al. 2012 ; Hély et al. 2010).

Le feu

Les variables du compartiment feux sont issues d'Ali et al. (2012). Il s'agit de :
(i) la fréquence de feu ou occurrence (*RegFF)* exprimée en nombre de feux par 1000 ans ;

(ii) la quantité de biomasse brûlée (*RegBB)* exprimée en nombre de jours ;

(iii) la taille des feux (*FS* index) obtenue par le ratio *RegBB/FF*.

Les variables climatiques (RCTA, PANN, SJJA) inférées par les assemblages polliniques sont exprimées en anomalies par rapport à la période de référence 1961-1990. Les valeurs moyennes sont indiquées pour chaque variable de feux (*RegFF, RegBB, FS* index). Les variations (+,-,0) des variables climatiques et de feux sont illustrées respectivement par rapport à leur valeurs actuelles et moyennes.

4.2.2 La végétation (Chapitre 3)

Notre région d'étude appartient à la Grande Ceinture d'Argile constituée de dépôts argileux laissés par la vidange finale du lac proglaciaire Ojibway et dont la vidange finale est datée à 8470 ans AA (Barber et al. 1999).

L'histoire de la végétation de la région de la pessière à mousses de l'ouest du Québec a débuté par une phase d'afforestation entre 8500 et 7000 ans AA, suivi par une phase forestière (7000–2000 ans AA). Au cours de cette dernière, le couvert forestier s'est densifié progressivement pour atteindre un maximum vers 4500–4000 ans AA (formation de la pessière à mousses). Le couvert forestier a commencé à s'ouvrir il y a environs 2000 ans AA (Fig. 4.1).

Les changements dans la composition et la structure d'âge des espèces forestières boréales reflètent les interactions climat-feu-végétation, avec notamment des effets de rétroaction entre eux et l'influence d'autres facteurs locaux tels que les conditions édaphiques et le contexte topographique (Blarquez and Aleman 2015; Asselin et al. 2016; Remy et al. 2017b).

4.2.3 Historique des relations climat-végétation-feu

Sur l'ensemble des derniers 8500 ans, les reconstitutions climatiques et du régime de feux postglaciaires de la forêt boréale de l'ouest du Québec montrent un refroidissement graduel de la température estivale (RCTA), lequel peut s'expliquer par la diminution progressive de l'intensité de l'insolation dans cette région (Ali et al. 2012). Une baisse graduelle de l'ensoleillement estival (SJJA), de l'indice de sécheresse (DC), de la fréquence de feux (*RegFF*) et de la biomasse brulée (*RegBB*) est également constatée. À l'inverse, une augmentation des précipitations annuelles (PANN) et de la taille des feux (*FS* index) est enregistrée (Fig. 4.1).

La période entre 8500 et 4500 ans AA

Cette période identifiée comme le Maximum Thermique de l'Holocène (HTM) (Chapitre 3), est marquée par des conditions climatiques chaudes (max. RCTA, SJJA) et plus sèches (min. PANN, max. DC) (Fig. 4.1). La circulation atmosphérique anticyclonique est plus intense et les vents d'ouest plus forts (comme suggéré par le maximum de SJJA), ce qui engendre un ciel ensoleillé, une faible nébulosité et un déficit dans les précipitations (Montero-Serrano et al. 2010; Fréchette et al. 2018). Malgré une interruption causée par l'événement climatique froid vers 8200 ans AA (refroidissement d'environ 2 °C), les températures estivales maximales sont supérieures de 2,6 °C aux températures actuelles (Chapitre 3).

La phase d'afforestation avant 7000 ans AA se caractérise par une végétation plus ouverte et hétérogène où *Pinus banksiana*, *Betula* et *Populus* étaient bien représentés sur le territoire (cf., Chapitre 3; Fréchette et al. 2018). La phase forestière relevée à partir de 7000 ans AA montre une densification de la végétation où *Picea* (probablement *Picea*-type *mariana*) devient de plus en plus abondant (Chapitre 3).

La présence d'espèces davantage thermophiles comme *Pinus strobus* avec une représentation pollinique maximale entre 7000 et 5000 ans AA, suggère un climat chaud et ensoleillé (chapitre 3). L'abondance d'espèces non adaptées au feu comme le *Thuja occidentalis* (Fréchette et al 2018) entre 6500 et 5500 ans AA souligne aussi une activité peu intense de feux (*RegFF* proche de la moyenne et *RegBB-).*

De surcroit, entre 5500 et 4500 ans AA, les moindres précipitations, un indice de sécheresse et des températures plus élevées semblent avoir été des facteurs propices à une fréquence importante (*RegFF++)* de petits feux (*FS* index<1) et une plus longue saison des feux (indice de sécheresse DC élevé) (Fig. 4.1, Ali et al. 2012).

