Université de Montréal

Joindre le passé et le présent par les études paléoécologiques dans un contexte d'aménagement écosystémique de la forêt boréale du Québec

par

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Joindre le passé et le présent par les études paléoécologiques dans un contexte d'aménagement écosystémique de la forêt boréale du Québec

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Résumé

Les enjeux actuels de protection et d'aménagement des écosystèmes, notamment en forêt boréale, se heurtent à des incertitudes liées aux changements climatiques. En effet, les changements climatiques ont et vont avoir des conséquences appréciables sur la composition, la structure et le fonctionnement dynamique des écosystèmes boréaux (Figure I.1).

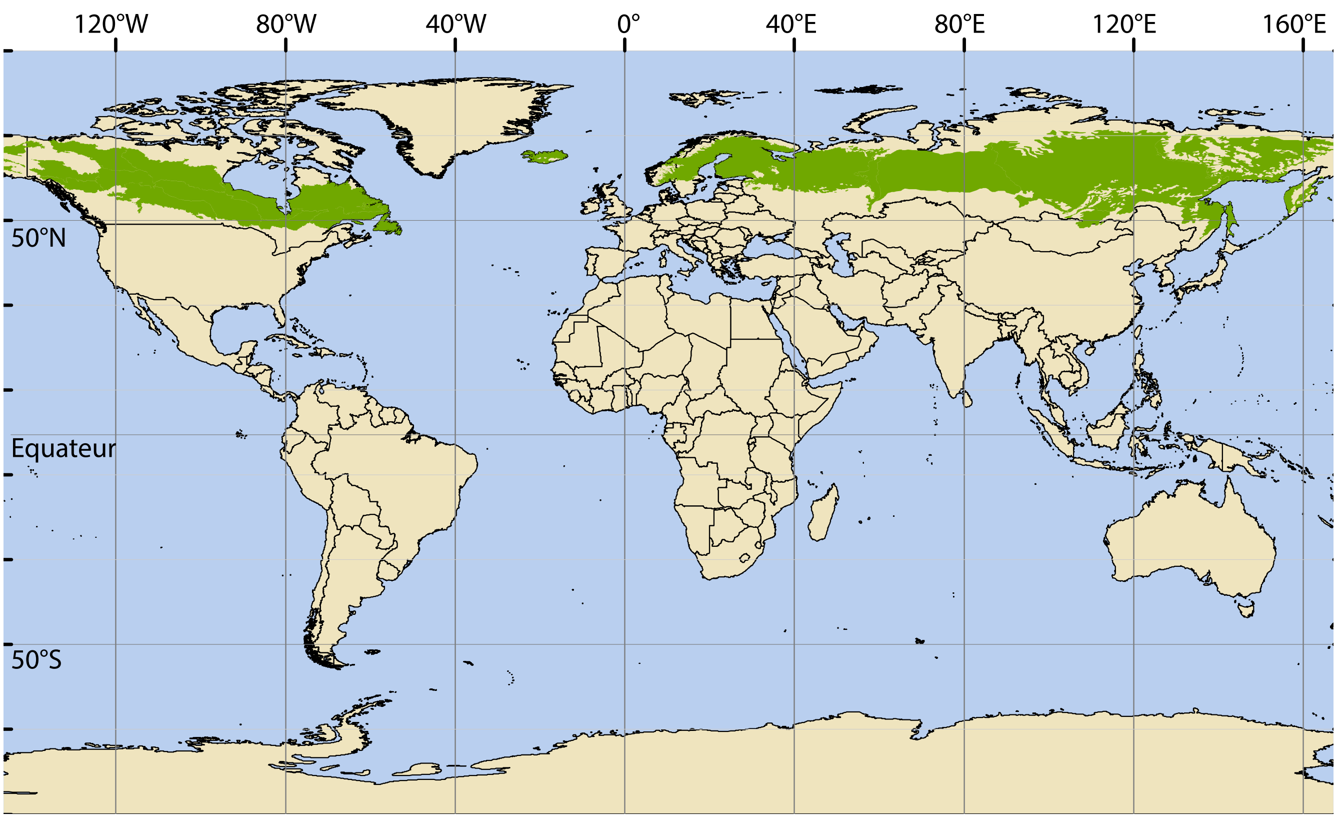

Figure I.1. Répartition du biome boréal (en vert) dans le monde

La dynamique de ces écosystèmes dépend aussi de perturbations telles que les feux, les épidémies d'insectes ou encore les chablis dont les régimes naturels (occurrence, surface, sévérité...) sont modifiés par les changements climatiques. À cela s'ajoutent les impacts directs et indirects des activités humaines qui ne cesseront d'augmenter et d'interférer avec le fonctionnement des écosystèmes. Dans ce contexte, il est donc difficile de savoir jusqu'à quel point les capacités de résistance et de résilience des écosystèmes seront altérées. De cette problématique émerge des préoccupations relatives à la préservation de l'intégrité des écosystèmes et à la pérennisation des usages que nous en avons. De nombreux efforts ont déjà été menés en réponse à ces interrogations par, entre autres, la création d'un aménagement écosystémique des forêts au Québec dont l'objectif est de réduire l'écart entre les forêts naturelles et les forêts aménagées. Il ne faut cependant pas négliger le fait que les écosystèmes sont des entités dynamiques qui possèdent des capacités de résistance et de résilience (adaptation) en réponse à des contraintes environnementales (climat, perturbations...). Ces interactions se manifestent depuis le retrait du dernier glacier qui recouvrait le Québec pendant la dernière ère glaciaire. Très rapidement les écosystèmes se sont différenciés et ont suivi leur propre dynamique jusqu'aux forêts que nous pouvons observer aujourd'hui. Pour préserver durablement ces écosystèmes il faut donc en comprendre l'état actuel et le fonctionnement écologique à long-terme posant ainsi la question des méthodes qui permettent de reconstruire cette histoire écologique. Ces méthodes peuvent être déployées suivant deux échelles : l'échelle spatiale et l'échelle temporelle, souvent considérées comme antagonistes (Figure I.2).

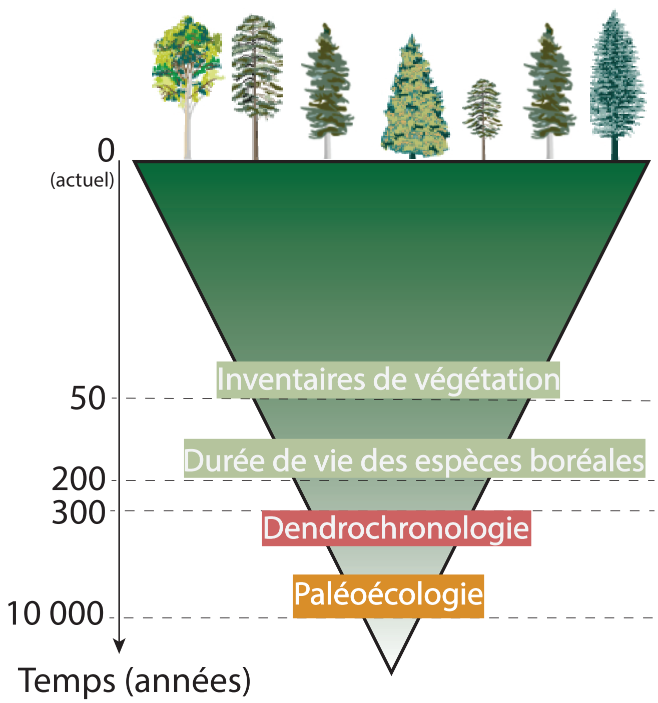

Figure I.2. Représentation schématique de l'abondance relative des données de description des écosystèmes actuels en fonction du temps, symbolisée par le triangle que l'on parcourt de la base (données abondantes) à la pointe (données plus rares). Avec le temps les témoins des écosystèmes actuels deviennent de plus en plus indirects. Ces témoins sont symbolisés par le dégradé de couleur qui s'étire du vert (témoins directs) au blanc (témoins indirects).

En effet, il est de coutume de remplacer l'échelle temporelle par l'échelle spatiale comme par exemple avec des inventaires extensifs de végétation qui donnent une image des écosystèmes contemporains. Au contraire, vouloir décrire la dynamique d'un écosystème sur le long terme s'effectue au détriment de l'échelle spatiale comme en paléoécologie. Plus la profondeur temporelle étudiée est importante, moins les données sont abondantes et plus les reconstructions doivent se baser sur des témoins indirects des variables d'intérêt (e.g. végétation, feux, etc..) dont la présence et l'abondance doivent être interprétées via des bio-indicateurs, notamment le pollen et les charbons (Figure I.2).

L'objectif de ce doctorat est de réconcilier les échelles, temporelle et spatiale, dans les études paléoécologiques et écologiques récentes avec pour territoire d'étude les écosystèmes forestiers boréaux du sous domaine de la pessière à mousses de l'Ouest du Québec (PMO). Dans un premier temps une étude de la diversité écosystémique actuellement présente et de son histoire pluri-millénaire permet d'appuyer la mise en place de cibles d'aménagement écosystémique à plus petite échelle. Les reconstructions holocènes de la végétation et des feux utilisées dans ce premier chapitre ont mis en évidence des difficultés dans l'analyse conjointe de plusieurs bio-indicateurs. Ces difficultés sont principalement liées au manque de connaissances du rôle des processus taphonomiques dans les enregistrements de bio-indicateurs retrouvés dans les archives sédimentaires. Les deux autres chapitres de ce doctorat ont permis de mieux comprendre ces liens qui existent entre les écosystèmes et certains des bio-indicateurs qu'ils génèrent. Il a ainsi été possible de développer des outils méthodologiques pour faciliter l'interprétation des bio-indicateurs. À terme, ces outils permettront de mieux comprendre les dynamiques à long-terme des écosystèmes forestiers boréaux de la PMO.

Contributions de chaque chapitre

Chapitre 1 : Utiliser la paléoécologie afin d'améliorer les états de référence pour l'aménagement écosystémique dans la pessière à mousses de l'Ouest du Québec.

Les objectifs de ce chapitre sont de mettre en évidence (1) la diversité actuelle des écosystèmes au sein d'une unité forestière : la pessière à mousses de l'Ouest et établir (2) la dynamique holocène de ces écosystèmes au regard de la végétation et des feux et (3) la pertinence de ces analyses au regard des cibles d'aménagement écosystémique mises de l'avant par le Ministère des Forêts, de la Faune et des Parcs. Pour répondre au premier objectif, des données d'inventaires écoforestiers ont été analysées à l'aide d'une RDA (Analyse de Redondance) pour comprendre les liens entre, d'une part, la végétation et, d'autre part, les variables environnementales formées par le milieu physique, le climat, les perturbations naturelles et anthropiques (Figure I.3).

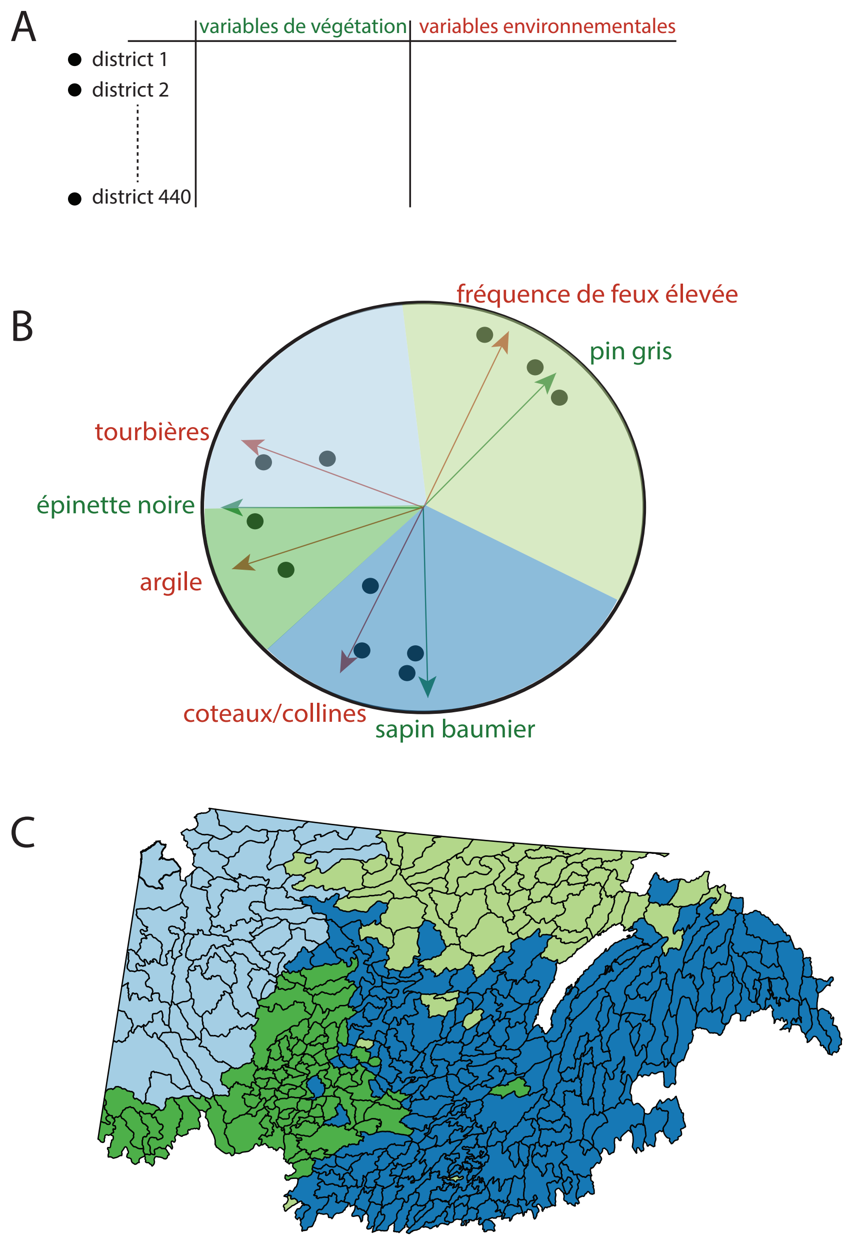

Figure I.3. (A) Description des districts écologiques (polygones sur la carte en (C)) selon la végétation et les conditions environnementales utilisées (B) afin d'exprimer les gradients écologiques à l'origine de la répartition de la végétation sur le territoire d'étude et (C) de regrouper les districts similaires pour former des territoires homogènes. Les résultats de B et C proviennent d'une Analyse de Redondance (RDA) réalisée sur les éléments définis en A.

Ce chapitre consiste aussi en une méta-analyse de données paléoécologiques de pollen et de charbons pour reconstruire les dynamiques pluri-millénaires de la végétation (Figure I.4) et des feux (Figure I.5) et ainsi établir la variabilité naturelle des écosystèmes forestiers du territoire à l'étude.

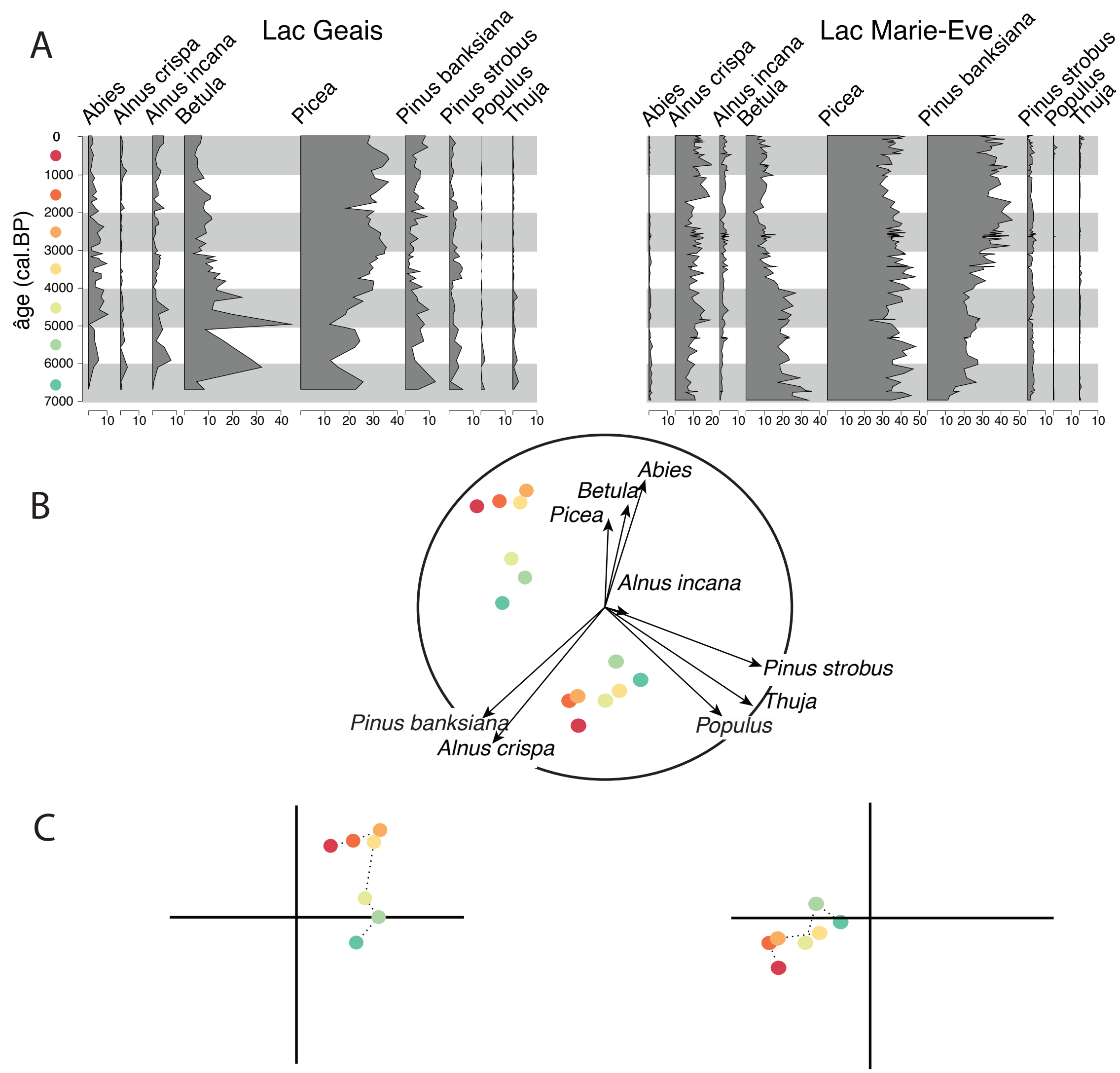

Figure I.4. Illustration, à partir de 2 lacs contrastés, montrant (A) le découpage par millénaire de données polliniques, (B) le positionnement des données millénaires des 2 lacs dans une ACP (Analyse en Composantes Principales) et (C) l'établissement des trajectoires de végétation correspondantes au cours des 7 derniers millénaires. Le lac Geai se situe dans la zone bleu pâle (dominance de tourbières et de pessières noires) et le lac Marie-Eve dans la zone vert pâle (reliefs plats et abondance de pinèdes grises) de la Figure I.3.

Pour répondre au dernier objectif, les reconstructions des cibles d'aménagement forestier ont été comparées avec la variabilité naturelle des écosystèmes.

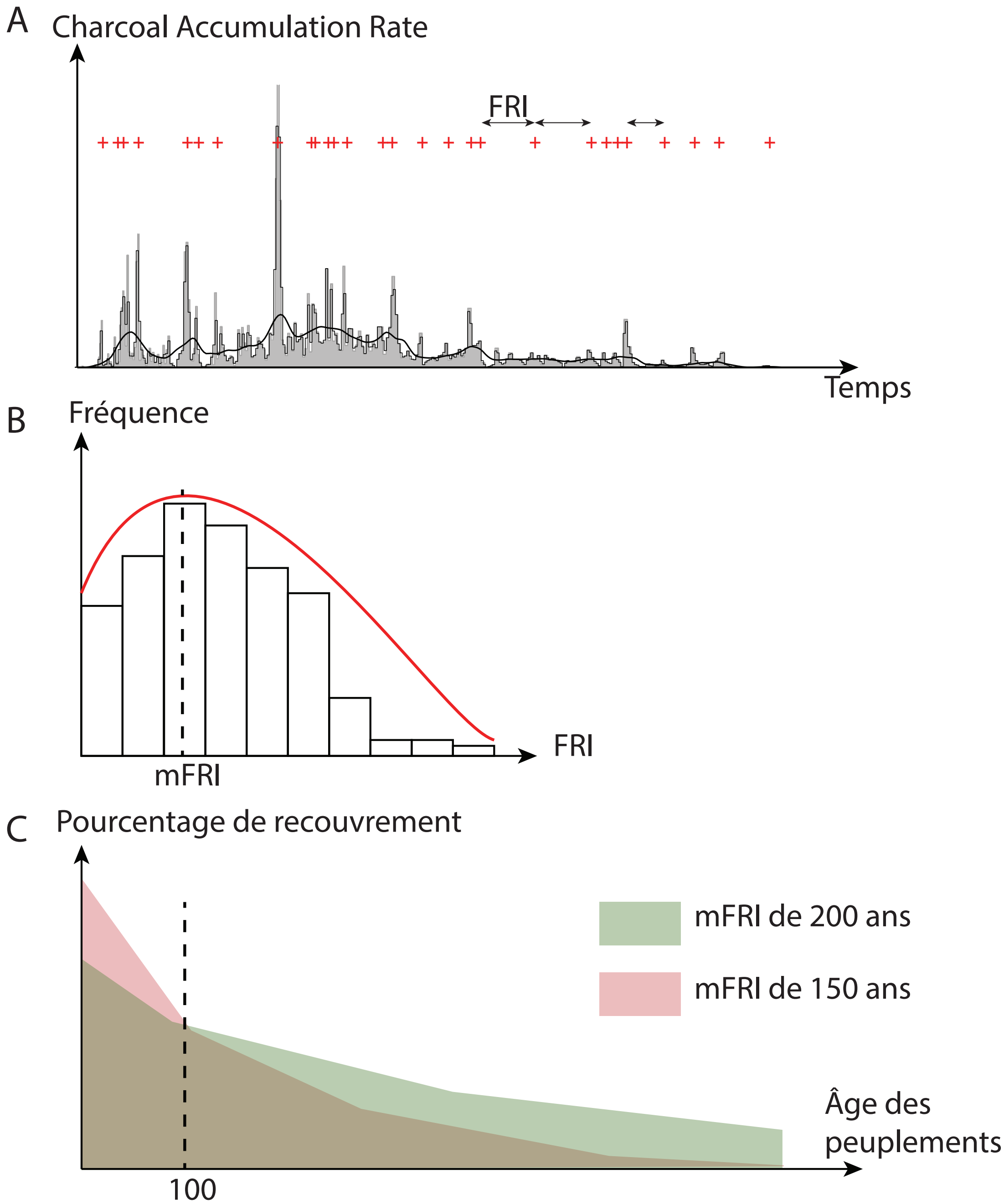

Figure I.5. (A) Illustration de la détection des feux à partir des données de charbon de la séquence du lac Nano. (B) Diagramme de fréquence des FRI pour des lacs localisés dans la même zone (Figure I.3) avec en rouge la courbe de regréssion de type Weibull. (C) Distribution relative des âges des peuplements pour un mFRI de 150 ans (en rouge) et un mFRI de 200 ans (en vert).

Ce chapitre a permis de montrer que la diversité écologique aujourd'hui observée au sein de la PMO s'est mise en place très tôt au cours de l'Holocène. Cette structuration devrait être considérée dans la définition des cibles d'aménagement écosystémique pour rendre l'exploitation des forêts plus durable. Ce chapitre montre également que la proportion de vieilles forêts (> 100 ans) a toujours été relativement élevée, peu importe le territoire homogène.

Chapitre 2 : Reconstructions de la surface brûlée et de la sévérité des feux à partir de charbons provenant de lacs boréaux.

Dans ce chapitre, il s'agit de mieux comprendre les processus taphonomiques qui affectent les particules de charbons entre le moment où elles sont produites par la combustion incomplète de la matière organique et le moment où elles se déposent à la surface des lacs. Il s'agit ainsi de comprendre (1) comment la surface brûlée et la sévérité d'un feu modulent le signal de charbon observée dans les lacs, (2) jusqu'à quelle distance du lac les particules d'un feu peuvent être captées et (3) quel est le délai qui existe entre l'émission des particules et leur dépôt à la surface des lacs.
Pour ce faire, des trappes placées sous la surface de l'eau ont été récoltées tous les ans entre 2011 et 2016 pour mesurer l'influx annuel de charbons. Ces influx ont été comparés à des données de surface brûlée et de sévérité de feux mesurées à 3, 15, 30 km autour des lacs pour des feux ayant eu lieu jusqu'à 5 ans précédant chaque relevé de trappes (Figure I.6).

Nous avons pu établir des liens statistiques significatifs entre la surface médiane des charbons calculée dans les enregistrements avec la sévérité et la surface brûlée des feux ayant eu lieu dans un rayon de 30 km autour des lacs l'année où les influx de charbons ont été mesurés.

Chapitre 3 : Calibration des charbons sédimentaires avec les caractéristiques des feux environnants : défis et nouvelles opportunités

Ce chapitre a pour objectif de mieux comprendre comment les processus de production, de transport et de stockage des charbons dans une archive sédimentaire influencent le signal de charbons.
En se basant sur les résultats du second chapitre, la surface brûlée et la sévérité des feux jusqu'à 30 km autour des six nouveaux lacs ont été reconstruites et comparées avec des données de charbons de sédiments de surface (Figure I.6). Dans ce chapitre, nous avons mis en évidence des liens marginalement significatifs entre le nombre de particules de charbons dans les sédiments et la surface brûlée et la sévérité des feux.
L'expérience acquise de ce chapitre et du précédent permet d'effectuer un bilan sur notre compréhension de la taphonomie des particules de charbons et leur potentielle utilisation dans la reconstruction de caractéristiques de feux comme la surface brûlée et la sévérité.

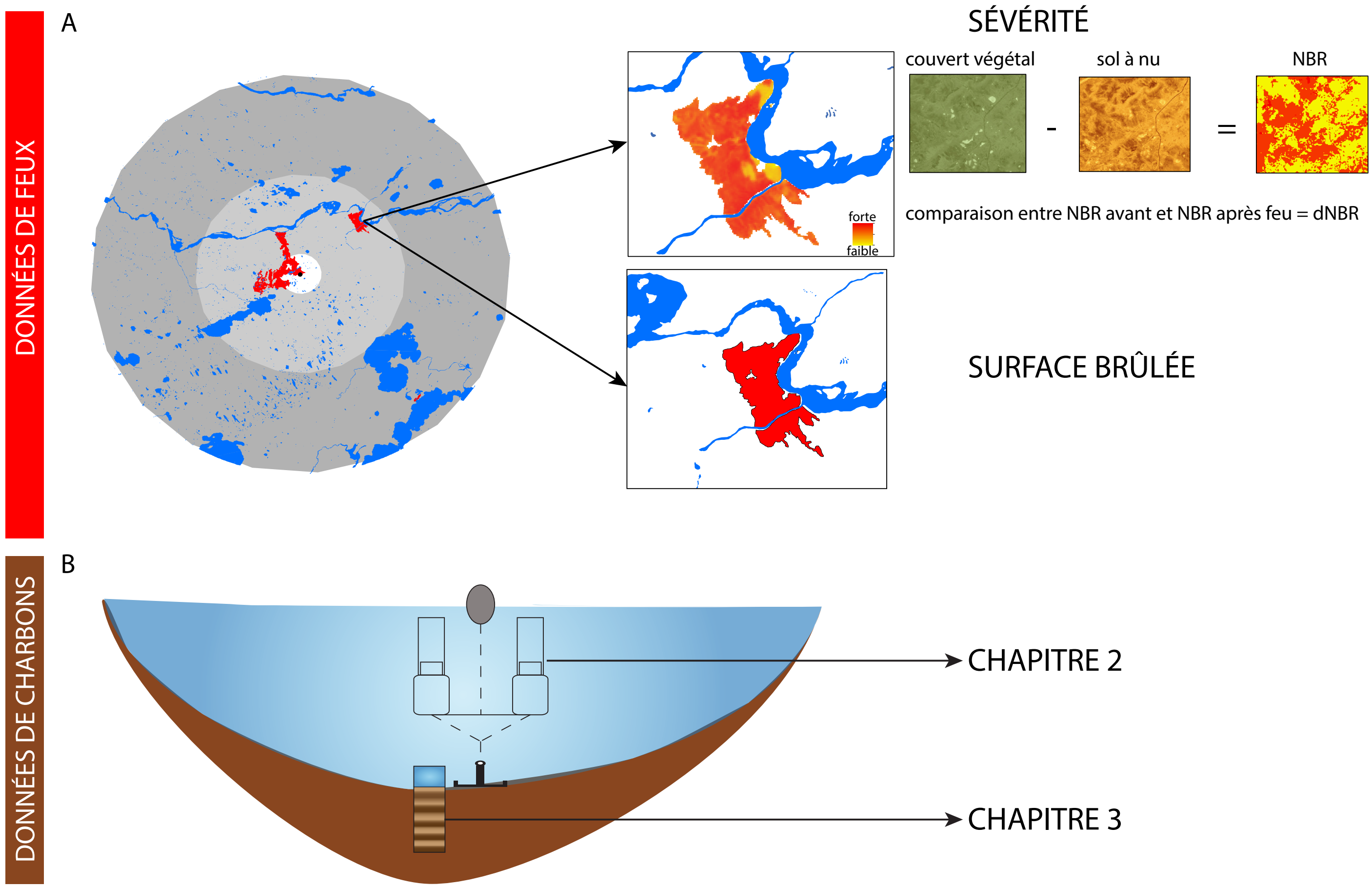

Figure I.6. (A) Caractéristiques principales des feux, surface brûlée et sévérité, utilisées dans le doctorat (pour les mesures de surface par classe de sévérité voir ***Chapitre 2***) qui seront comparées aux (B) données de charbons qui se déclinent sous deux formes, les enregistrements annuels utilisés dans le ***Chapitre 2*** et les sédiments de surface dans le ***Chapitre 3***.

MOTS-CLES : paléoécologie, taphonomie, calibration, pollen, charbons, aménagement, forêt, feu

Abstract

In the boreal forests, current objectives in terms of protection and management of ecosystems are facing uncertainties due to climate change. Indeed, ongoing and future climate change have and will have noticeable consequences on boreal ecosystems composition, structure and dynamic (Figure I.1). Ecosystem dynamic is also influenced by natural disturbances such as fire, insect outbreaks and windthrows for which regimes (occurrence, surface, severity...) will be modified by climate change. Moreover, direct and indirect impacts of human activities will keep on increasing and interfering with ecosystems functioning. Thus, knowing how the resistance and resilience of ecosystems will be affected is challenging. By the same token, protecting ecosystems integrity and sustaining the usages we have of them raise concerns. Many efforts have been put in place as an answer to these questions such as in Québec with the establishment of an ecosystem based management of forest which aims at reducing the gap between natural and managed forests. Nevertheless, one should not neglect that ecosystems are dynamic entities with resistance and resilience capacities (adaptation) in response to environmental constraints (climate, disturbances...). These interactions are occurring since the retreat of the glacier that was covering Québec during the last Ice Age. Quickly, ecosystems differentiated and followed their own path until reaching their current state. In order to protect the ecosystems we need to understand their current state and their long-term dynamic thus asking the question of the methods available to access ecological history of the ecosystems.

Methods can be applied following spatial and temporal scales often considered as antagonistics (Figure I.2). Indeed, temporal scale is often replaced by spatial scale such as for extensive inventories. On the contrary, the description of long-term ecosystem dynamic can be done at the expense of spatial scale such as in paleoecology. The longer the temporal scale is, the less the data are abundant and the more reconstructions rely on indirect indicators of (e.g: fire, vegetation, ...) which presence and abundance must be described via proxies as pollen or charcoal (Figure I.2).

The objective of this thesis is to reconcile the two scales, temporal scale and spatial scale, in paleoecological studies and contemporary ecological studies with the Quebec western spruce-feathermoss subdomain (PMO) as study area. First, the current ecosystem diversity and its pluri-millennial history have been studied and support the establishment of low scale ecosystemic management targets. The Holocene reconstructions of vegetation and fire from the first chapter highlighted the challenges of multi-proxy analyses. These difficulties are mostly due to the lack

of knowledge concerning the influence of taphonomic processes in the recording of bio-proxies in a sedimentary archive. The two other chapters composing this thesis helped to understand the links existing between the ecosystems and the bio-proxy signals they generate in order to develop methodological tools to facilitate their interpretation. Overall, these tools will allow us to better understand long-term dynamics of boreal forest ecosystems in the PMO.

Contributions of each chapter

Chapter 1: Using paleoecology to improve reference conditions for ecosystem-based management in western spruce-moss subdomain of Québec

The objectives of this chapter are to highlight (1) the current diversity of the ecosystems located in a forest unit : the western spruce-feathermoss domain and to establish (2) the Holocene dynamic of the ecosystems regarding the vegetation and fires and (3) the relevance of these analysis regarding the ecosystem-based management targets promoted by the Ministry of Forests, Wildlife and Parks. To meet the first objective, vegetation inventories data were analyzed using a RDA (Redundancy Analysis) to understand the relationships between vegetation and physical environment-climate-disturbances (natural and anthropogenic) (Figure I.3).