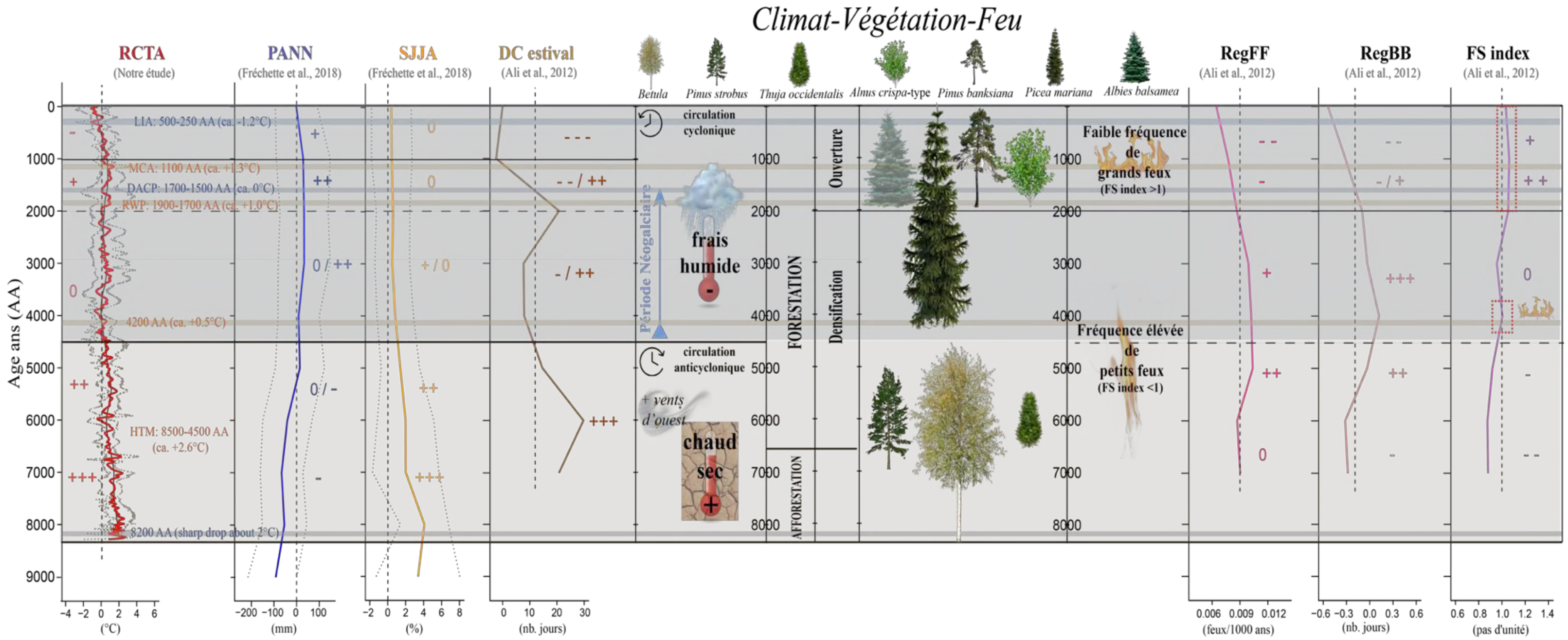

Figure 4.1 Synthèse des interactions climat-végétation-feu dans la forêt boréale de l'ouest du Québec. Les variables climatiques sont représentées par la Reconstitution Combinée de la Température du mois d'Août (RCTA ; notre étude), les précipitations annuelles (PANN ; Fréchette et al. 2018), l'ensoleillement des mois de juin, juillet, août (SJJA ; Fréchette et al. 2018) et l'indice de sécheresse estival (DC ; Ali et al. 2012). Les types de circulation sont indiqués par leur sens horaire (anticyclonique) et antihoraire (cyclonique). La végétation est illustrée par des espèces clés en lien avec le climat et l'activité des feux. La taille des espèces représentées correspond à leur période de présence dans la région de l'ouest du Québec. Les variables du régime des feux sont représentées par la fréquence des feux (*RegFF* ; Ali et al. 2012), la biomasse brûlée (*RegBB* ; Ali et al. 2012) et la taille des feux (*FS* index ; Ali et al. 2012).

La combinaison d'une légère augmentation des précipitations annuelles et d'une sécheresse estivale élevée entre 6500 et 4500 ans AA semble avoir favorisée par ailleurs un accroissement de la biomasse brûlée, quoique insuffisante pour engendrer de grands feux (Fig. 4.1). D'autre part, une plus grande abondance de *Betula* (espèce feuillue limitant la propagation des feux) entre 8500 et 4500 ans AA (Chapitre 3) a pu contribuer à réduire de la taille des feux (Remy et al. 2017b).

La période entre 4500 et 2000 ans AA (Fig. 4.1)
Cette période est marquée par un affaiblissement de la circulation atmosphérique cyclonique au niveau des pôles, entrainant une recrudescence des masses d'air froid en provenance de l'Arctique et donnant lieu à un déplacement vers le sud du courant-jet (Pratte et al. 2017 ; Fréchette et al. 2018).

C'est à cette époque que débute la période Néoglaciaire, en général plus fraîche et plus humide (cf., Chapitres 1 et 3; Ali et al. 2012; Blarquez et al. 2015; Pratte et al. 2017). Le Néoglaciaire est caractérisé par une baisse de l'insolation estivale (SJJA+/0) et des températures (RCTA 0), une nébulosité accrue et une recrudescence des précipitations annuelles (PANN 0/++). De surcroit, la longueur de la saison des feux (référée par l'indice de sécheresse DC estivale) diminue progressivement (Fig. 4.1).

Aux alentours de 4500-4000 ans AA, le couvert forestier devient plus homogène avec une densité maximale. Il est alors dominé par le *Picea* accompagné par le développement des populations d'*Abies balsamea* (Chapitre 3; Fréchette et al. 2018). C'est aussi à cette époque que se développe la pessière à mousses de l'ouest du Québec comme nous la connaissons aujourd'hui (Chapitre 3; Garralla and Gajewski 1992; Fréchette et al. 2018). En contrepartie, certaines espèces comme *Thuja occidentalis* et *Pinus strobus* voient leurs abondances décliner. Les petits feux ont une fréquence élevée, à l'exception de l'événement climatique chaud centré vers 4200 ans AA durant lequel leur taille augmente (*FS* index =1).

Cet événement climatique (+0,5 °C) est corrélé à des précipitations proches de celles actuelles et une chute abrupte de l'indice de sécheresse. Une fréquence de feux et une biomasse brûlé élevées faisant écho à cette augmentation de la taille de feux sont aussi notées (Fig. 4.1). Par ailleurs, la domination d'espèces conifériennes comme *Picea* et *Pinus banksiana* (Chapitre 3) inflammables a probablement contribué à l'augmentation de la taille de feux (Remy et al. 2017b).

Toutefois, de manière générale, entre 4500 et 2500 ans AA, la biomasse brûlée maximale couplée à une faible sécheresse ne semble de pas avoir favorisé les larges feux. D'autre part, la plus grande abondance de conifères et l'augmentation des précipitations annuelles au début de la période Néoglaciaire ont sans doute permis une accumulation de matière organique accrue sur les sols.

Ceci pourrait explique le déclin de *Thuja occidentalis,* en raison de la diminution de la surface des sols argileux disponibles favorables à son développement (Liu 1990). L'augmentation de la nébulosité a pu également participer à son déclin, puisque cette espèce est connue pour sa sensibilité à l'ombrage (Fréchette et al. 2018). En revanche, le déclin de *Pinus strobus* peut s'expliquer par le refroidissement, la couverture nuageuse, la fréquence de feux élevée et probablement la compétition entre espèces (Chapitre 3; Fréchette et al. 2018).

Entre 2000 et 1000 ans AA (Fig. 4.1).