This chapter also consists in a meta-analysis of paleoecological pollen (Figure I.4) and charcoal data (Figure I.5) for reconstructing multi-millennial vegetation and fire dynamics and thus for establishing the natural range of variability of the forest ecosystems. To meet the last objective, ecosystem-based management targets were reconstructed and compared with ecosystems natural range of variability.

This chapter allowed to highlight that the current ecological diversity characterizing the western spruce feathermoss domain set up early during the Holocene. This structuring should be considered in the definition of the ecosystem-based management targets in order to sustain lumbering. This chapter also shows that the proportion of old growth forest ($>$ 100 years) has always been relatively high in all the homogeneous territories.

Chapitre 2: Reconstruction of burned area and fire severity using charcoal from boreal lake sediments

In this chapter, the objective is to understand the taphonomic processes that affect charcoal particles between the production by incomplete combustion of the organic matter and the deposition at the lake surface. Thus it aims at understanding (1) how the burned area and the fire severity influence the charcoal signal observed in lakes, (2) how far away from the fire the particles produced can be transported and (3) what is the delay between the particles production and the deposition at the lakes surface. To do so, trapps were placed under the water surface and collected annually between 2011 and 2016 in order to measure the annual charcoal influx. These influx were compared to the burned area and the fire severity data measured at 3, 15 and 30 km around the lakes for fire events that happened up to 5 years before each charcoal influx measurement (Figure I.6).

We found significant relationships between charcoal median surface area calculated for each record and fire severity and burned area for fires that occured up to 30 km from the lakes the year of the charcoal influx measurement.

Chapitre 3: Sedimentary charcoal calibration with surrounding fire characteristics : challenges and new opportunities

This chapter aims at better understanding how the taphonomic processes of production, transportation and storage in a sedimentary archive influence the charcoal signal.

Based on the results of the previous chapter, the burned area and the fire severity within a 30-km radius around six new lakes were measured and compared to the surface sediments charcoal data (Figure I.6). In this chapter, we highlighted marginally significant links between the number of sedimentary charcoal particles and the fire severity and burned area.

The output of this chapter and the previous one helped to better understand the charcoal particles taphonomy and their potential use for the reconstruction of fire characteristics such as the burned area and the fire severity.

KEYWORDS : paleoecology, taphonomy, calibration, pollen, charcoal, management, forest, fire

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Liste des sigles et des abréviations

ACP	Analyse en Composantes Principales
BP	Avant aujourd'hui sachant que 0 BP = 1950, de l'anglais *Before Present*
FRI	Intervalle de retour de feu *Fire Return Interval*
KB	Kajak Brinkhurst
MFFP	Ministère de la Faune, de la Forêt et des Parcs
ONU	Organisation des Nations Unies
PMO	Pessière à mousses de l'Ouest
RDA	Analyse de Redondance (Redundancy Analysis)

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Et il y a ceux qui sont là depuis toujours et que j'aime d'autant plus, vous êtes la raison qui me pousse à persévérer et à surmonter les difficultés. Vous avez été d'un soutien sans faille malgré la distance qui nous sépare. Je veux remercier ma famille, mervilloise et québéco/-clermontoise. Merci d'avoir soutenu mes choix de poursuivre des études qui m'ont menées loin de vous. Maman, Papa, Alexis, je vous aime, je vous dédie cette thèse, et sans oublier bien sûr ce plat pays qui est le mien.

Et...quand la thèse se fait trop pesante, il est bon de la quitter pour mieux la retrouver. Durant ces périodes, j'ai eu la chance de pouvoir partir pour faire un point sur les raisons qui me poussent vers elle. Merci donc à Nathalie Paulin et André Turcotte pour leurs accueils à L'Auberge Boisé Rivière à Magog pour ces retraites plus que nécessaires, ces soirées autour du feu à écouter le ruisseau et déguster des bières de micro-brasserie (oui encore la bière) ! Je n'ai de cesse que de me remémorer votre magnifique forêt.

Ces années ont été l'occasion pour moi de voyager et d'expérimenter l'auto-stop, je remercie donc très chaleureusement l'ensemble des personnes qui m'ont ramassé sur le bord des routes canadiennes. Que ce fut pour 5 minutes ou plusieurs jours, ces moments échangés avec vous sont très précieux à mes yeux, merci de m'avoir permis de découvrir ce magnifique pays. C'est en tout environ 6000 km que j'ai pu parcourir grâce à vous les 32 ramasseurs de pouceux ! Un immense merci à vous tous ! Merci aussi aux 15 autres ramasseurs de pouceux pour les quelques 800 km autour de la Gaspésie.

Figure I.7. Mon sac de voyage devant un panneau de la route 132 qui fait le tour de la Gaspésie

Ces voyages ont été pour moi un moyen de me questionner sur les raisons qui m'ont poussées à entreprendre de telles études. Me remémorer de la raison pour laquelle je me suis lancé dans cette aventure m'a aidé à surmonter ces moments plus difficiles.

Et aussi une anecdote parce que j'aime raconter ma vie : Je venais d'arriver dans la vallée de l'Okanagan en Colombie Britannique. By the way, Roshan just in case you pass by, thank you for welcoming me in Kelowna. I really enjoyed my staying, the people, the Wu-Tang Clan concert and the mountains ! À ce stade de mon voyage, mon objectif était de rallier Kelowna pour y passer quelques jours. Cette région est connue dans tout le Canada pour son micro-climat plutôt chaud et sec ce qui a tendance à favoriser les feux de forêt. Vous me voyer venir, quand je suis arrivé aux alentours de Kelowna il y avait un feu. Un peu plus tard dans la même journée j'étais sur le bord d'un lac et je discutais avec un local, c'était presque le coucher du Soleil et les couleurs étaient incroyables. De notre point de vue, on ne pouvait pas voir les flammes directement mais juste le panache de fumée qui couvrait le Soleil et en diffusait les rayons d'une manière que je n'avais jamais vue auparavant. Ce spectacle de lumière se reflétait sur l'eau du lac qui était troublée par une multitudes de particules sombres. Et là, j'ai eu un flash, le feu qui brûle une forêt que je ne vois pas directement, le panache de fumée qui transporte des particules de charbon qui se retrouvent dans un lac. Ces morceaux de charbons qui ensuite allaient se déposer au fond du lac et être incorporés aux sédiments. C'était ça, les phénomènes que je cherche à comprendre et à reconstruire dans presque tous les chapitre de cette thèse étaient en train de se passer là devant mes yeux !

Et pour finir, parce que je pense qu'il est de bon ton de terminer par une phrase qui se veut énigmatique et profonde, car au fond on aime tous la philosophie de comptoir, j'aimerais tout simplement dire ceci : « Malgré le doute, les difficultés voire même les accidents de parcours, il est important de retenir qu'il ne faut pas lâcher, rien, jamais, pas pour les mauvaises raisons. Il faut mettre le pied dans la porte avant que la porte de l'ascenseur social se ferment et qu'il parte sans vous ». En d'autres termes YOLO !

Introduction

Afin de comprendre les enjeux et problématiques soulevés dans ce doctorat, il faut au préalable faire un état des connaissances que nous avons de la zone géographique étudiée au travers du prisme de la végétation.

1. Contexte biogéographique de la pessière à mousses de l'Ouest

La pessière à mousses de l'Ouest (PMO) est un vaste territoire qui présente de grands ensembles de végétation contemporaine qui se développent sous les effets combinés du climat, des variables du milieu physique ainsi que des perturbations naturelles et humaines (anthropiques). L'un des objectifs de ce doctorat est de déterminer ces grands ensembles sur la base de l'écologie numérique et de ré-analyser les sédiments lacustres et tourbeux qui y ont été étudiés afin de définir des liens entre ces connaissances et la gestion forestière.

1.1. Contrôle climatique de la répartition de la végétation (effet top-down)

En forêt boréale et en particulier au sein de la PMO (Figure I.8), la température est le facteur le plus limitant de la croissance végétale (D'Orangeville et al., 2018; Buechling et al., 2017). Il existe un fort gradient de température orienté du Sud vers le Nord qui va induire un découpage latitudinal de la végétation. Le principal effet visible est la transition de la forêt boréale mixte (domaine de la sapinière à bouleau blanc) vers la forêt coniférienne (domaine de la pessière noire) orienté du Sud vers le Nord (Grondin et al., 2007; Saucier et al., 2009). La disponibilité en eau est le second facteur le plus limitant de la croissance végétale en forêt boréale (Seddon et al., 2016). Il s'exprime notamment le long d'un gradient longitudinal et permet de distinguer les influences des climats océaniques (plus humides, à l'Est du Québec) des climats plus continentaux (plus secs, à l'Ouest). Au Québec, ces gradients climatiques sont à la base d'une régionalisation du régime de feux, avec un cycle de feu plus court à l'Ouest qu'à l'Est (Portier et al., 2016). En réponse à ces conditions climatiques, l'Ouest se distingue par ses peuplements d'épinette noire et de pin gris qui cèdent la place à des peuplements d'épinette noire et de sapin dans l'Est (De Grandpré et al., 2000; Saucier et al., 2009; Couillard et al., 2019). Ainsi, au Québec, plusieurs découpages successifs de la végétation sont possibles sur la base des facteurs qui régissent la répartition des espèces les plus abondantes. Le gradient de température détermine un découpage latitudinal de la végétation et représente le premier niveau de perception c'est à dire les zones, sous-zones, et domaines

Figure I.8. Localisation du sous-domaine bioclimatique de la pessière à mousses de l'Ouest (en vert) au sein du Québec (en gris).

bioclimatiques de la végétation au Québec (Grondin et al., 2007; Saucier et al., 2009). Le second gradient, orienté Ouest-Est, est quant à lui le reflet de changements liés aux précipitations, aux variables du milieu physique et aux régimes des perturbations naturelles (Grondin et al., 2014b).

Ces trois facteurs sont à la base de la reconnaissance des sous domaines bioclimatiques, dont le sous-domaine de la pessière à mousses de l'Ouest sur lequel porte le présent doctorat (Figure I.8).

1.2. La diversité des peuplements forestiers dans les paysages de la PMO est tributaire des conditions locales de l'environnement (effet bottom-up)

La PMO est un territoire de 154 184 km^2 qui présente de grands ensembles de végétation qui se développent plus localement sous les effets combinés du climat, des variables du milieu physique ainsi que des perturbations naturelles et humaines (Grondin et al., 2014a,b; Couillard et al., 2019). Le (***Chapitre 1***) de cette thèse cherche à définir ces grands ensembles en utilisant des techniques d'écologie numérique et les connaissances actuelles sur les écosystèmes présents.

Le territoire de la PMO présente des conditions climatiques froides et modérément humides, caractéristiques des forêts boréales, ce qui limite la dégradation de la matière organique et favorise son accumulation au cours du temps. Ce phénomène, nommé paludification (Simard et al., 2009; Fenton et al., 2005), est d'autant plus favorisé lorsque la topographie est plane et que le substrat sous-jacent est de texture fine. Ces caractéristiques du milieu limitent la circulation verticale de l'eau et favorisent la formation d'une nappe phréatique proche de la surface. C'est le cas notamment dans la ceinture d'argile qui occupe la portion Ouest du territoire d'étude et où les tourbières se sont développées sur de vastes territoires. Ces dernières sont souvent forestières et dominées par l'épinette noire avec le mélèze laricin (*Larix laricina* (Du Roi) K.Koch) en espèce compagne (Belleau et al., 2011; Gauthier et al., 2000). À la marge de ces tourbières, sur les argiles mieux drainées et un relief faiblement ondulé, le peuplier, en mélange avec l'épinette noire et le pin gris, domine le territoire. Vers le centre-nord, la topographie est relativement plane à ondulée, les dépôts sont bien drainés et de texture grossière, (sables) ce qui favorise le pin gris (Le Goff and Sirois, 2004). Dans les zones où le drainage est déficient à mauvais, l'épinette noire abonde (Frelich and Reich, 1999). L'Est de la PMO se caractérise essentiellement par un relief de coteaux et de collines recouverts de tills. Les sapinières à bouleau blancs dominent les plus hautes altitudes ; les pessières noires à sapin sont inféodées aux altitudes et pentes intermédiaires ; alors que les terrains les plus plats, et majoritairement couverts de dépôts fluvio-glaciaires, sont couverts d'épinette noire et de pin gris dont la dynamique est liée à une fréquence plus élevée de feux (Couillard et al., 2016; Martin et al., 2018). Les sols de mi-versants possèdent une plus grande capacité de rétention de nutriments, ce qui favorise le sapin baumier qui forme des peuplements mélangés avec l'épinette noire (Gauthier et al., 2000; Saucier et al., 2009; Martin et al., 2018). La connaissance de la répartition des dépôts de surface couplée à la topographie permettent d'appréhender la diversité écosystémique locale que l'on peut exprimer le long de toposéquences (Saucier et al., 2009).

1.3. Les perturbations, vecteurs de dynamisme des écosystèmes forestiers

À l'échelle du paysage, les écosystèmes forestiers boréaux présentent une mosaïque de peuplements d'âges variés et de stades allant de début de succession à la fin de succession (Cyr et al., 2009). Cette hétérogénéité s'explique en partie par les régimes de perturbations, notamment les feux, les épidémies d'insectes ou encore les chablis (Grondin et al., 2014b). Dans la PMO, le cycle moyen de retour de feu est de 150 ans, celui de la Tordeuse des Bourgeons de l'Épinette (*Choristoneura fumiferana* Clem.) (TBE) est de 2860 ans et celui du chablis est de 4165 ans (Boucher et al., 2011). Plus la fréquence de ces perturbations est importante dans le paysage, plus l'âge moyen des forêts tend à diminuer (Johnson, 1996; Bergeron, 1998; Gauthier et al., 2000). Dans la PMO, plusieurs types de successions forestières peuvent être identifiés (Lecomte and Bergeron, 2005). Dans la plaine tourbeuse de la ceinture d'argile, la dynamique forestière est contrôlée par le processus de paludification. Sur les sites où la tourbe est peu épaisse, l'argile est exposée lors des feux et la paludification se poursuit (paludification secondaire) alors que les sites les plus fortement entourbés (paludification primaire) montrent une diminution graduelle de la croissance et de la densité des épinettes noires jusqu'à devenir une tourbière ouverte ou non forestière (Le Stum-Boivin et al., 2019; Magnan et al., 2018). Dans le centre-nord, un régime de feu trop court conduit ici et là à l'ouverture des forêts et à leur transformation en landes (Lecomte and Bergeron, 2005). Dans l'Est, tous les peuplements bien pourvus de sapin sont dynamisés par les épidémies de TBE (De Grandpré et al., 2000). Ces forêts âgées abritent une grande diversité de plantes vasculaires (Gauthier et al., 2000), non-vasculaires (Fenton et al., 2005) et d'animaux (Drapeau et al., 2009).

1.4. Les perturbations anthropiques : conséquences du passé de l'activité forestière sur la diversité des peuplements forestiers de la PMO

Depuis le début du XXième siècle, la mécanisation progressive permet une exploitation industrielle des ressources forestières québécoises (Boucher et al., 2015) notamment via des coupes rases. Il suffisait après exploitation de laisser la régénération naturelle s'implanter et, lorsque cette dernière était insuffisante, d'effectuer des plantations d'espèces commerciales. La forêt était alors gérée comme une ressource inépuisable selon une rotation forestière de 100 ans. Dans la PMO par exemple, ce mode de gestion a entraîné un rajeunissement des peuplements et une modification de la structure d'âge des paysages forestiers (Cyr et al., 2009; Martin et al., 2019) en plus de favoriser l'expansion des espèces feuillues dans les peuplements les plus riches et des éricacées dans les peuplements plus pauvres au regard du régime nutritif. Une rotation de 100 ans implique en théorie une absence complète de peuplements plus âgé que 100 ans alors qu'un cycle de feu de 100 ans génère une mosaïque complexe d'âge avec au moins 37% des peuplements plus âgés que 100 ans (Bergeron et al., 2007). L'exploitation forestière a donc eu pour effet d'accroître l'écart entre la forêt aménagée et celle évoluant sous une dynamique naturelle observée sur plusieurs millénaires (Cyr et al., 2009). De manière plus générale au Canada, la gestion équienne des forêts ne semble plus répondre aux objectifs de préservation des caractéristiques des forêts actuelles et futures ; les coupes partielles favorisant le maintien de forêts à structure inéquienne devraient être favorisées (Martin et al., 2020; Bergeron et al., 2004).

Une des originalités de ce doctorat a été une grande intégration de la compréhension des écosystèmes. La connaissance de l'état actuel des écosystèmes va permettre d'avoir plus de recul sur les reconstructions paléoécologiques de long, moyen et court termes. La régionalisation va permettre d'analyser comment les résultats de la paléoécologie se joignent aux résultats de l'écologie numérique.

2. Application des principes de la paléoécologie à la conservation et la gestion des écosystèmes

2.1. Principes généraux de la paléoécologie

La paléoécologie se base sur l'analyse de bio-indicateurs émanants d'une composante d'un écosystème comme la végétation (pollen) ou le feu (charbons de bois) et qui sont stockés dans une archive (ex : sédiments lacustres). Un bon indicateur doit pouvoir se conserver sans être altéré pendant une longue durée. Une fois produits, les bio-indicateurs sont émis dans l'environnement, puis transportés par exemple par le vent ou l'eau et déposés dans une archive où ils sont stockés. L'ensemble de cette dynamique de production, de transport et de sédimentation constituent les processus taphonomiques spécifiques à chacuns des bio-indicateurs (Anderson, 2014; Conedera et al., 2009). Le milieu dans lequel les bio-indicateurs sédimentent respecte généralement le principe de stratigraphie, c'est à dire que les couches les plus anciennes se trouvent sous des couches plus récentes. Le respect de ce principe permet de reconstituer l'âge de chaque niveau sédimentaire par datation au radiocarbone et la constitution d'un modèle âge-profondeur. Ainsi, les lacs accumulent des sédiments lacustres (gyttja) alors que les tourbières accumulent de la matière organique. Les charbons de bois qui s'accumulent dans les sols minéraux forestiers ne sont pas stratifiés de sorte que l'analyse de cette archive nécessite la datation d'un nombre important de charbons de bois. Ils sont néanmoins des témoins directs de la présence locale des espèces identifiées mais le risque de rebrûlage limite le reconstruction de longues séquences de feux.
La nature de l'élément daté va dépendre de l'âge estimé de la carotte. Ainsi pour les longues séquences, le ^{14}C sera favorisé (Reimer et al., 2004). Pour la partie supérieure, donc plus récente, de ces carottes, mais aussi pour les carottes de sédiments de surface (voir ***Chapitre 3***), l'élément mesuré sera principalement le plomb : ^{210}Pb (Appleby, 1997).

2.1.1. *Principes de la palynologie*

Les grains de pollens sont constitués de sporopollénine, une substance presque indestructible et imputrescible qui présente une grande variabilité de morphotypes. Les structures et textures des grains de pollens, ou ornementations, sont variées et permettent leur identification plus ou moins précise à l'espèce ou au genre ; on parle alors de taxon pollinique (Von Post, 1946; Lézine, 2008). Les grains de pollens des taxa les plus fréquents dans la zone d'étude sont suffisamment légers pour être transportés par le vent sur de plus ou moins grandes distances. De cette manière, l'identification et le dénombrement des pollens dans des échantillons prélevés le long de la carotte sédimentaire vont permettre de reconstituer l'évolution de la composition des forêts des alentours du site au cours du temps. Les données de comptages sont souvent exprimées dans un diagramme pollinique soit sous forme de pourcentages ou d'influx polliniques. Les pourcentages permettent d'analyser les dynamiques des espèces selon un même référentiel (de 0 à 100%). Or les pourcentages polliniques de toutes les espèces sont liés car la somme des tous ces pourcentages doit faire 100%. Ainsi, l'augmentation en pourcentage d'une espèce va faire diminuer mathématiquement les pourcentages des autres espèces sans que cela soit lié à un changement de composition dans les forêts aux alentours. Exprimer les abondances de chaque espèce en terme d'influx permet de palier à ce phénomène mais réduit la capacité de comparaison entre les sites car les influx des taxa polliniques vont dépendre de la biomasse de chaque espèce présente autour des sites. Par conséquent, cela réduit notre capacité à dégager des dynamiques plus régionales de la végétation.

2.1.2. *Principes de l'anthracologie*

Lors d'un feu de forêt, la biomasse aérienne brûle, mais sa consumation incomplète génère des particules de charbons qui vont, au même titre que les grains de pollen, être transportées par le vent et éventuellement se déposer, sédimenter et être incorporées aux archives. Le dénombrement et la mesure de la taille de ces particules sont à la base de la reconstruction de l'historique des feux de forêts. En paléoécologie, les analyses de charbons sédimentaires lacustres portent généralement sur les particules de taille supérieure à 150 μm (Lynch et al., 2004) afin de ne considérer que les feux locaux (Carcaillet et al., 2001). Pour reconstruire l'historique des feux, le traitement des données de charbons se base sur la détection de pics d'accumulation sédimentaire de charbons, en terme de nombre de particules. L'écart entre deux pics successifs permet de reconstruire un FRI (Intervalle de Retour de Feu) qui est l'intervalle de temps qui sépare deux feux successifs (Higuera et al., 2010). De plus, un ensemble de méthodes statistiques existe afin d'optimiser la détection de ces pics de charbons (Blarquez et al., 2013) (voir ***Chapitre 1***).

En analysant conjointement plusieurs bio-indicateurs, comme les charbons et les pollens, il sera donc possible de décrire les interactions entre la végétation et les feux sur le long-terme et de mieux comprendre l'état actuel des écosystèmes (***Chapitre 1***). D'autres bio-indicateurs permettent de reconstruire les variations de température (chironomides) et de précipitations (thécamoebiens) mais ces derniers n'ont pas été considérés dans ce doctorat.

2.2. L'aménagement écosystémique des forêts boréales et l'utilisation de données à temporalité variable

Le nouveau régime forestier du Québec voté en 2013 a pour objectif de réduire l'écart qui existe entre les forêts naturelles (préindustrielles) et les forêts aménagées. Pour évaluer cet écart, il est

nécessaire de pouvoir comparer les deux types de forêts. Au travers d'états de référence, consignés dans un registre (Boucher et al., 2011), le MFFP décrit l'état préindustriel des forêts attribuables. Les auteurs définissent la composition relative en espèces, la structure des forêts au travers de la distribution des âges des peuplements et les longueurs des cycles des perturbations. La composition forestière est décrite grâce à une succession de programmes décennaux (débutée en 1970) de mesures de placettes-échantillons réparties sur tout le territoire de la forêt méridionale québécoise. Le régime des feux est reconstruit à l'aide d'études dendrochronologiques qui visent à établir, sur un territoire donné, les surfaces brûlées par les feux qui ont affecté les peuplements locaux (Le Goff et al., 2007; Bergeron et al., 2001). Ces études permettent de définir un cycle de feu régional qui rend compte du temps nécessaire pour brûler entièrement un territoire donné (Keeley, 2009). La connaissance du cycle de feu permet de définir une dernière cible d'aménagement relativement au pourcentage de vieilles forêts. Ces dernières sont des peuplements âgés de plus de 100 ans qui possèdent des caractéristiques spécifiques notamment en terme de composition et de structure (Kneeshaw and Gauthier, 2003).
Les données actuellement utilisées pour définir les cibles d'aménagement écosystémique prennent en considération les 200-300 dernières années soit l'équivalent de 1 à 2 cycles de feu, ou 1 à 2 cycles de vies des espèces forestières. Or, les écosystèmes sont des entités dynamiques, et par conséquent, la variabilité naturelle à long terme de ces écosystèmes n'est actuellement pas prise en compte et mène à une gestion aveugle (Gillson and Marchant, 2014). Le (***Chapitre 1***) de cette thèse vise à explorer cet aspect en utilisant les outils de la paléoécologie.

Au Québec, les modèles montrent que le climat devrait être plus chaud et plus humide à l'avenir. Cependant, l'augmentation des précipitations ne permettrait pas de compenser l'augmentation des températures. Ainsi, le climat tendrait à devenir plus sec ce qui favoriserait un régime de feu plus soutenu (Girardin and Mudelsee, 2008). Or par le passé, et depuis le début de l'Holocène, le climat a connu des variations notamment en terme de températures et de précipitations (Bajolle et al., 2018; Ali et al., 2012). Ces conditions climatiques ont modulé le régime des feux et les dynamiques de végétation qui ont pu être enregistrées dans les sédiments (Remy et al., 2017; Ali et al., 2012). Ainsi, par des reconstructions pluri-millénaires, la paléoécologie donne accès à des écosystèmes qui se sont développés sous certaines conditions climatiques qui pourraient correspondre au climat du futur.
Les études paléoécologiques permettent de reconstruire l'histoire de la mise en place et de la dynamique de la végétation à l'échelle d'un territoire. Ces études ont été menées dans de nombreux types d'écosystèmes, comme les écosystèmes Méditerranéens (Vanniére et al., 2016; Colombaroli and Tinner, 2013) ainsi que les savanes et les forêts tropicales (Aleman et al., 2011). L'étude des paléofeux à grande échelle a déjà permis d'identifier des dynamiques régionales pluri-millénaires (Marlon et al., 2016; Daniau et al., 2012; Power et al., 2008). L'ensemble de ces études offre une vision à plus long terme de la dynamique des écosystèmes, de leur variabilité naturelle et de leur relative stabilité (***Chapitre 1*** ; (Gillson and Marchant, 2014)). À terme, ces connaissances vont

guider les politiques de restauration, de protection et d'aménagement des écosystèmes (Aleman and Staver, 2018; Willis et al., 2010).

3. La calibration de bio-indicateurs : le présent comme clé de décryptage du passé

Le second objectif de mon doctorat était de comprendre comment les processus taphonomiques de production, de transport et de sédimentation conditionnent les signaux de charbons (influx annuels, accumulations dans les sédiments). De plus, il s'agissait de comprendre comment ces signaux peuvent nous renseigner sur les caractéristiques des feux qui les ont généré afin, à terme, de pouvoir reconstruire quantitativement les caractéristiques de ces feux sur une échelle pluri-millénaire.

3.1. Des reconstructions paléoécologiques principalement qualitatives des écosystèmes du passé

Le FRI, calculé à partir des pics de charbons sédimentaires, traduit le régime de feu reconstruit indirectement à l'échelle d'un site mais ne permet pas de localiser géographiquement un événement de feu dans le bassin versant. Ce faisant, le FRI n'est pas spatialement explicite et n'est pas l'équivalent du cycle de feu (cible d'aménagement), ce qui freine l'utilisation des données de FRI en aménagement. Plus généralement, la méconnaissance de l'emprise spatiale des reconstructions permises par les bio-indicateurs peut aussi mener à des interprétations contradictoires qui mettent en évidence la nécessité de travaux de calibrations entre les charbons et les caractéristiques des feux qui les ont générés (Hawthorne and Mitchell, 2016) ; ***Chapitre 2 et 3***) ; et les pollens et les quantités relatives de biomasse spécifiques.

La représentation pollinique des taxa peut être exprimée soit en pourcentage, soit en influx (nombre de grains par unité de surface de sédiment et par unité de temps). Chacune de ces représentations possède des avantages et des inconvénients. Exprimer les données en pourcentage permet par exemple de mieux comparer des sites entre eux (***Chapitre 1***) ; mais ne permet pas de rendre compte de l'abondance des espèces autour du site d'étude, ce que permettent les influx polliniques par espèce. En effet, chaque espèce a une production pollinique qui lui est propre, ce qui permet, à partir de la représentation pollinique d'une espèce, d'en déduire son abondance dans les paysages. Néanmoins, ces reconstructions de végétation restent principalement qualitatives. Sur la base de techniques de comparaison entre les assemblages polliniques de surface et la composition actuelle de la végétation, il est possible d'attribuer à un assemblage pollinique plus ancien, un analogue de la végétation actuelle correspondante. Cette technique des analogues modernes permet de reconstruire indirectement et de manière quantitative les dynamiques de végétation au cours de l'Holocène (Simpson, 2007; Blarquez and Aleman, 2015). L'efficacité de cette méthode repose sur la quantité disponible de données polliniques de surface et de leur répartition spatiale pour couvrir la diversité des climats et des végétations contemporaines. En effet, la principale limite de cette méthode est que les conditions climatiques passées ont pu favoriser des types de végétation qui n'ont pas de pareil dans le présent, on parle alors de non-analogue (Simpson, 2007; Gavin et al., 2003). Dans ce cas, il n'est pas possible d'attribuer de végétation actuelle à un assemblage pollinique ancien, ce qui limite la capacité de reconstruction de cette méthode, d'où la nécessité de recourir à des méthodes de calibration pour développer des reconstructions plus directes et précises de la végétation.

3.2. Calibration statistique des liens qui existent entre un processus écologique et les bio-indicateurs

Dans le cadre du présent doctorat, la reconstruction de l'histoire postglaciaire d'un site repose sur l'analyse de carottes sédimentaires lacustres desquelles on a extrait le pollen et les charbons de bois à plusieurs profondeurs afin de reconstituer la dynamique de la composition de la végétation et du régime des feux. Ces études peuvent se faire à l'échelle d'un seul site (Bajolle et al., 2019), de plusieurs sites d'une même région (Carcaillet et al., 2001) ou d'un nombre important de sites couvrant de vastes territoires (Fréchette, 2015; Remy et al., 2017). Afin d'être en mesure d'analyser correctement les résultats livrés par ces différentes échelles de perception, il est important de caractériser l'ensemble des processus écologiques impliqués dans la production, le transport, le dépôt et le stockage dans une archive sédimentaire et ses bio-indicateurs. Les études qui étudient ces processus composent une discipline récente, nommée taphonomie.

3.2.1. *Biais de production*

La production des deux bio-indicateurs à l'étude, soient le pollen et les charbons de bois, ont en commun qu'elle est dépendante des espèces concernées. En d'autres termes chaque espèce a des stratégies spécifiques de production de pollen et de charbons de bois (Sugita, 2007b,a). Le peuplier ne produit qu'une très faible quantité de pollen qui a la particularité d'avoir une exine très mince et donc de se dégrader au cours du temps lorsqu'ils sont stockés dans les sédiments. Le sapin baumier est lui aussi un faible producteur et est ainsi sous-représenté dans les diagrammes polliniques. Au contraire, le bouleau est un très bon producteur de pollen ce qui explique pourquoi il est souvent sur-représenté dans les diagrammes polliniques (Richard and Grondin, 2009). La quantité globale de biomasse spécifique autour d'un lac détermine les influx polliniques relatifs à chaque taxon, (Seppä et al., 2009; Webb III et al., 1981). Le climat (température et précipitations) de l'année en cours et précédente va lui aussi moduler la quantité de pollen produite par une espèce donnée voire par un même individu. Par ailleurs, les caractéristiques des feux vont influencer la production de charbons. La surface brûlée (***Chapitre 2 et 3***, (Higuera et al., 2010)) ainsi que la sévérité (***Chapitre 2 et 3***, (Higuera et al., 2005) modulent la quantité de biomasse brûlée et par conséquent la quantité de particules de charbons émise.

3.2.2. *Biais de transports*

Le principal mode de dispersion des bio-indicateurs depuis leur lieu de production jusqu'au lieu de dépôt est assuré par le vent (charbons : ***Chapitre 2***, (Clark, 1988; Lynch et al., 2004; Higuera et al., 2007) ; pollen : (Prentice, 1985; Sugita, 1993; Bunting et al., 2004)). Lorsqu'ils se déposent sur le sol, les bio-indicateurs peuvent être transportés de manière secondaire par les précipitations et le réseau hydrographique (Anderson, 2014) ce qui assure un influx faible mais relativement régulier de bioindicateurs qui ont été transportés sur une plus ou moins grande distance. Ces particules font partie d'un signal de fond lors des analyses des séquences sédimentaires. Des méthodes statistiques permettent de détecter ce bruit de fond et de l'extraire du signal sédimentaire de charbons pour ne conserver que les influx provoqués par des événements de feux, ou pics de charbons (Higuera et al., 2010; Blarquez et al., 2013).

3.2.3. *Biais de remobilisation et bioturbation*

Sous l'effet de variations saisonnières de températures, des différences de températures se créent entre la surface et le fond du lac. Au printemps et à l'automne, l'eau de surface peut être soumise à des températures inférieures à celle de l'eau plus en profondeur (Hostetler and Bartlein, 1990). L'eau froide étant plus dense que l'eau chaude, des mouvements de convection entre les eaux de surface et de profondeur vont se créer. Ce phénomène peut causer une remobilisation des couches superficielles de sédiments, en contact avec l'eau, et qui sont encore très liquides. De plus, le passage d'animaux tels que des ongulés comme les orignaux, cerf, caribous etc. . . ; d'animaux fouisseurs comme certaines espèces de poissons qui remuent les sédiments pour se nourrir ; ou encore d'animaux bâtisseurs comme les castors peuvent participer à perturber une plus ou moins grande épaisseur de sédiments, on parle alors de bioturbation.

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Ainsi, plusieurs études ont souligné la difficulté de réaliser des études paléoécologiques multi-sites et impliquant plusieurs bio-indicateurs (ex : charbons et pollen). En effet, il semble probable que des processus taphonomiques viennent perturber les influx de bio-indicateurs et ce même à faible échelle.