Le climat qui prévalait à cette époque est notamment marqué par deux événements plus chauds : la Période chaude dite Romaine (RWP, 1900-1700 ans AA, +1,0 °C, Chapitre

3) et l’Anomalie Climatique Médiévale (MCA, autour de 1100 ans AA, +1,3 °C, Chapitres 1 et 3). Ces deux épisodes sont séparés par un évènement plus frais, soit la Période froide de l’Âge Sombre (DACP, 1700-1500 ans AA, anomalies de température proche des températures actuelles, Chapitre 3). Les précipitations maximales (PANN++), le pic de sécheresse et le faible ensoleillement ont probablement entrainé une diminution de la fréquence des feux (*RegFF-*) mais les feux étaient de plus grandes tailles (*FS* index >1) autour de 2000 ans AA.

À cette époque, le couvert forestier s’ouvre graduellement en raison d’une forte activité de feux (Bremond et al. 2010; Ali et al. 2012; Fréchette et al. 2018). L’abondance d’espèces pyrophiles telles que *Pinus banksiana, Picea mariana*, *Alnus crispa* et *Betula* suggère l’ouverture du milieu influencé par la sévérité du régime de feux (Remy et al. 2017b). Toutefois, l’abondance d’*Abies balsamea* connue pourtant pour être sous-représentée (<10 %) polliniquement (Richard 1993; Chapitre 3) peut montrer une présence soutenue au sein de zones refuges liées à un relief plus accidenté et peu sujettes aux feux sévères (Asselin et al. 2001; Bergeron et al. 2004; Remy et al. 2017b).

A partir de 1000 ans AA (Fig. 4.1).

L’événement froid du Petit Âge Glaciaire (LIA, 500-250 ans AA, -1,2 °C) (Chapitres 1 et 3) est marqué par une chute des températures, des précipitations annuelles et de la sécheresse estivale. La fréquence des feux et la biomasse brûlée continuent de diminuer alors que la taille de feux baisse légèrement.

Pour conclure, conformément aux résultats de plusieurs études sur les relations climat-feu, les changements dans les régimes de feux sont influencés par une instabilité climatique principalement menée par les variations saisonnières des précipitations et de l’irrégularité des épisodes de sécheresse (Carcaillet and Richard 2000; Ali et al.

2012; Remy et al. 2017a). La température estivale ne semble pas jouer un effet direct sur les variables feux. Toutefois, les grands feux (*FS* index >1) ou les feux sévères pointés vers 4200 ans AA et à partir de 2000 ans AA coïncident avec des évènements climatiques ponctuels relevés par notre reconstitution RCTA (4200 ans AA, RWP, DACP, MCA et LIA).

4.3 Perspectives de recherche dans un contexte d'aménagement écosystémique durable

Au vu du renforcement des reconstitutions quantitatives des paléotempératures avec l'utilisation des assemblages de Chironomidae (Chapitres 1 et 2) notamment dans une approche combinée (Chapitre 3), des travaux sont à envisager. Il faudrait tout d'abord pouvoir améliorer l'homogénéité du jeu de données modernes.

Pour ce faire, il serait nécessaire d'échantillonner de nouveaux lacs référentiels pour couvrir les températures d'août manquantes entre 16,8 et 19 °C (Chapitre 1). Un affinement des optimums donnés par les taxons pourrait être obtenu par l'élargissement du niveau d'identification taxonomique. Le genre *Tanytarsus* par exemple, peut regrouper plusieurs espèces aux valences écologiques très diverses.

En revanche, dans l'attente de futures investigations d'échantillonnage et d'identification, une solution peut être proposée pour améliorer la fonction de transfert actuelle : l'utilisation d'une fonction de transfert combinée regroupant deux jeux de données modernes (Heiri et al. 2011; Larocque-Tobler et al. 2015). L'application d'une fonction de transfert combinée a déjà fait ses preuves (Larocque and Finsinger 2008; Hernández-Almeida et al. 2017).

À titre d'expérimentation (Appendice A), la fonction de transfert combinée Est Canada-Pologne (Larocque-Tobler et al. 2015, 2016) a été utilisée dans le cadre d'une étude comparative avec la fonction de transfert initiale Est canadienne (Larocque 2008) et celle canadienne (Fortin et al. 2015). Le jeu de données polonais a permis de compléter les températures d'août manquantes entre 16,8 et 19 °C, et de fournir de meilleurs optimums de température et donc probablement une meilleure reconstitution. Récemment, cette fonction de transfert a fait également ses preuves (Hernández-Almeida et al. 2017). Toutefois elle est encore controversée en raison des niches écologiques probablement différentes (échelle intercontinentale) pour les taxons communs aux deux jeux de données et regroupant éventuellement des espèces différentes.

Au vu de nos résultats du Chapitre 3, l'approche combinée (Chironomidae-pollen) fournit une reconstitution quantitative robuste des températures régionales passées. La mise en évidence de périodes et évènements climatiques clés survenus depuis plus de 8000 ans rend la méthode pertinente. Toutefois, en matière de méthodologie croisée (Chironomidae-pollen), dans l'optique de maintenir une cohérence dans la sélection des analogues modernes pour les assemblages polliniques et donc de renforcer l'approche combinée, il pourrait être utile de contraindre le choix des analogues modernes des assemblages polliniques fossiles par les valeurs de températures d'août inférées par les assemblages de Chironomidae. En effet, en Europe des travaux sur les reconstitutions des précipitations (Guiot et al. 1993 ; Magny et al. 2009) ont pu mettre en évidence l'efficacité de contraindre le choix des analogues modernes des assemblages pollinique par des données de niveaux lacustres.

Enfin, la multiplication des sites d'études dans la région considérée est nécessaire afin d'améliorer la caractérisation des périodes et évènements clés (en chronologie et en amplitude) au regard notamment des changements de régime des feux. Une attention particulière doit être portée sur les évènements climatiques suivants : 4200 ans AA, RWP, DACP, ou encore les évènements Bonds, moins connus dans la région d'étude.

Et pour conclure ?

Ce présent travail de recherche s'est attaché à fournir des résultats paléoclimatiques qui alimentent la recherche sur le registre des états de références (Boucher et al. 2009) établis par le Ministère des Forêts, de la Faune et des Parcs du Québec. Dans un contexte d'aménagement forestier aux enjeux environnements et socio-économiques majeurs, ses résultats participent à la caractérisation de la variabilité naturelle et l'évaluation de la capacité adaptative (résilience) d'un écosystème forestier (Gauthier et al. 2008). Elle cherche à apporter les connaissances nécessaires à la caractérisation de l'évolution climatique durant l'Holocène (durée, amplitude thermique et conséquences des évènements clés).