Problème 1 : Pour des sites relativement proches, il peut exister des différences non négligeables en termes de reconstruction de FRI (Fire Return Interval) (Carcaillet et al., 2010). Par ailleurs, certaines études réalisées sur des lacs faiblement distants ont permis de montrer l'effet du milieu physique (argile vs till) sur la dynamique holocène des écosystèmes (Senici et al., 2013).

Problème 2 : De la même manière, des périodes aux FRI plus longs i.e : des feux moins fréquents, ne correspondaient pas systématiquement à des périodes où les espèces de fin de successions étaient plus abondantes, ce qui est contraire aux observations dans les écosystèmes actuels (***Chapitre 1***, (Ali et al., 2008)).

Problème 3 : En effet, cela montre qu'il est probable d'avoir des perturbations qui n'affectent qu'une partie de l'aire de provenance des bio-indicateurs et qui peut ainsi mener à des messages contradictoires comme une forte proportion d'espèces de début de succession (pin gris) alors que l'occurrence de feu est faible. Il apparaît donc de plus en plus indispensable de réaliser des études de calibration (Hawthorne and Mitchell, 2016) afin de mieux comprendre la provenance des particules en fonction des processus taphonomiques (***Chapitre 2 et 3*** : charbons ; pollen).

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Chapitre 1

Using paleoecology to improve reference conditions for ecosystem-based management in western spruce-moss subdomain of Québec

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Abstract

Ecosystem based management in Québec is framed by reference conditions defining percentage of old-growth forest (>100-years-old) and forest composition characterizing pre-industrial forest landscapes. In the western spruce-moss bioclimatic subdomain (154 184 km^2) a fire cycle estimated at 150 years was used to target that 49% of the landscape has to be composed of old-growth forest. Yet, this target was developed using past (19^{th}-20^{th} C.) climate and vegetation data and assume that environment and ecosystem processes are homogeneous for the entire western spruce-moss bioclimatic subdomain. The wide spatial and narrow temporal windows limit the application of reference conditions under ongoing climate change. Our aim was to classify current vegetation heterogeneity of the western spruce-moss subdomain into homogeneous zones and to study the long-term history of fire and vegetation within these zones. This approach will help to refine forest management targets that are based upon short-term records by providing a long-term perspective that is needed for the forests to be managed within their natural range of variability. Modern forest inventories data were used along with climate, physical variables, and natural and human disturbances to study the current vegetation-environment interactions among the western spruce-moss subdomain. We also used 18 published sedimentary pollen and charcoal series to reconstruct Holocene vegetation and Fire Return Intervals (FRI). Contemporary data revealed 4 zones with homogeneous interactions between vegetation and environment. Pollen analysis revealed three long-term vegetation paths : early successional species dominance, late to early species transition and late successional species dominance. These suggest that modern forest composition results from Holocene trajectories occurring within each zone. Holocene mean FRI (mFRI) ranged from 222 to 258 years across the subdomain, resulting in old-growth forests ranging between 64% and 68%, depending upon the zone. Paleoecological and contemporary results support that to make forest management more sustainable, current landscape heterogeneity that arises from millennial forest composition trajectories and fire cycle dynamics should be taken into account by down-scaling the previously established reference conditions.

KEYWORDS : lacustrine and peatland charcoal particles, pollen, paleoecology, forest management, spruce-moss subdomain, reference conditions registry

1. Introduction

Conservation and sustainable management of ecosystems is a major concern for stakeholders and policy makers thus leading to the establishment of reference conditions used as guidelines for ecosystem restoration (Kuuluvainen, 2009; Pollock et al., 2012), conservation, and management (Goebel et al., 2005). In the province of Québec, these reference conditions consist of an average fire cycle and associated percent of old-growth forest (> 100-years-old) at the spatial scale of vegetation subdomains (average area of 77 587 km^2, (Boucher et al., 2011). Old-growth forest stands, mostly composed of late successional species, shelter high biodiversity and, therefore, are valuable for conservation of vascular plants (Gauthier et al., 2000), non-vascular plants (Fenton et al., 2005), and animals (Drapeau et al., 2009). These reference conditions are used by forest managers as a scientific framework for measuring and bridging the gap between natural and managed forest landscapes, the main goal of which is maintaining these forests within their natural range of variability according to the pre-industrial period (19th-20th C.).

In Québec, the western spruce-moss subdomain is one of the largest subdomains (154 184 km^2) located in the northwestern portion of Québec's commercial forests (Saucier et al., 2009). Its reference conditions have been established from inventory data covering the 19th-20th centuries and showed that pre-industrial landscapes prior to the advent of industrial forestry were composed of

89% resinous species, 9% mixed stands, and 2% broadleaf stands (Boucher et al., 2011). A 150-year fire cycle for the last 200-300 years was estimated for this subdomain using dendrochronology (Bergeron et al., 2001) and the resulting percentage of old-growth forests was $\approx$ 49% (Boucher et al., 2011). Old-growth forests are mostly composed of late successional species such as balsam fir (*Abies balsamea* [L.] Miller) and black spruce (*Picea mariana* [Mill.] BSP). The latter species can also be considered as early successional (Gagnon and Morin, 2001). Conversely, early-successional forest stands are composed of jack pine (*Pinus banksiana* Lambert), black spruce, trembling aspen (*Populus tremuloides* Michaux), and paper birch (*Betula papyrifera* Marshall) that eventually transit into black spruce forests in lowlands and flat topography zones, and black spruce stands mixed with balsam fir in uplands (Cogbill, 1985; Saucier et al., 2009). In this subdomain, vegetation composition and fire regime are highly spatially heterogeneous. Indeed, vegetation distribution within the region is driven by topography, coupled with climate, soil conditions and disturbance regimes (Palik et al., 2000; Grondin et al., 2014a). As the main disturbance, fire interacts with age-class distribution of the stands (Bergeron, 2000), which in turn influence the percentage of old-growth forests (Cyr et al., 2005). Fire effects also display high spatial heterogeneity in southern Québec and at vegetation subdomain scales (Bergeron et al., 2004; Gauthier et al., 2015). Interestingly, mixed and coniferous zones of western Québec are characterized by different fire regimes and contrasting vegetation trajectories that were established after the retreat of the last glaciers, and persisted during the Holocene (Carcaillet et al., 2010; Blarquez and Aleman, 2015). For this subdomain, there is therefore a need to increase the resolution of landscape analyses and their associated millennial trajectories to ascertain whether the short time period that is currently used to define reference conditions is sufficient to cover the natural variability of these forest ecosystems (Landres et al., 1999).

Indeed, reference conditions are based upon data that date back to the Little Ice Age (1600-1850 CE), when climate was cooler and drier, and fire frequency was higher than what is currently observed (Bergeron and Archambault, 1993). This type of climate differs from the forecasted one since the predicted future climate of Québec is likely to be characterized by higher temperature and higher precipitation (IPCC, 2013). However, the increase in precipitation would not necessarily offset the increase in temperature, thereby leading to potentially higher fire activity (Girardin and Mudelsee, 2008). As wildfire frequency and intensity are major drivers of forest dynamics, a modification of fire regimes can deeply modify forest composition and dynamics for example by favoring the establishment of post fire early successional species (Cogbill, 1985). Thus, the choice of baseline data that are used to define management targets is critical and should provide information regarding the state of the targeted ecosystem, regardless of whether it is currently stable or transient (Gillson and Marchant, 2014). There is then a need for a higher temporal coverage of the above-mentioned reference conditions. Long-term information regarding ecosystem dynamics, therefore, can inform ecosystem range of variability according to past climate and fire regime changes (Dearing and Zolitschka, 1999). Thus, paleoecology represents an important source of data and methodological approaches for providing multi-millennial information on ecosystem functioning

and improving guidelines for biodiversity conservation and management (Willis et al., 2010).
Here we used pollen analysis for long-term vegetation reconstructions in order to bring insights regarding post-glacial vegetation dynamics (Carcaillet et al., 2010) and to reconstruct regional vegetation trajectories that are followed by forests (Jamrichová et al., 2017). Charred particles that are contained in lake sediments and peatlands cores were used to reconstruct the Holocene Fire Return Interval (FRI) (Ali et al., 2012) and to calculate the long-term dynamics of old-growth forests within the landscape (Cyr et al., 2009).
We hypothesize that regional differentiation of vegetation in time and space would occur within the western spruce-moss subdomain under the multi-scalar influence of the environment, climate, and disturbances regimes. These regional differences would result from ecological legacies that have persisted after the retreat of Lake Barlow-Ojibway (i.e., ≈ 8000 cal. years BP in the area ; by convention, the present is 1950 CE). If long-term vegetation and fire dynamics explain current landscape heterogeneity, then this data will help to redefine current forest management targets that would comply with ecosystem-based management principles and objectives (Cyr et al., 2009; Bergeron and Fenton, 2012). Therefore, to inform forest managers regarding the long-term dynamics of ecosystems, the Holocene history of boreal forest ecosystems should be reconstructed. In particular, our aims are to (1) highlight and describe current landscape heterogeneity in the western spruce-moss bioclimatic subdomain forest of Québec, (2) to define and classify Holocene vegetation trajectories that have led to current vegetation heterogeneity, (3) to reconstruct FRIs to identify homogeneous fire regimes and analyze their consequences on vegetation distribution and finally (4) estimate the range of variability of the percentage of old growth forest for redefining reference conditions based on Holocene variability.

2. Material and Methods

2.1. Study area

The western spruce-moss subdomain covers 154 184 km^2 of Québec, extending from 70° W to 80° W and from 48° N to 52° N (Figure 1.1). This territory ranges from mixedwood boreal forest in the south to the spruce-lichen subdomain in the north (Saucier et al., 2009), which corresponds to the northwestern portion of Québec's commercial forests. Climate is characterized by low annual temperatures that range from -5° C to 3° C, with a clear North-South gradient. Total precipitation exhibits an East-West gradient, i.e., from 1300 mm to 600 mm, which is linked to increasing distance from the Atlantic Ocean (Grondin et al., 2007). Elevation ranges from 15 m a.s.l. (meter above sea level) with a flat topography in the West to 630 m a.s.l. with a hilly topography in the East. The northwestmost region is dominated by organic deposits that diminish eastward. The Clay Belt is located in the southwest part of the study area and is characterized by a layer of clay left by the pro-glacial Lake Barlow-Ojibway. The central and eastern parts of the study area are dominated by till. Wildfires are abundant in the northern part of the study area and are less abundant elsewhere, particularly in the western part dominated by peatlands (Gauthier et al., 2015).

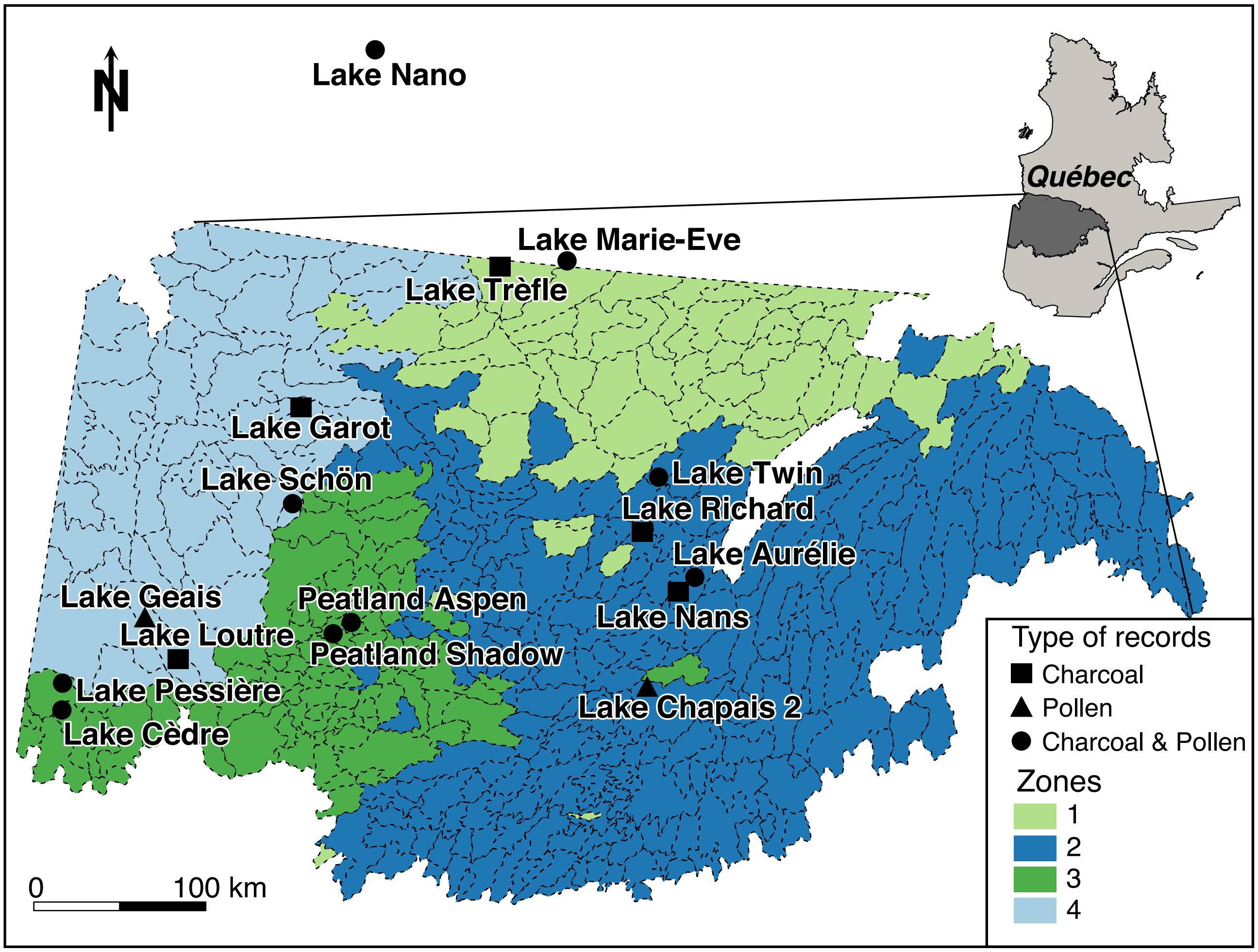

Figure 1.1. Contemporary homogeneous zones (numbers 1–4 and associated colors) of the western spruce-moss subdomain obtained by RDA and k-means partitioning that were applied on ecological districts (n=440). The study area (upper right hand map) represents the western spruce moss subdomain of Québec (Saucier et al., 2009), and paleosites used in this study are denoted according to the type of proxy studied, squares for charcoal, triangle for pollen and circles for both charcoal and pollen.

2.2. Contemporary zonation of the ecological districts

All modern data that are used were provided by the Ministère des Forêts, de la Faune et des Parcs (Ministry of Forests, Wildlife and Parks) of Québec and are defined at the district scale (Grondin et al., 2007). Photo-interpretation of 1 :60 000 scale surficial deposits and the analysis of 1 :50 000 scale physiography on topographic maps permitted delineation of ecological districts (Robitaille, 1988). The study area is composed of 440 ecological districts, which have a mean surface of 300 km^2, and that have been characterized with respect to their current vegetation, climate, physical environment, and natural and human disturbances. Vegetation data consist in relative importance of species basal area and forest stand cover. The two last sets of vegetation variables have been defined by using forest plot inventories and forest maps recorded during the 1980's. Climate data were generated using BioSIM 10 (Régnière and Bolstad, 1994), which interpolates climate information from stations at a cell size of 2 km^2. Climate data that were used range from 1961 to 1990. Physical environment data described surficial deposit relative abundance (percentages) and topography variables described the slope and elevation. Human disturbances referred to anthropogenic fires (Ministry archives 1938-1999) and to forest use through the creation of partial and clear-cuts, and plantations (1970-1980 cartographic data). Natural disturbances consisted of natural fires, outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)) and windthrows, and are expressed as the percentage of a district's surface area that was affected by those disturbances during the 1980s

2.3. Statistical analysis on contemporary data

All statistical analyses were performed in R 3.3.2 (R Core Team, 2018). Redundancy analysis (RDA) was used to analyze the relationships between the response, vegetation data (Y matrix, 26 variables), and the explanatory, environmental data (X matrix, 46 variables) of the 440 districts forming the study area. Before applying RDA, the vegetation variables were Hellinger-transformed, which is recommended when dealing with species abundance data (Legendre and Gallagher, 2001). Forward selection, using the adespatial package version 0.0-8 (Dray et al., 2017), was also carried out on the explanatory variables to select the most significant ones, according to two criteria, based upon their P-values ($P < 0.05$) and the adjusted coefficient of multiple determination (adjR2thresh = 0.54) obtained after performing a preliminary RDA on all the variables (Blanchet et al., 2008). This selection allowed for the identification of more parsimonious and therefore more interpretable links between the vegetation and explanatory environmental variables. The RDA was performed using the *vegan* package (Oksanen et al., 2014). To group the ecological districts according to their specific vegetation-environment interactions, iterative k-means partitioning was performed on the constrained RDA axes scores. This procedure was run for 2 to 12 groups (or clusters) with 100 iterations to strengthen each result and evaluate the consistency of the number of groups (Borcard et al., 2018).