Désormais, il est admis que la recrudescence des feux dans la zone boréale canadienne est soumise à l'influence du climat (Girardin et al. 2013). Il est toutefois important de souligner que la résilience d'un écosystème forestier (face aux changements du régime des feux) dépend également de facteurs locaux (conditions édaphiques, disponibilité du combustible, topographie, hydrographie, etc.). De ce fait, la gestion forestière actuelle visant à lutter contre l'éclosion et la propagation des feux utilise plusieurs pratiques connues (suppression des feux, coupes de récupération, régénération artificielle ; Gauthier et al. 2008). Ces pratiques en perpétuelle amélioration cherchent à diminuer la vulnérabilité des écosystèmes forestiers afin de maintenir leur résilience. Ces stratégies d'aménagement devront être nécessairement soutenues par une recherche paléoécologique encore plus développée.

Par ailleurs, la hausse des températures et des précipitations a des conséquences directes sur la résilience forestière ainsi que la productivité de la forêt. La croissance des arbres est allongée et certains paramètres (succès de reproduction, distribution et abondance des espèces, assemblages d'espèces et migration) sont modifiés (Gauthier et al. 2008). Ces constatations rendent la recherche paléoécologique absolument nécessaire, car elle apporte les informations essentielles sur le fonctionnement pluriséculaire des écosystèmes forestiers (Hennebelle et al. 2018).

Pour aller plus loin dans l'objectif d'une gestion forestière davantage améliorée, de récents modèles de dynamique globale de la végétation proposent des scénarios mettant en lien les perturbations climat-feu et la végétation. C'est par exemple le cas du modèle LPJ-LMfire de Chaste et al. (2018). Dans cette perspective, la détermination des paramètres climatiques modulant le régime des feux au sein de la forêt boréale représente une grande utilité pour le développement de stratégies d'aménagement écosystémique visant à minimiser l'impact de la perturbation feu. Toutefois, les modèles climatiques actuels peinent à mettre en évidence en haute résolution temporelle les principaux changements de température qui ont ponctué l'Holocène.

Des données paléoclimatiques basées sur des bio-indicateurs thermiques performants sont donc fondamentales pour contraindre et diminuer les incertitudes dans les projections climatiques futures (Gajewski 1993). Il est évidemment nécessaire que les reconstitutions simulées des paléotempératures soient réalistes et fiables et qu'elles soient validées par des données thermiques indépendantes. Dans cet objectif, l'utilisation depuis peu, de la systématique des Chironomidae pour la reconstitution des paléotempératures semble avoir répondu à ces attentes.

Aujourd’hui, la caractérisation de la résilience d’un écosystème forestier au Québec à travers une démarche intégrative et pluridisciplinaire est au centre des préoccupations scientifiques. On ne peut donc qu’insister davantage sur la nécessité de renforcer la recherche fondamentale en vue d’acquérir de nouvelles données paléoclimatiques toujours plus robustes basées sur des bio-indicateurs thermiques, comme cette thèse a cherché à le démonter, et de renforcer sa relation avec la recherche appliquée.

APPENDICE A

USING THE COMBINED TRANSFER FUNCTION (EAST CANADA - POLAND) ON THE CHIRONOMID ASSEMBLAGES FROM THE *LAC AURÉLIE:* COMPARISON BETWEEN THREE TRANSFER FUNCTIONS

Introduction

To provide the most accurate temperature reconstruction, the transfer function method was used. In the last decade, this method has been widely used and criticized (Brooks *et al.*, 2012; Velle *et al.*, 2010). In recent years, means of improving the accuracy of inferences have been tested. One solution is to obtain temperature optima as realistic as possible. To do so, chironomists have started to combine transfer functions (Heiri *et al.*, 2011) and to apply the transfer functions obtained with combined training sets on sites outside the geographical range of the training set (Larocque and Finsinger, 2008).

Validating this method is still needed at multiple sites. Our study site offers the possibility of testing this new approach by using three training sets: a regional set consisting of lakes from eastern Canada (Larocque, 2008), a Canadian set consisting of lakes from the Arctic to the coniferous boreal forest (Fortin *et al.*, 2015) and a combined training set data comprising the lakes used in Larocque (2008) and Polish lakes (Eastern Canadian Polish model: Larocque-Tobler *et al.*, 2015). An underlying goal of this study is thus to provide a critical assessment of the regional versus combined method of Holocene climate reconstruction using chironomids.

Method

The study is investigated on the same site *Lac Aurélie* (central Québec) and the conditions are similar than chapter 1 (*Major postglacial summer temperature changes in the central coniferous boreal forest of Quebec (Canada) inferred using chironomid assemblages*). The mean annual temperature from the closest meteorological station

[Chapais 2: 1971-2000, 49°47’N; 74°51’W] is 0.0 ± 1.3 °C with an August temperature average of 14.9 °C ± 1.4 °C. Further details can be found in chapter 1.

Three published chironomid-based transfer functions were used to reconstruct mean August air temperature and estimate their reliability to infer past climate changes. These transfer functions were performed using weighted-averaging partial least squares regression (WAPLS) with bootstrapping using the C2 program (Juginns 2003; 2013). All models performed better with two components. Details on statistics and performance can be found in each of the published papers and summarized in Table A.1. Zones illustrated (Fig. A.1) have been taken from chapter 1 (chironomid diagram at *Lac Aurélie*).

For each of the transfer functions, the temperature optima for each taxon were calculated using weighted average (WA). Based on these optima, each taxon was described as “cold” if its optimum was lower than the present-day temperature (15°) and “warm” if its optimum was warmer than today Table 2.

Why use of the combined Eastern Canada and Poland transfer function?

The third combined (Eastern Canada and Poland; afterwards called Combined EastCanPo) transfer function published by Larocque-Tobler *et al.* (2016) was used to provide a complete coverage of temperatures along the existing gradient (23.5 °C), the Eastern Canadian transfer function having no lakes between 16.8 and 19 °C.

All polish lakes have August temperatures between 16.3 and 19 °C and the chironomid assemblages were imbedded in the Eastern Canadian training set, completing the coverage of the temperature gradient. Combining both training set provided a data set of 122 lakes (72 from Canada and 50 from Poland) and 95 taxa. Temperature optima for taxa should be more realistic (*i.e.* less biased toward warmer or colder lakes) for quantitative reconstruction from subfossil assemblages since the number of lakes completing the gradient and the taxonomy was increased (Heiri and Lotter, 2010).

In an ideal world, samples from Canadian lakes would have been imbedded to the Eastern Canadian training set; however, no funding has been secured to do so. The combined EastCanPo transfer function has a r^2_{boot} = 0.74, a RMSEP = 2.3 °C and a maximum bias of 2.9 °C. The Combined EastCanPo transfer function has been used to infer temperatures in a Polish varved lake for comparison with instrumental data, and the differences between reconstructed and measured temperatures were in average 0.75 °C (Larocque-Tobler *et al.*, 2015; 2016). The Combined EastCanPo transfer function was also used to reconstruct climate of the past millennium (Hernández-Almeida *et al.*, 2016) and the last 2000 years (Larocque-Tobler et al. *in prep*) with a good correlation to the PAGES 2k reconstruction (PAGES 2k Consortium, 2013).

Results

The patterns of temperature reconstructions obtained by the three transfer functions were similar (Fig. 1), the correlation coefficient (r_{Pearson}) between the combined EastCanPo and the Fortin et al. (2015) reconstruction which contains only 52 out of 485 lakes from EastCanPo, was 0.68. However, the Canadian transfer function provided estimates which were 2-3 °C colder than the two other models. The temperature anomalies obtained from the Canadian model were mostly inferred colder than today.

Cold temperatures were recorded before 8 k cal a BP (Fig. 1). Temperatures increased to reach a maximum around ca. 8 k cal a BP and remained warm until ca. 6.73 k cal a BP with an average anomaly of 2.3 °C (Combined EastCanPo) and 1.7 °C (Eastern Canadian). During zone Ach-2 (ca. 6.73 – 5.47 k cal a BP), temperatures were generally colder than in the previous zone with an average anomaly of 1.4 °C (Combined EastCanPo) and 0.4 °C (Eastern Canadian). During zone Ach-3 (ca. 5.47 – 4.88 k cal a BP), the inferred temperatures were still higher than today's temperature with average anomaly of 1.8 °C (Combined EastCanPo) and 0.8 °C (Eastern Canadian). In zone Ach-4, values oscillated around today's temperature (average anomaly of 0.56 °C (Combined EastCanPo) and -0.6 °C (Eastern Canada) and remained more or less constant. Changes occurred at around 1 k cal a BP (average anomaly of 1.6 °C (Combined EastCanPo) and 2.2 °C (Eastern Canadian). Zone 4b has an average anomaly of 0.9 °C in Combined EastCanPo while it was 0.5 °C in zone 4a. During zone Ach-5 (ca. 0.55 k cal a BP – present) the average anomaly was -0.8 °C (Combined EastCanPo) and -1.6 °C (Eastern Canadian).

With the Combined EastCanPo transfer function, today's temperature inferred by chironomids in the surface sample is 15.2 °C, only 0.2 °C warmer than the instrumental measured temperature (15.0 ± 1.4 °C) while it is 1.4 °C colder (13.8 °C) with the

Eastern Canadian transfer function and 2.2 °C (12.8 °C) colder with the Canadian model of Fortin *et al.* (2015).
The amplitude of inferred-temperature changes was larger with the Eastern Canadian transfer function (-6.9 to 6.1 °C) and the Canadian transfer function (-7-5 °C to 1.2 °C) than the Combined EastCanPo transfer function (-3.8 °C to 4.1 °C).

Discussion

With the Combined EastCanPo transfer function, many taxa had higher temperature optima than those modelled with the Eastern Canadian data set (Table A.2). Since the gradient of temperature was better covered with more lakes imbedded into the 16.3 to 19 °C temperatures, the distribution of taxa along the gradient had better chances to be unimodal and the combined EastCanPo possibly provided more accurate optima than in the Eastern Canadian model. Most of the colder than today indicators are similarly characterized in Brooks *et al.* (2007) except for the warmer than today indicator, *Tanytarsus lugens*-type, which has been characterized as a cold stenotherm by Brooks *et al.* (2007).

However, this description could be partly based on an older taxonomy as *T. lugens*-type and *C. oliveri* were not differentiated as they are today in literature older than 2007. Furthermore, most of the training sets in the Northern Hemisphere contain lakes with temperatures at a maximum of 18 °C (Swiss-Norwegian combined, Heiri *et al.* (2011) and possibly do not provide the complete unimodal distribution of the taxon. In the Eastern Canadian transfer function, *T. lugens*-type was found in lakes between 19 and 24 °C, and in higher abundances in the EastCanPo lakes (16.3 to 19 °C) which suggest that *T. lugens*-type is not a typical cold stenotherm. This illustrates the importance of obtaining the largest possible gradient to get the most realistic distribution of all chironomid taxa.

The Eastern Canadian transfer function (Larocque, 2008) is an extended version of the 52 lakes from Larocque *et al.* (2006) used in the Canadian model of Fortin *et al.* (2015). It contains a few lakes north (3 °C) and south (25 °C), increasing the gradient of temperature (3-27.5 °C). Although it comprises less lakes (72) than the Canadian transfer function, the increased gradient might provide more accurate optima. The temperature optima in the Eastern Canadian model vary between 7.4 and 25.9 °C (Table A.2). However, this training set does not comprise any lake with August temperature between 16.8 and 19 °C, temperatures which might have been experienced at *Lac Aurélie* in the past. To obtain the best coverage (larger gradient and lakes evenly distributed along the gradient) of possibly experienced temperatures, and temperature optima possibly more realistic, lakes should be added between 16 and 19 °C. Unfortunately, this data was not available in Canada. The data from the Norwegian-Swiss combined transfer function is not freely provided, and its maximum temperature is limited to 18 °C (Heiri *et al.*, 2011). Thus, came the idea of merging the Eastern Canadian lakes with a training set of 50 lakes in Poland with August temperatures between 16.3 and 19 °C.

Why Poland?

First, because the data is freely available from the NOAA website, which is not the case for any other transfer function data, either from the American or the European continents. Second, the same analyst has identified the chironomids in *Lac Aurélie* and in both transfer functions. It might appear trivial to those who never tried to merge data sets together, but the consistency in taxonomy makes the application of the transfer function to the downcore samples more accurate. The lower amplitudes in the combined EastCanPo transfer function suggest that the obtained optima are more realistic, as exemplified by the gradient of optima obtained by merging the two transfer functions (9.1 to 21.1 °C; Table A.2). Third, the combined EastCanPo transfer function has previously been used to infer climate in a varved Polish lake and compare to instrumental data with a very good correlation (Larocque-Tobler *et al.*, 2016).