2.4. Paleoecological study sites

Fourteen lakes and 2 peatlands within the study area have been studied to reconstruct long-term vegetation and fire regime dynamics (Table S1.2, Figure 1.1). The lacustrine sites were cored with a Livingstone sampler and the water-sediment interface was sampled with a Kajak-Brinkhurst corer. Sampling of peatlands was conducted by excavating a trench with a shovel, and then cutting peat monoliths from top to bottom (mineral soil). AMS (Accelerated Mass Spectrometry) radiocarbon dating was used to date lacustrine or peat sediments (Table S1.1 : macroremains, charcoal or gyttja samples) and to derive age-depth models. All ages were calibrated against calendar ages using the IntCal04 dataset (Reimer et al., 2004). Radiocarbon dating and age-depth models were accessed from the original publications for each studied lake or peatland, and have been listed in Table S1.1 S3. Ages were expressed in calibrated years before present (hereafter : BP) with a reference year set at 1950 CE (0 BP = 1950 CE).

2.5. Paleoecological data

To reconstruct the Holocene vegetation history, only the most common tree and shrub species observed in the studied area were kept (Saucier et al., 2009) and represent the main pollen signal measured in the sediment. Overall, the objective is to guide forest managers and stakeholders that preferentially base their management plans on trees rather than on herbaceous species. These nine pollen taxa are : 1-*Abies* related to pollen from *Abies balsamea*. 2–3 *Alnus crispa* (Current designation : *Alnus viridis* [Chaix] DC. ssp. *crispa* [Aiton] Turrill) and *A. incana* [L.] Moench, were taken individually since they are adapted to respectively dry and humid soils ; this characteristic was of interest in the current study since both soil types widely typify the study area surficial deposits. 4-*Betula* encompassed pollen for *Betula papyrifera*, *B. glandulosa* (Michaux) and *B. alleghaniensis* (Britton), with the latter species being rare in our study area. 5-*Picea glauca* (Moench) Voss and *P. mariana* were combined in the taxon *Picea*, since *Picea glauca* is scarce in the study area. 6–7 *Pinus strobus* and *P. banksiana* were differentiated since their autoecologies differ according to fire characteristics (surface, severity, cycle) (Pausas et al., 2004), and their geographical distributions. *Pinus strobus* is found where fires are less severe and rare, while *Pinus banksiana* dominates where fires are both more frequent and severe. 8-The taxon *Populus* refers to *Populus tremuloides* Michaux, and to a lesser extent, *Populus balsamifera* L., with no distinction being made between the two species. 9-*Thuja* and *Juniperus* are indistinguishable using pollen analysis ; however, *Juniperus* is rare in the boreal forest, and as such, we can infer that the *Thuja*/*Juniperus* pollen type mainly corresponded to *Thuja occidentalis* L. Thus, the taxon was denoted *Thuja*. Taxa pollen percentage where originally calculated for each pollen spectra considering all the taxa identified, then we retained only the previously cited ones. The total percentage for the nine taxa were not adjusted to 100 so that the relative abundance variations for those taxa were not over-estimated. As the distinction between two species can be tedious, sometimes undifferentiated pollens were reported mostly for *Pinus*, *Picea* and less frequently for *Alnus*. In that case, the undifferentiated percentage were attributed to the other identified species of the same taxon according to the percentage ratio between each identified species and the percentage for the whole taxon. Pollen percentages were calculated to permit between-site comparisons and were used to plot pollen diagrams with the R package *rioja* (Juggins, 2015).

2.6. Statistical analysis on paleoecological data

2.6.1. *Pollen data*

We performed PCA (Principal Component Analysis) on all pollen assemblages after performing chord-distance transformation (Legendre and Gallagher, 2001). Confidence ellipses (95%) on the taxonomic variables were then calculated to depict the position that was occupied by each site within PCA space. Pollen assemblage coordinates were aggregated using thousand-year periods, including [0-1000), [1000-2000), … [7000-8000) BP, by calculating the mean position along the first and second axes of all samples within each period. These consecutive 1000-year time window means were then connected to display long-term ecological trajectories.

2.6.2. *Charcoal data*

For each sedimentary sequence, mean Fire Return Intervals (mFRI) (i.e., number of years between two consecutive fire events) were calculated. To compare mFRI sequences between zones and then between sites located in the same zone, the mFRI sequences of all respective sites that were located in each zone and individual sites were fitted against a two-parameter Weibull function, and their scale parameters were compared (here we assumed that the shape parameter equals to 1) (Schafer and Sheffield, 1976). The iterative comparison of mFRI sequences for two zones or two sites relied upon calculating the difference between (1) the sum of the log-likelihood for the two zones or sites that we wanted to compare and (2) the log-likelihood of the pooled sequence. If the P-value of the previously calculated log-likelihood difference is less than the threshold set to $P = 0.05$, then Holocene fire dynamics for the two zones or sites were considered to be significantly different. Forest stand age-class distributions were related to the fire return interval using a Weibull-type function :

$$A(t) = 1 - \int_{t}^{\infty} exp\left(-\frac{t}{b}\right)^{c} dt \qquad (1.1)$$

where A is the proportion of landscape stands that were older than t (years), b is the scale parameter and is equal to the mFRI, and c is the shape coefficient, which is not significantly different from 1, even between periods with different fire cycles (Johnson and Gutsell, 1994) (hereafter c = 1) (Cyr et al., 2009). By setting t to 100, the formula allowed us to calculate the proportion of old-growth forests within a landscape under a given mFRI, and the 95% confidence interval was calculated by bootstrap resampling.

3. Results

Refining the current vegetation classification of the western spruce-moss subdomain represents a spatial framework of the current vegetation heterogeneity that can be used later to analyze the regionalization of the Holocene vegetation trajectories and fire dynamics, while guiding the downscaling of reference conditions from subdomain to homogeneous zones of vegetation.

3.1. Contemporary vegetation-environment interactions to characterize homogeneous territories

When coupled with k-means partitioning that was applied to vegetation and environmental data for the districts of the western spruce-moss subdomain, RDA showed four zones where links between forest composition and environmental constraints are homogeneous (Fig.1). Zone number one (Z1) concentrates 29% of *Pinus banksiana* and 63% of *Picea mariana*, which are respectively the highest and lowest proportions of these species within the western spruce-moss subdomain, on a substratum dominated by till (51%). The second zone (Z2) has a lower percentage of *P. banksiana* than zone 1

(12%), a higher proportion of *P. mariana* than zone 1 (71%), and surficial deposits are also mostly till (45%). Zone three (Z3) has a substantial proportion of *P. mariana* (73%), together with *P. banksiana* (9%) and *P. tremuloides* (7%), on clay deposit (45%). Indeed, this zone belongs to the Clay Belt. In Zone number four (Z4), forests are mostly composed of *P. mariana* on organic soil (85%). For a complete description of ecological variables that were retained by forward selection, together with the relationship between paleoecological sites and environmental variables, the reader is referred to Figure S1 and to Grondin et al. (2014b).

3.2. Holocene vegetation histories

The two first axes of the PCA that was applied to the pollen assemblages represent 44% of the variance (the first three axes represent 60% ; Fig. 1.2). Pollen taxa are well discriminated by the PCA (Fig. 1.2A). Three groups can be distinguished : *Betula-Alnus incana-Thuja-Pinus strobus-Abies* ; *Picea-Populus* ; and *Pinus banksiana-Alnus crispa.* The vegetation history that was observed for Marie-Eve Z1, Nano Z1 and Twin Z2 is characterized by a dominance of the fire-prone taxa *P. banksiana* and *A. incana.* The second vegetation history is characterized by an increasing proportion of *P. banksiana* since 4000-3000 BP. The assemblages (and consequently, the ellipses) span the length of PCA1 with several taxa that can be described as light-demanding species (*Populus* and *Betula*) for sites in Zones 2 (Aurélie Z2), 3 (Aspen Z3, Shadow Z3) and 4 (Schön Z4). A third vegetation history, mostly characterized by a high abundance of late-successional species (*Thuja* and *Abies*, and to a lesser extent, *Picea*), characterizes sites on the right side of the ordination, i.e., zones 2 (Chapais Z2), 3 (Cèdre Z3, Pessière Z3), 4 (Geais Z4).

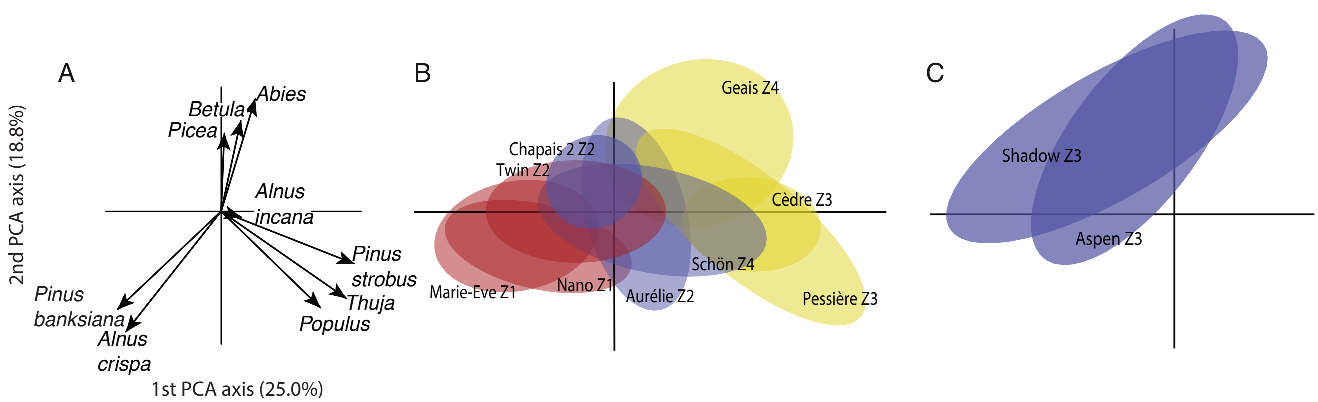

Figure 1.2. Holocene vegetation histories assessed by a PCA applied to the pollen assemblages of lakes and peatlands. (A) Projection of species (pollen taxa) onto the first two axes of the PCA, using scaling 2 thus reflecting the correlation between pollen taxa. (B) 95% confidence ellipses for the lakes. (C) 95% confidence ellipses for the peatlands, using scaling 1 to observe the Euclidean distance between the pollen assemblages. Ellipse color highlights three vegetation histories : red is characterized by a forest composition dominated by *Pinus banksiana.* Blue ellipses represent sites with both late successional species and *P. banksiana* ; yellow refers to vegetation that is mostly composed of late-successional species. The numbers following sites names refers to the zone in which they are located.

3.3. Holocene vegetation trajectories

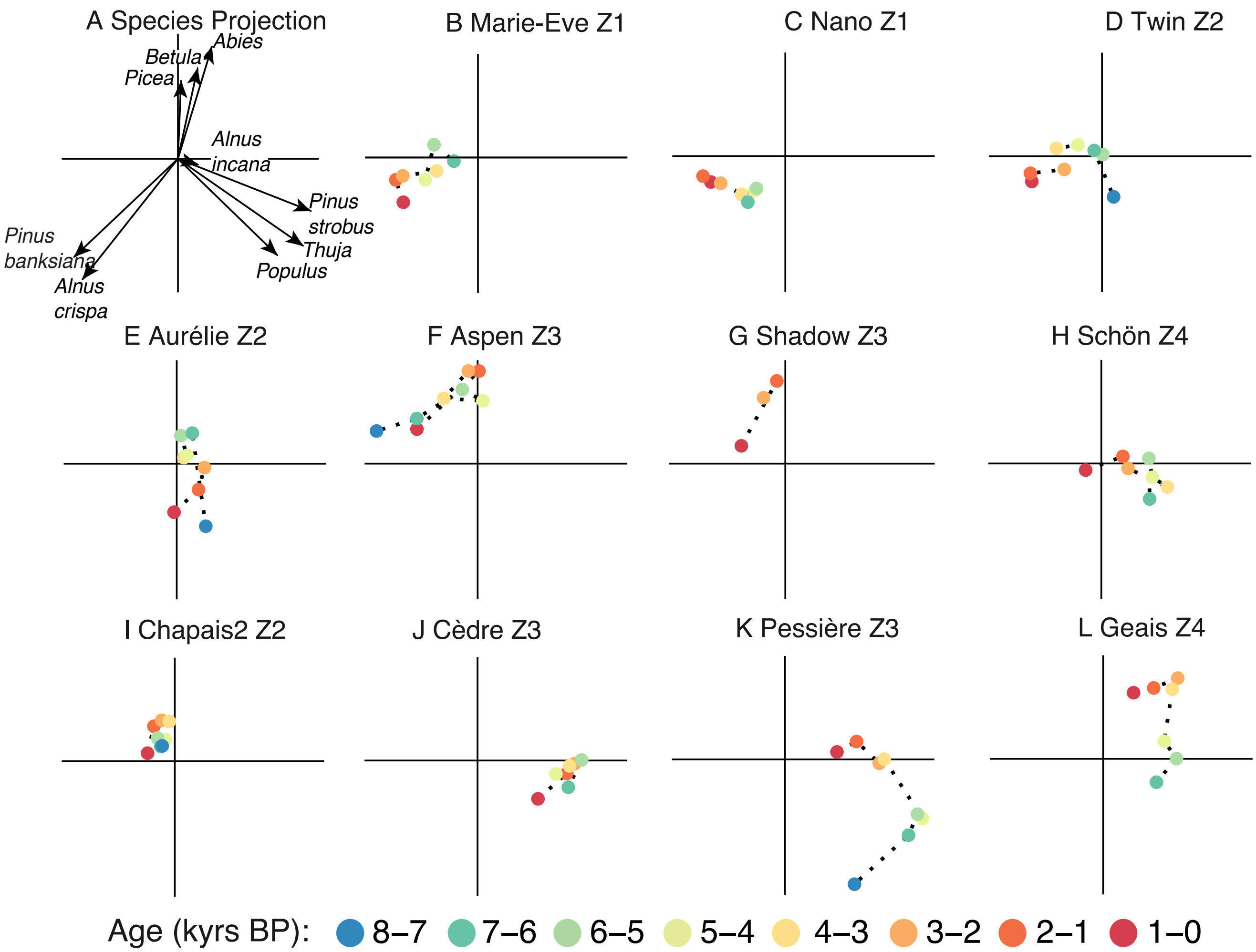

Figure 1.3. Vegetation trajectories corresponding to 1000-year pollen assemblage means projected onto PCA axes 1 and 2 for each paleoecological site. Panels B to L show vegetation trajectories followed by each site, which are represented by dashed lines using scaling 1. Each millennium is represented by a dot, red for the most recent assemblages and blue for the oldest ones. Species were projected onto the PCA (Panel A) using scaling 2 (same as Fig. 2). First raw of panels corresponds to the dominance of jack pine during Holocene, the second one (and lake Chapais 2 in panel I) to the transitional trajectory (from late to early successional species) and the third row (except lake Chapais 2) corresponds to dominance of late successional species.

3.3.1. *1$^{(st)}$ vegetation trajectory : dominance of jack pine over the entire Holocene*

Marie-Eve (Fig. 3B) and Nano (Fig. 3C) exhibit vegetation that is dominated by *A. crispa* and *P. banksiana*. From the beginning of the Holocene to 6000-5000 BP, Marie-Eve vegetation exhibited a higher proportion of *Populus* and *Betula*, subsequently converging towards stands strongly dominated by *P. banksiana*, such as in Nano. For Twin (Fig. 3D), the early Holocene pollen assemblages reveal more mixed stands, which then converged toward Marie-Eve and Nano since 4000-3000 BP.

Overall, these three sites (Marie-Eve, Nano, Twin) have their whole vegetation dynamics contained within the early successional portion of the ordination and evolved toward or have always been dominated by *P. banksiana* and *A. crispa*.