In theory, one would expect that species have different ecological niches at intercontinental scales, thus a model composed of lakes located in the same country should perform better. We do agree with this statement and would appreciate having the opportunity to add samples to the Eastern Canadian training set, if only funding could be secured. However, the taxonomy of subfossil chironomids is not developed to the species but to a coarser level, such as genus. A species name (*i.e. Chironomus anthracinus*-type) is given to an identified head capsule, but the word “type” is added to the scientific name. It means that a morphotype can regroup several species having the same morphological traits. When the optima of these pseudo species are compared in different training sets, for example in Canada and Europe (Larocque-Tobler *et al.*, 2015), it seems that most taxa have similar range of temperature preferences [cf., cold (optimum <10 °C, intermediate (10.1-14,9 °C) and warm (>15 °C)].

These different numbers are due to temperature gradient and coverage of lakes within a training set. The most realistic optima can only be obtained from training sets with a large number of lakes, in a large temperature gradient, with a good coverage of lakes within this gradient and with the highest possible level of taxonomy (Birks, 1998; Heiri and Lotter, 2010), which is the case in the combined EastCanPo transfer function compared to the Eastern Canadian transfer function. These different optima should lead to temperature reconstructions with similar patterns of changes, but with different amplitudes, as seen by Lotter *et al.* (1999) and in this study. In studies using the Eastern Canadian model on Swiss and Italian lakes (Larocque and Finsinger, 2008; Larocque-Tobler *et al.*, 2011), it was shown that the temperature reconstructions using the Eastern Canadian model was more accurate than by using a Swedish or Swiss model because the Eastern Canadian model had more of the downcore taxa present in the training set.

Similar results were obtained in Poland (Płóciennik *et al.*, 2011) where three training sets (Norwegian, Russian, Swiss) were used to reconstruct temperatures and where very similar patterns of changes were obtained. Taxonomy might also be a restrictive factor in the Canadian transfer function. To combine the different training sets, Fortin *et al.* (2015) had to reduce the taxonomic level for *Chironomus* spp, *Micropsectra* spp, *Heterotrissocladius* spp and many of the Tanytarsisni (Table A.2). This grouping provided less realistic optima. For example, the many Tanytarsini are grouped under the name "Tanytarsina" with a temperature optimum of 8.3° while the optima varied from 14.1 to 16.4 °C with the combined EastCanPo transfer function (Table A.2).

Combining training sets to obtain better temperature optima for most taxa is not a new idea. For example, it has been attempted with success from Norwegian and Swiss lakes (Heiri *et al.*, 2011). This Norwegian-Swiss model has been used to reconstruct Holocene climate in France (Gandouin *et al.*, 2016), Ireland (van Asch *et al.*, 2012) and Romania (Tóth *et al.*, 2012). The combined EastCanPo transfer function has already been applied to a Polish lake where inferences were successfully compared with instrumental data (Larocque-Tobler *et al.*, 2016), suggesting that the "inter-continent model" is a valid method. These results strengthen the hypothesis already assumed by Lotter *et al.* (1999) that chironomid transfer functions developed on a continent can be applied to fossil records from the other continent with similar results.

In this study, the combined EastCanPo transfer function provided an inference of the surface sample closer to the meteorological data (0.2 °C) than the Eastern Canadian transfer function (-1.4 °C), although the latter was still within the variability of today's average August temperature (15.0 ± 1.4 °C). The amplitude of changes was smaller with the combined EastCanPo model, which seems more realistic when compared with a simulated regional Holocene climate reconstruction (Ali *et al.*, 2012). Consequently, in the following sections, only the output data from the combined EastCanPo model will be discussed.

The absence of modern analogues stays a problem, which needs to be considered in evaluating the accuracy of a model. Eighteen of the 179 samples (located in the lower portion of the sedimentary) had poor or no modern analogues (Fig. 1). It is assumed that WA-PLS methods calculate well in non-analogue situations because the estimates are based on modelled taxon temperature optima assuming unimodal responses to temperature in order to infer temperatures outside the range of the calibration set (Birks, 1998). The use of the combined EastCanPo transfer function to the *Lac Aurélie* samples was further assessed using goodness-of-fit to temperature. All downcore samples were located within the combined EastCanPo training set samples (Fig. A.2).

This analysis suggests that if only the Eastern Canadian transfer function was used, most of the downcore samples would be located outside the CCA, but by adding the Polish lakes with temperatures between 16.8 and 19 °C, it allowed the training set samples to cover the *Lac Aurélie* samples. None of the *Lac Aurélie* samples was above the 10th percentile, thus all downcore samples had good fit to temperature.

Conclusions

Three transfer functions have been used to reconstruct chironomid-inferred mean August air temperature of the past 8000 years in boreal northeastern Canada from *Lac Aurélie*. This study provides a critical assessment on the use of different transfer functions: A regional transfer function (based on an Eastern Canada data set), a Canadian transfer function including part of the Eastern Canada data set and an intercontinental one based on merged data set of lakes from Eastern Canada and Poland; EastCanPo). We found that this combined EastCanPo transfer function provided more accurate temperature inferences based on comparison between the surface sample and the instrumental data.

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Table A.1 Summarize of three transfer functions used in this study

	1. Eastern Canada (Larocque, 2008)	**2. Canada (Fortin et al., 2015)**	**3. Combined EastCanPo (Larocque-Tobler et al., 2015, 2016)**
Training set	72 lakes 82 taxa	485 lakes 78 taxa	122 lakes 72 (Canada) and 50 (Poland) 95 taxa
August air temperature gradient °C	23.5: (3 – 27.5)	16: (-0.3 – 15.7)	23.5: (3 – 27.5)
Correlation coefficient (r^2_{boot})	0.79	0.73	0.74
Root-mean-squared error of prediction (RMSEP) °C	2.4	1.8	2.3
Maximum bias °C	3.7	2.9	2.9
Used to reconstruct paleotemperatures	**Arctic Canada** (Rolland et al. (2009), **Northern Quebec** (Saulnier-Talbot et al., 2015), **Southern Quebec** (Hausmann et al., 2011), **Switzerland** (Larocque-Tobler et al., 2010) **Northern Italy** (Larocque and Finsinger, 2008).	4 **arctic Canadian lakes** (Fortin et al., 2015)	**Poland** (Hernández-Almeida et al., 2016)
Comments	- (16.3 – 19) °C	Different training sets reduce the taxonomic level (Table 2)	+ (16.3 – 19) °C Combined training set in intercontinental scales (***cf*** **discussion)**
Lac Aurélie 179 samples analysed 63 taxa identified 17 samples (9.5 %) with less than 30 head-capsules)			**Minimum distance to modern assemblages** (Overpeck et al., 1985) Details in chapter 1 **Goodness-of-fit** was calculated by passively adding downcore samples of *Lac Aurélie* into a CCA analysis of the EastCanPo transfer function samples constrained to temperature (Heiri and Lotter, 2010,), using the Canoco 4.5 program (details in chapter 1) **17 samples (10 %) had poor or no-analogues**
Temperature optima	Weighted average (WA)		
Categories (Table 2)	" Cold " (< the present-day temperature, 15 °C) and " Warm" (> 15 °C)		

Table A.2 Occurrence of taxa in the sediment of *Lac Aurélie* (total of 179 samples), comparison of temperature optima obtained with WA for the three transfer functions: (a) Combined EastCanPo transfer function (Larocque-Tobler *et al.,* 2016), (b) Eastern Canadian transfer function (Larocque, 2008), (c) Canadian transfer function (Fortin *et al.,* 2015) and temperature categories.

Taxa identified in sediment	Occurence in sediment	Optima			Category	
		(a) Combined EastCanPo	(b) Eastern Canada	(c) Canada	Colder than today (15 °C)	Warmer than today (15 °C)
Ablabesmyia spp	131	16.5	15.6	4.5		X
Allopsectrocladius spp	33	16.2	16.1			X
Brillia spp	2	14.4	14.4	10.4		
Chaetocladius spp	34	15.8	14.1	9.2		X
Chironomus spp				9.7		
Chironomus anthracinus-type	164	16.3	12.9	*merged with Chironomus* spp		X
Chironomus plumosus-type	147	16.7	14.8	*merged with Chironomus* spp		X
Cladopelma lateralis-type	75	15.9	13.6	10.2		X
Cladotanytarsus mancus-type	87	16.3	12.2	9.3		X
Constempellina spp	34	15.3	14.6	11.2		X
Corynocera oliveri-type	45	11.7	10.4	8.3	X	
Corynoneura spp	43	15.6	8.1	7.9		X
Cricotopus/Orthocladius				7.7		
Cricotopus spp	96	15	11.8	*merged with Orthocladius* spp		
Cryptochironomus spp	48	15.9	14.9	11.3		X
Dicrotendipes nervosus-type	119	16	14.5	10		X
Einfeldia spp	11	13.4	12.9	11.8	X	
Endochironomus tendens-type	54	16.9	15.6	11.1		X
Glyptotendipes pallens-type	36	17.3	14.7	10.9		X
Heterotrissocladius spp				7.7		
H. grimshawi-type	17	12.5	12.5	*merged with Heterotrissocladius* spp	X	
H. marcidus-type	17	12.1	12.4	*merged with Heterotrissocladius* spp	X	
H. subpilosus-type	6	9.5	8.3	*merged with Heterotrissocladius spp*	X	

Labrundinia spp	2	17.5	*not in model*	13.9		X
Lauterborniella spp	60	19.5	22.9	13.4		X
Limnophyes spp	19	17.4	17.3	8.6		X
Mesocricotopus spp	8	10.3	10	8.7	X	
Micropsectra spp				6.2		
Micropsectra bidentata-type	19	15.1	14.9	*merged with Micropsectra* spp		
Micropsectra insignilobus-type						
Micropsectra radialis-type						
Microtendipes pedellus-type	130	15.4	13.6	11		X
Nanocladius spp	3	14.2	12.7	10.8	X	
Orthocladius spp	39	14.4	13.6		X	
Pagastiella spp	26	14.7	14.6	11.2	X	
Parachaetocladius spp	2	*not in model*	*not in model*	*not in model*		
Parachironomus varus-type	5	16.8	13.6	10.4		X
Paracladius spp	1	9.1	7.4	4.5	X	
Paracladopelma spp	2	13.5	13.5		X	
Paracricotopus spp	1	12.2	10.4	9.6	X	
Parakiefferiella spp	40	14	10.7	8.4	X	
Paratanytarsus spp	96	15.4	12.9	*merged with Tanytarsina*		X
Paratendipes nudisquama-type	13	17.4	*not in model*	11.9		X
Pentaneurini spp	83	15.3	14.9	9.3		X
Phaenopsectra spp	9	17.7	19.2	11		X
Polypedilum nubeculosum-type	101	17.7	18.8	11		X
Procladius spp	168	15.4	14.6	9.5		X
Psectrocladius septentrionalis-type	55	13.3	12.9	10.6	X	
Psectrocladius sordidellus-type	141	13.8	12.5	10.9	X	
Pseudochironomus spp	63	17.7	*not in model*	11.9		X
Pseudosmittia spp	7	17	16.1	8.5		X

Rheocricotopus spp	1	*not in model*	*not in model*	9.1		
Sergentia coracina-type	20	21.2	25.9	7.1		X
Smittia spp	5	15.1	11.6	*not in model*		
Stempelinella spp	21	17.6	14.7	10.6		X
Stenochironomus spp	2	*not in model*	*not in model*	*not in model*		
Stictochironomus spp	10	13.4	7.9	7.4	X	
Tanytarsina				8.3		
Tanytarsus lugens-type	145	16.3	13.4			X
Tanytarsus mendax-type	145	15.7	14.1			X
Tanytarsus pallidicornis-type	74	14.8	13.7		X	
Tanytarsus spp	173	14.1	12.7		X	
Tanytarsus sp.C	95	15.8	15.8			X
Tanytarsus with spur on antenna	44	16.4	15.5	9.9		X
Thiennemaniella spp	16	*not in model*	*not in model*	*not in model*		
Thiennemanyia spp	3	15.1	12.5	*not in model*		
Xenochironomus spp	1	*not in model*	*not in model*			
Zalutschia mucronata spp	49	13.3	13.1	8.2	X	
Number of taxa not included in the training set		**5**	**8**	**19**		
Maximum temperature (°C)		**21.2**	**25.9**	**13.9**		
Minimum temperature (°C)		**9.1**	**7.4**	**4.5**		