3.3.2. *2$^{(nd)}$ vegetation trajectory : increase of jack pine during the Holocene*

Aurélie (Fig. 3E) and Schön (Fig. 3H) lakes present similar vegetation paths. Both are dominated by *Betula* and *Picea* and are moving towards vegetation during the last millennia characterized by an abundance of *P. banksiana* and *A. crispa*. *Pinus strobus* and *Thuya* are also present in these two lakes. Similar pattern is observed for Aspen (Fig. 3F) and Shadow (Fig. 3G). These latter two peatlands exhibit very similar vegetation trajectories that are mainly characterized by *Picea* and early successional species (*Pinus banksiana* and *Betula*), even when considering that the Shadow sequence has only covered the last 4000 years (Asselin et al., 2016). Chapais 2 vegetation composition is largely dominated by *Betula* until 3000 BP. *Picea* become abundant after this period and *Pinus banksiana* increased mainly since 1500 BP. Lake Chapais 2 remains difficult to interpret because of the high amount of undifferentiated *Pinus* (Garralla and Gajewski, 1992; Fréchette, 2015). For this reason, we do not see the migration from the right side of the PCA to the left quadrant during the last millennia (Fig. 3).

3.3.3. *3$^{(rd)}$ vegetation trajectory : dominance of late successional species over the Holocene*

The sites Cèdre (Fig. 3J), Pessière (Fig. 3K) and Geais (Fig. 3L) have their entire vegetation dynamics contained within the late-successional portion of the ordination. Pessière and Geais have shown very variable landscape composition during the Holocene, but started to converge towards the same trajectory than Cèdre around 2000 BP. These lakes are also characterized by the similarity of the main species vegetation (*Picea*, *Betula*, *Alnus incana*) between the late and the early Holocene. In all of them, *Pinus banksiana* increased during the last millennia, but never enough to migrate to the left side of the PCA.

3.4. Holocene fire regime variability

Following mFRI (mean fire return interval) reconstructions, it appears that all zones show distinct but not significantly different Holocene fire dynamics (Fig. 4). Nevertheless, it is worth noting that all zones exhibit a period from the beginning of the Holocene until 4000-3000 BP, during which the mFRI was shorter than between 3000 and 1000 BP. Since the last millennium, some zones have exhibited a slight increase in mFRI, except for Z3 sites (Fig 4 A). Consequently, the percentage of old-growth forest has also increased (Fig 4 E). The mFRI for the entire western spruce-moss subdomain is 240 years, with a 95% confidence interval of (222, 258), which corresponds to 66% old-growth forests, with a 95% confidence interval of (64, 68) (Table 1.1). Comparison of the mFRI distributions did not reveal significant differences among zones. The same analysis has been led on sites FRI sequences and differences appeared between lakes that were located in the same zone

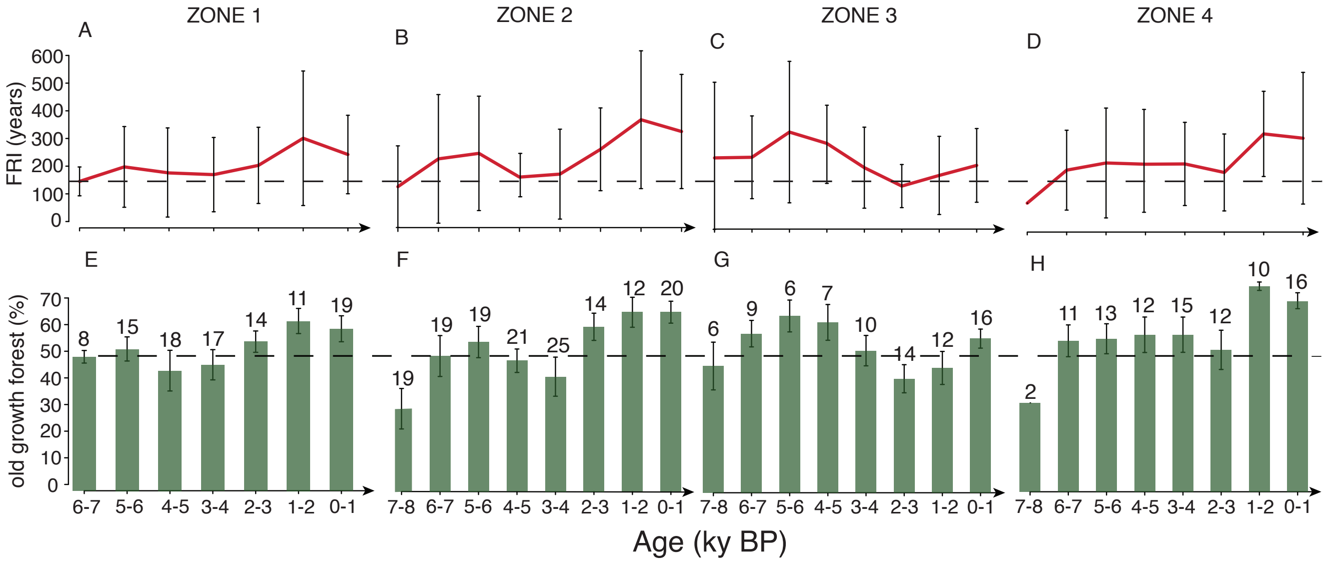

Figure 1.4. Graph showing the Holocene evolution of mFRI (upper row of panels) and the evolution of old-growth forest percentage (lower row of panels). Dashed line in the first row of panels represents a fire cycle of 150 years, in the lower row it represents the 49% of old-growth forest both corresponding to the reference conditions established for the western spruce-moss subdomain. Numbers above each histogram correspond to the number of individuals used to calculate the mean and standard deviation of the data.

(see Table S1). In Zone 2, Aurélie showed a significant difference with respect to other sites that were located in the same zone : Richard ($P = 0.00045$), and Twin ($P = 0.048$).

Tableau 1.1. Regional Holocene mFRI (mean and 95% confidence interval) and percentage of old-growth forest (hereafter OF : mean and 95% confidence interval) for each zone in the western spruce-moss subdomain.

Zone	mFRI(years)	95%CI	OF(%)	95%CI
1	227.3	[194.6 , 260]	64.4	[59.8 , 68.1]
2	234.9	[201.7 , 268]	65.3	[60.9 , 68.9]
3	226.7	[189.2 , 264.2]	64.3	[58.9 , 68.5]
4	266.2	[226.4 , 305.9]	68.7	[64.3 , 72.1]
Mean	240.1	[221.9 , 258.3]	65.9	[63.7 , 67.9]

Discussion

In this study, we showed that it is possible to (1) highlight and describe current landscape heterogeneity in the western spruce-moss bioclimatic subdomain forest of Québec, (2) to define and classify Holocene vegetation trajectories that have led to current vegetation heterogeneity, (3) to reconstruct FRIs to identify homogeneous fire regimes and analyze their consequences on vegetation distribution and finally (4) estimate the range of variability of the percentage of old growth forest for redefining reference conditions based on Holocene variability.

Current landscape heterogeneity

We demonstrated that the contemporary vegetation could be divided into four main zones where relationships between forest composition and physical characteristics, climate and disturbances regimes are homogeneous. Interestingly, this zonation shows important similarities with the third vegetation level of division that was developed for the whole southern Québec (Grondin et al., 2007). Yet, this is not the spatial scale that is currently used for establishing management targets in Québec (Boucher et al., 2011). Developing restoration and management targets at the scale of homogeneous vegetation-environment interactions has been shown to be relevant to ecosystem restoration for identifying disturbed ecosystems and prioritizing the interventions to restore the most disturbed sites among them (Palik et al., 2000). We therefore suggest using the zonation proposed in our analysis for developing new management targets in the western spruce- subdomain.

Holocene vegetation trajectories leading to contemporary vegetation heterogeneity

The first vegetation path that corresponds to northernmost sites that were located in Zone 1 and Lake Twin (Zone 2, close to Zone 1), boreal species migration resulted in an unprecedented increase in *P. banksiana* and *A. crispa* abundance within the vicinity of the sites (Remy et al., 2017), driving the vegetation to deviate toward early-successional species. This corresponds to the first vegetation path identified in this study (Fig.2), and is consistent with the current vegetation type observed in this region of the spruce-moss subdomain. This vegetation path is characterized by early Holocene differentiation and subsequent cyclical dynamic involving frequent fires (Gauthier et al., 2015).

The second vegetation path was found in lakes and peatlands that are located in Zones 2 and 3. Peatlands Aspen and Shadow located in Zone 3, as well as Schön located at the border between Zones 3 and 4 and Aurélie located in Zone 2. This dynamic is characterized by « transitional » vegetation dynamics for which the surrounding vegetation was initially dominated by broad-leaved species that changed towards stands with an increasing proportion of *Pinus banksiana* since 2000-1000 BP. This increase in *P. banksiana* has been noticeable for the three vegetation paths and has been more precisely dated to around 1800 BP. Its increase is usually interpreted as the development of boreal forest as currently observed or « borealization »(Carcaillet et al., 2010) coupled with more frequent fire (Payette et al., 2017), or less frequent but larger and more severe fires (Remy et al., 2017). Since then, a diminution of *Abies balsamea* and an increase in *Pinus banksiana* (Blarquez and Aleman, 2015; Asselin et al., 2016) has been reconstructed highlighting the transition from late- to early- successional dominated landscapes (Fig. 3). The similarity of vegetation between the Late Holocene and the early Holocene has also been observed by some authors, such as Payette et al. (2017) in temperate forests.

The third vegetation path that was identified is characterized by vegetation dynamics involving late successional species that are located in the right part of the ordination (Fig. 2) and corresponds to lakes Geais located in Zones 4 and by extension to lakes Cèdre and Pessière located in Zone 3 and that represent landscapes dominated by peatlands. After the retreat of Lake Barlow-Ojibway, forest stands of southernmost sites (e.g., lakes that were located in Zone 3) were dominated by broad-leaved species, mixed with *Thuja* and *P. strobus* (Carcaillet et al., 2001). For the Clay Belt (Zone 3), *Thuja* reached a maximum extent in 6000-5000 BP and retreated around 2000 BP to its current extent. Between 5000 and 3000 BP, its relative abundance was mostly explained by low fire frequency, which overrode the effects of climate and carbonate soils. The two latter factors thus explain not only that *Thuja* persists today in the Clay Belt (Zone 3) (Carcaillet et al., 2001; Paul et al., 2014), but also to a lesser extent around Lakes Geais and Schön located in Zone 4. *Pinus strobus* was present at 50° N latitude around 6000 BP, but this species is currently found in the southern part of the boreal forest in mature forests characterized by surface fires (Bergeron et al., 1997). With the end of the Holocene Thermal Maximum (HTM ; ca. 10 000 – 6000 BP (Kaufman et al., 2004) and the occurrence of a less favorable climate associated with less frequent and more severe fires, *Pinus strobus* retreated to its current limits (Carcaillet et al., 2010). Interestingly, the Holocene dynamics of *Thuja* and *Pinus strobus* suggest that all site trajectories withdrew from the upper-right quadrant of the PCA ordination (Fig. 2). For Geais, Cèdre, Pessière and Chapais 2, other species, such as *Picea*, *Betula* and *Alnus crispa*, increased in abundance following the retreat of Lake Barlow-Ojibway, around 8000 BP (Carcaillet et al., 2010; Blarquez and Aleman, 2015). *Picea* became the dominant taxon, which is often associated with *Abies balsamea* (Ali et al., 2008; Remy et al., 2017). The period 7000-6000 BP is marked by the settlement of various species that enhance biodiversity (Blarquez et al., 2014), which is also consistent with variations in ROC (Rate of Change) that were observed in the study area during this period (Carcaillet et al., 2010; Remy et al., 2017).

Our results have shown that current vegetation patterns are the results of the Holocene dynamics of vegetation, particularly those of forest species. Indeed, during the Holocene, the climate underwent changes that initiated vegetation settlement and dynamics (Blarquez et al. 2015) that differ regarding their location in the western spruce-moss subdomain. In the following section, we will discuss the Holocene fire dynamics that might have influenced the previously identified vegetation trajectories.

Long-term variation of FRI

These changes in vegetation composition followed climate changes during the Holocene, but were also determined by interactions with fire dynamics. In particular, fire return intervals can strongly influence forest composition (Bergeron and Charron, 1994; Carcaillet and Blarquez, 2017), thereby determining the percentage of old-growth forest that has been retained in the landscape and its associated biodiversity (Cyr et al., 2009). Surprisingly, Zone 1 has one of the shortest mFRI, i.e., 227.3 years (95% confidence interval : 194.6, 260 ; Table 1), but this fire return interval is not significantly shorter than the one reconstructed for the entire western spruce-moss subdomain (240.1). However, the current fire cycle distribution is of 67.4 years as reconstructed using fire archive data ranging from 1938 to 1998 (recalculation from Gauthier et al. (2015). Interestingly, the width of the 95% confidence interval window (194.6 – 260 years) is no larger than the one reconstructed using archive data. Indeed, Mansuy et al. (2010) identified three different fire zones that encompassed our Zone 1, with fire cycles ranging from 90 years (95% confidence interval : 57, 208) to 149 years (95% confidence interval : 86, 257). In both instances, these estimates are among the lowest observed in southern Québec (Gauthier et al., 2015). Lakes located in Zone 1 show only one slightly significant difference, i.e., between Lakes Trèfle and Nano (Table S1), thereby revealing a relatively homogeneous long-term fire dynamics history for this zone.

The second zone has a Holocene fire mFRI of 235 years (95% confidence interval : 202, 268) for a current fire cycle of 198.1 years (recalculation from Gauthier et al. (2015)). It is located around Mistassini Lake where surficial deposits exhibit heterogeneity, leading to a wide range of fire cycles. These cycles span a range from 90 years (95% confidence interval : 57-208,) on tills to 715 years (95% confidence interval : 353, infinity) on organic soils (Mansuy et al., 2010). Lake-to-lake comparisons showed significant differences between Lake Aurélie and the other lakes that were located in the zone, i.e., Richard and Twin, thereby revealing in-between zone heterogeneity in long-term fire dynamics.

Zone 3, reconstructed FRI dynamics and mFRI (226.7, 95% confidence interval : 189.2, 264.2) were surprisingly lower than the current fire cycle, which is of 1272.3 years (recalculation from Gauthier et al. (2015). Bergeron et al. (2001) have reconstructed a fire cycle prior to 1850 with an estimate of 101 years (95% confidence interval : 79, 129) and 398 years (95% confidence interval : 302, 527) since 1920, where some sites located on till or sand deposits tended to have a shorter fire cycle. Cyr et al. (2005), who also reconstructed fire events in this area, found a fire cycle estimated to be 446 years (95% confidence interval : 190, 1047) with local differences explained by firebreaks, such as paludified areas, which can contribute to lengthening fire cycles.

Zone 4 has a reconstructed mFRI of 266.2 years (95% confidence interval : 226.4, 305.9) which is not significantly different from the current fire cycle estimated at 242.1 years (recalculation from Gauthier et al. (2015)). Also, the site-to-site comparisons show no significant differences thus highlighting a relatively homogeneous Holocene mFRI for the zone.

Overall, our FRI values must not be taken as a strict equivalent of the fire cycle. Indeed, fire cycle, which represents the time for burning an area of interest is equivalent to FRI only if each past fire (from charcoal records) burned the entire study area, which is probably not always the case here. This conceptual difference and others, related for example to the spatial scale of paleoecological proxies, may explain the observed differences. Indeed, the spatial scale at which ecological processes had occurred in the past from lake records (Hawthorne et al., 2018), depends on local-scale effects, such as fuel load dynamics or ignition conditions (Gavin et al., 2007), vegetation (Girardin et al., 2013), and climate (Ali et al., 2012). More generally, the record of paleoecological proxies is influenced by taphonomical processes, which include transportation of particles, watershed characteristics, lake hydrographic connectivity, and physiognomy (Higuera et al., 2007; Anderson, 2014). This might explain the differences in reconstructed FRI, for example, for two lakes located in Zone

3 (Cèdre and Pessière, Table S1) that are only 20 km apart. Alternatively, the differences in reconstructed mFRI might represent real local differences in fire occurrences. Despite these differences, paleofire reconstructions from charcoal data constitute a unique way of assessing past fire regimes at a temporal scale that is not accessible by any other means (Conedera et al., 2009).

Integration of Holocene ecosystem range of variability in the definition of reference conditions for the western spruce-moss subdomain

With the combined contemporary and paleoecological approaches that were developed in this study, we aimed at defining more local (homogeneous vegetation-environment interactions) reference conditions that also would consider the long-term natural variability of boreal forest ecosystems. Our results showed that long-term fire return interval had a mean value of 240 years and a narrow 95% interval (221.9, 258.3) (Table 3), but the provincial reference conditions registry targets a fire cycle for the whole western spruce-moss subdomain at 150 years, based upon inventories that were conducted in the 1970s (Boucher et al., 2011). Our long-term approach allowed us to define a mean FRI for the entire subdomain, together with estimates for the individual zones that we defined.