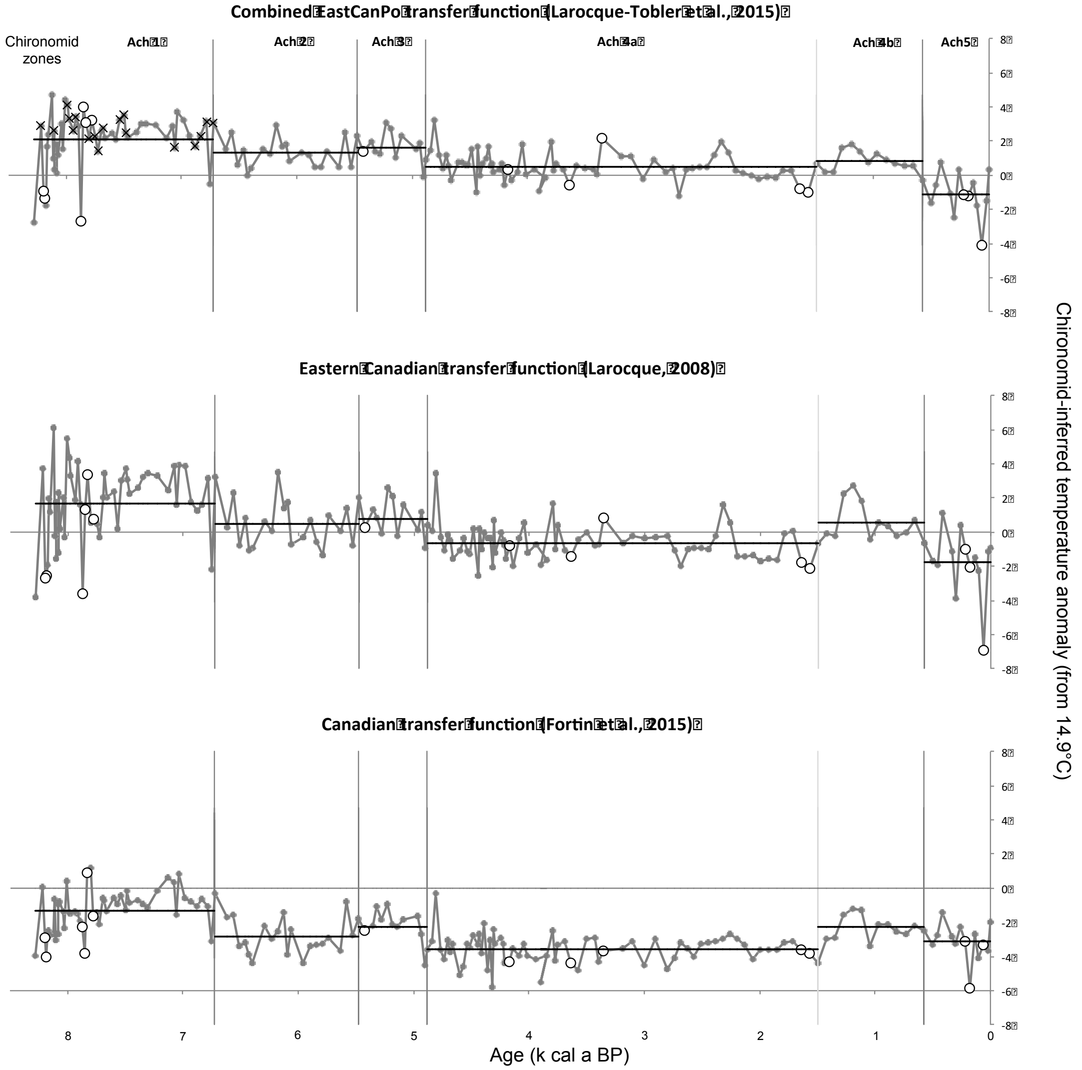

Figure A.1 Chironomid-inferred August air temperature anomaly (C°) at *Lac Aurélie* using a combined EastCanPo (upper graph) transfer function, the Eastern Canadian transfer functions (middle graph) and the Canadian transfer function of Fortin *et al.* (2015) (lower graph). White circles correspond to samples with less than 30 head-capsules and crosses samples with “poor analogue”. The vertical lines indicate the zonation obtained from the chironomid stratigraphy (Fig. 2). The horizontal bold lines indicate the average anomaly during the chironomid zones.

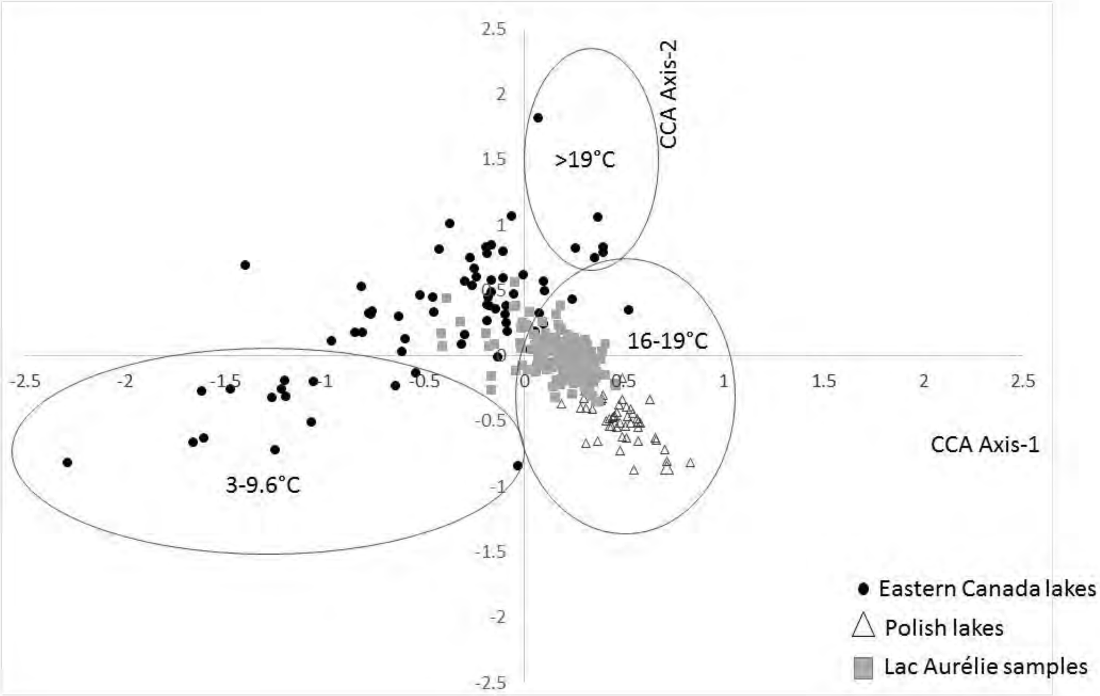

Figure A.2 Goodness-of-fit calculated by passively adding downcore samples of *Lac Aurélie* into a CCA analysis of the EastCanPo transfer function samples constrained to temperature. If the distance between downcore and transfer function samples were above the 10th percentile, the downcore sample was characterized as not having good fit to temperature. Here, only four of these 17 samples provided extreme inferences, so it was decided to leave them.

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