Moreover, this method also provides an interval of variation that encompasses the natural multi-millennial behavior of fire dynamics. From the FRI, it is possible to reconstruct how the percentage of old-growth forests changed through time and, as for the FRI, to provide intervals of variation through time. Therefore, it is possible to assess whether current management guidelines are well adapted or whether they are leading landscapes outside their natural boundaries (Cyr et al., 2009; Bergeron et al., 2010). Indeed, Cyr et al. (2009) indicated that old-growth forests cover only 13% of the current landscape south of the western spruce-moss subdomain, while they should conservatively represent between 40% and 70%. Our results suggest that the past mean percentage of old-growth forest for the entire area was 65.9% (95% confidence interval : 63.7, 67.9) which is included in the conservative range developed by (Cyr et al., 2009). This noticeable discrepancy in stand age-class distributions between the reference condition and the Holocene natural range of variability has prompted more questions regarding the use of present-day reference conditions to establish management targets. The reference conditions register actually reflects 19th and 20th century forests, a short time scale for boreal species for which life spans can exceed 200 years (Bergeron and Charron, 1994), and might not be well adapted for current and future conditions. Therefore, as percentage of old growth forest values derive from mFRI, they should be taken with perspective. Paleoecological studies can thus provide long-term variation in fire regimes and forest composition. We then suggest that management targets should be adapted to the long-term natural variability of boreal forest ecosystems.

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Supplementary material

Current inventories data analysis

The RDA that was used in this article has been applied to current vegetation and environment data available at the district scale for the entire western spruce-moss subdomain. To understand the current context of the paleoecological sites that were used in this study, we selected districts located within a 15 km-radius buffer around each site, together with the mean of their 1^{st} and 2nd RDA axis coordinates to obtain the following plots.
RDA applied to districts contained within a 15 km radius of the sites was used to display relative positions of the sites, with the arrows representing the species (Fig. 3A). Site projections along the first RDA axis strongly correspond to their longitudinal location, with their latitudinal locations following the second RDA axis. Thus, sites that are geographically located in the same zone are relatively close to one another in the projection, and vegetation surrounding the sites is relatively homogeneous. Except for black spruce, which can behave as early successional species under specific conditions (Gagnon and Morin, 2001), early successional species were located above the 1^{st} axis, while late successional species were located below it. Forward selection that was applied to environmental variables used in the RDA (Fig. 3B) retained 23 out of 48 explanatory variables. Lightning fires were mostly associated with jack pine stands that are found in Zone 1, while spruce budworm outbreaks were projected in the same direction as balsam fir and white birch. Very old-growth stands that were dated to the 1700s are mostly found in black spruce forests.

Paleoecological analysis : Fire Return Interval comparison

To compare mFRI sequences between zones and then between sites located in the same zone, the mFRI sequences of all respective sites that were located in each zone and individual sites were fitted against a two-parameter Weibull function, and their scale parameters were compared (here we assumed that the shape parameter equals to 1) (Schafer and Sheffield, 1976). The iterative comparison of mFRI sequences for two zones or two sites relied upon calculating the difference between (1) the sum of the log-likelihood for the two zones or sites (Table S1) that we wanted to compare and (2) the log-likelihood of the pooled sequence. If the P-value of the previously calculated log-likelihood difference is equal to or less than the threshold set to $P = 0.05$, then Holocene fire dynamics for the two zones or sites were considered to be significantly different.

Since 13 tests have been performed, a Holm (1979) correction has been applied to the P-values to avoid inflating of the risk of type I error (false positives). In Zone 2, Aurélie showed a significant difference with respect to Richard ($P = 0.00045$), and Twin ($P = 0.048$) thereby revealing in-between zone heterogeneity in long-term fire dynamics. No other difference is significant after the Holm correction.
In Zone 1, Trèfle and Nano were significantly different (P = 0.029) thereby revealing a relatively homogeneous long-term fire dynamics history for this zone. In Zone 2, Aurélie showed a significant difference with respect to the other sites that were located in the same zone : Nans (P = 0.023), Richard (P = 0.000035), and Twin (P = 0.0040) thereby revealing in-between zone heterogeneity in long-term fire dynamics. In Zone 3, Pessière and Cèdre are significantly different (P = 0.015), while no difference is indicated between lakes that were located in Zone 4.

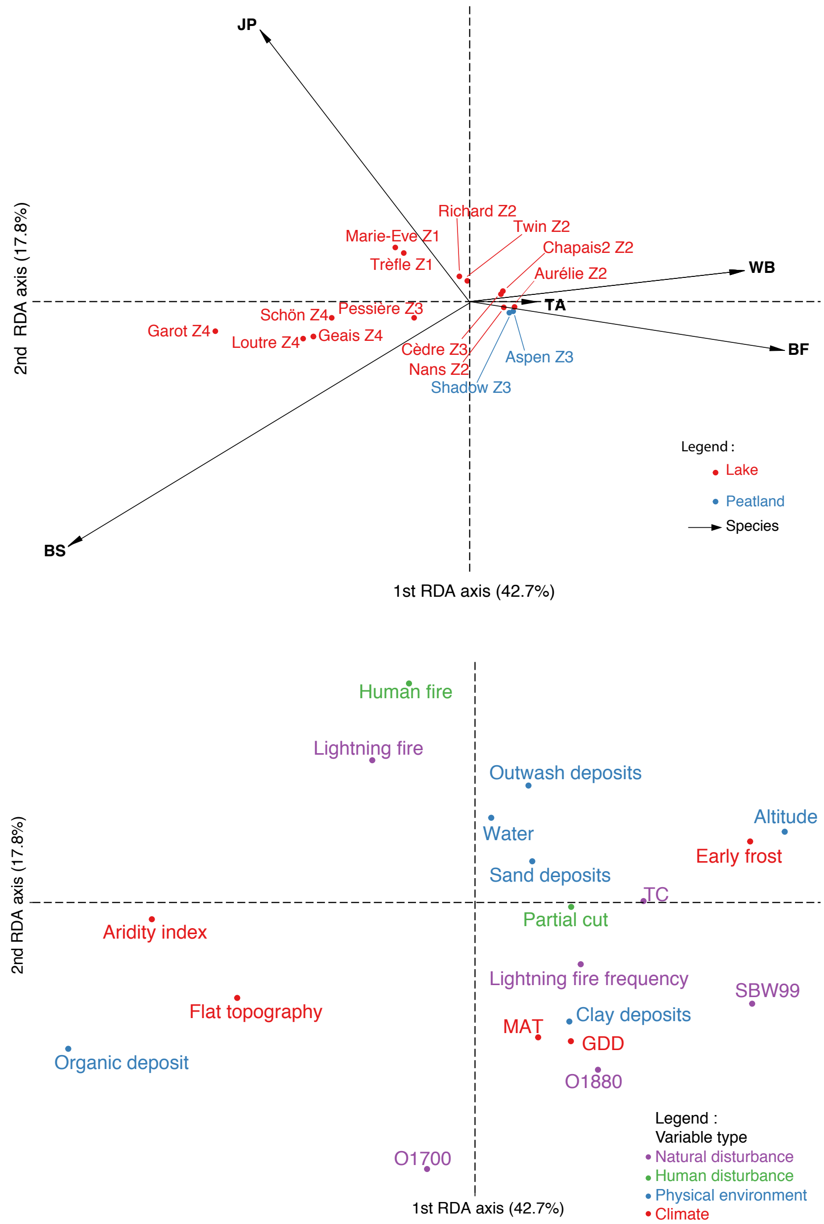

Figure S1.1. (A) Redundancy Analysis was applied to the ecological district dataset. Projections of districts within 15 km of a paleoecological site are plotted onto the two first axes of the RDA (red for lakes, blue for peatlands) using scaling 1. Species describing current vegetation (black arrows) are based on RDA coordinates (WB = White birch, BS = Black spruce, JP = Jack pine, BF = Balsam fir, TA = Trembling aspen). Values within parentheses correspond to the percentage variance explained by each axis. (B) Forward selection was performed on predictor variables, where purple refers to natural disturbances, green refers to human disturbances, blue refers to environment characteristics, and red refers to climate variables plotted in scaling 2. O1700 and O1880 refer to forest stands that are originated from fire that occurred respectively in the 1700s and in the 1880s. SBW99 refers to a spruce budworm outbreak that occurred in 1999, and LF to a forest tent caterpillar (Malacosoma disstria) outbreak. MAT = Mean Annual Temperature, GDD = Growing Degree-Days over 5° C (the paleoecological site locations are not represented here).

Tableau S1.1. Results of site-to-site comparison

		Zone 1			**Zone 2**				**Zone 3**		**Zone 4**		
		Nano	*Marie-Eve*	*Trèfle*	*Aurélie*	*Nans*	*Richard*	*Twin*	*Cèdre*	*Pessière*	*Garot*	*Loutre*	*Schön*
Zone 1	*Nano*	1	0.40	**0.03**									
	Marie-Eve		1	0.41									
	Trèfle			1									
Zone 2	*Aurélie*				1	**0.02**	**3.5E-5**	**0.004**					
	Nans					1	0.13	0.70					
	Richard						1	0.20					
	Twin							1					
Zone 3	*Cèdre*								1	**0.015**			
	Pessière									1			
Zone 4	*Garot*										1	0.10	0.52
	Loutre											1	0.61
	Schön												1

Tableau S1.2. AMS Radiocarbon dating for the palaeosites

Site	Sample depth (cm)	Sampled material	C date (years BP)	Calibration Range (cal. years BP)
Nano	35-35.5	gyttja	2575±35	2696-2761
	60-60.5	gyttja	3950±50	4245-4524
	90-90.5	gyttja	5025±35	5803-5892
	119.5-120	macroremains	6060±50	6777-7027
	139.5-140	macroremains	6530±50	7410-7514
Marie-Eve	59.5-60	gyttja	2330±30	2309-2369
	116-116.5	gyttja	2500±30	2468-2730
	176-176.5	gyttja	3440±30	3631-3780
	232-232.5	gyttja	4595±35	5275-5331
	289-289.5	gyttja	6110±40	6890-7034
Trèfle	40-40.5	gyttja	2480±35	2435-2718
	75.5-76	gyttja	3790±40	4075-4296
	100-100.5	gyttja	4325±35	4837-4972
	125-125.5	gyttja	5040±35	5710-5901
	150-150.5	gyttja	6280±40	7156-7308
Aurélie	43-44	macroremains	2870±30	2879-3136
	111-112	macroremains	3990±35	4319-4568
	163-164	macroremains	4750±35	5329-5586
	220-221	macroremains	6140±40	6931-7163
	236-237	macroremains	6490±40	7317-7476
	326-327	macroremains	7460±50	8185-8373
Chapais 2	40-50	gyttja	1480±90	
	140-150	gyttja	2530±90	
	240-250	gyttja	3880±100	
	355-365	gyttja	4660±100	
	415-423	gyttja	6520±100	
	446-452	gyttja	7660±100	
Nans	20-25	gyttja	1200±40	970-1180
	30-35	gyttja	1820±30	1610-1740
	50-51	gyttja	3290±40	3390-3570
	100-101	gyttja	4040±40	4550-4560
	130-131	gyttja	4630±40	5380-5460
	150-151	gyttja	4040±40	4410-4570
	150-151	gyttja	4720±40	5540-5570
	170-171	gyttja	5230±40	5900-6000

	212-213	gyttja	7800±40	8410-8600
Richard	0-5	gyttja	560±30	490-530
	20-25	gyttja	1220±30	980-1170
	80-81	gyttja	3800±30	4200-4230
	97-98	gyttja	4870±40	5470-5600
	131-132	gyttja	6770±40	7460-7580
	149-150	gyttja	6820±40	7550-7620
	159-160	gyttja	7560±40	8180-8350
Twin	24-25	gyttja	2415±30	2357-2679
	54-55	gyttja	3615±30	3848-4056
	74-75	gyttja	4105±30	4480-4806
	94-95	gyttja	4340±30	4851-5019
	114-115	gyttja	4435±30	4892-5264
	134-135	gyttja	5245±30	5931-6169
	164-165	gyttja	6285±30	7166-7267
	180-181	macroremains	6910±50	7654-7866
	183-184	gyttja	7625±45	8368-8531
Peatland Aspen	37-38	charcoal	180±30	136-224
	38-39	charcoal	75±15	33-73
	44-45	charcoal	235±20	281-307
	49-50	charcoal	955±20	796-874
	52-53	charcoal	915±15	840-910
	64-65	charcoal	2275±15	2306-2346
	77-78	charcoal	3590±20	3839-3929
	81-82	charcoal	4345±20	4856-4963
	84-85	charcoal	4705±20	5325-5409
	132-133	macroremains	7185±25	7956-8026
Peatland Shadow	21-22	charcoal	120±30	51-149
	24-25	charcoal	240±20	281-308
	32-33	charcoal	945±20	796-874
	41-42	charcoal	1760±20	1608-1724
	44-45	charcoal	1680±20	1539-1619
	45-46	charcoal	1655±15	1524-1573
	50-51	charcoal	2010±20	1920-1998
	85-86	charcoal	2790±25	2842-2956
	93-94	charcoal	3425±20	3613-3720
	94-95	charcoal	3745±25	4068-4157
Cèdre	6-14	gyttja	3850±90	3990-4520
	18-24	gyttja	3790±130	3780-4530

	43-49	gyttja	4730±90	5150-5650
	106-111	gyttja	3390±80	3450-3840
	237-242	gyttja	4260±80	4540-5040
	376-381	gyttja	5420±80	5990-6400
	479-484	gyttja	6150±90	6800-7260
	566.5-572.5	gyttja	6290±160	6800-7490
Pessière	75.5-80.5	gyttja	1510±90	1275-1565
	167.5-172.5	gyttja	2500±80	2345-2765
	290.5-295.5	gyttja	3410±60	3485-3835
	394.5-398.5	gyttja	4580±70	5040-5465
	487.5-492.5	gyttja	6010±70	6675-7010
	538.5-543.5	carbonated gyttja	7500±90	8155-8425
	545.5-550.5	macroremains	6720±80	7455-7685
Garot	18-18.5	gyttja	2060±30	1948-2118
	30-30.5	gyttja	3390±30	3562-3703
	45-45.5	gyttja	3795±35	4083-4295
	61-61.5	gyttja	4445±35	4956-5085
	78-78.5	gyttja	5200±50	5890-6031
	99.5-100	gyttja	6510±40	7323-7494
Loutre	66.5-67	macroremains	3450±40	3620-3830
	98-100	macroremains	4070±40	4430-4800
	103.5-105	macroremains	4480±40	4970-5300
	174.5-177	macroremains	5430±40	6180-6300
	220-225	macroremains	6900±40	7830-7670
Schön	35-35.5	gyttja	1820±30	1694-1825
	49.5-50	gyttja	3010±35	3136-3275
	67-71.5	macroremains	3515±35	3696-3881
	95-95.5	gyttja	4675±35	5315-5473
	110-110.5	gyttja	5280±40	5983-6183
	133-133.5	gyttja	6370±40	7247-7420

Tableau S1.3. Main features of the paleosites, together with cores and publications that were associated with the data that were used in this study

	Zone 1			Zone 2	
	Nano	*Marie-Eve*	*Trèfle*	*Aurélie*	*Nans*
Latitude	53° 01'25.5"N	52° 01'47.4"N	51° 57'54.7"N	50° 25'12.81"N	50° 22'03.87"N
Longitude	77° 21'51.3W	75° 31'14.6"W	76° 04'52"W	74° 13'47.64"W	74° 18'10.52"W
Elevation (m asl)	206	296	270	440	438
Local vegetation	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Betula papyrifera*
Surface are (ha)	0.4	16.5	6.8	0.12	4.5
Water depth (m)	3.2	8.7	5.4	5.65	5
Length of organic core (cm)	140	290	150	335	230
Mean deposition time (SE) ($yr.cm^{-1}$)	54±1.63	24±0.71	48±1.10	10	18
Publication	(Oris et al., 2014)	(Oris et al., 2014)	(Oris et al., 2014)	(Ali et al., 2012)	(Ali et al., 2012)

Zone 2		Zone 3		Zone 4		
Richard	*Twin*	*Cèdre*	*Pessière*	*Garot*	*Loutre*	*Schön*
50° 38'40.33" N	50° 56'42.27" N	49° 20'45"N	49° 30'11.54"N	51° 05'58.7"N	49° 42'42.1"N	50° 35'41.7"N
74° 40'42.94" W	74° 33'48.71" W	79° 12'30"W	79° 14'22.2"W	77° 33'12.9"W	78° 20'09.0"W	77° 34'06.1"W
432	376	305	305	248	274	291
Picea mariana, Pinus banksiana	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Pinus banksiana*	*Picea mariana, Larix laricina, Abies balsamea*	*Picea mariana, Pinus banksiana*
1.2	0.5	4	4	5.1	2.1	2.8
5.28	5.71	16	16	6.9	10.63	7
165	230	315	302	100	227	133
25	21	12±6.4	13±0.11	74.7±3.0	36.6±0.76	55±0.12
(Ali et al., 2012)	(Ali et al., 2012)	(Ali et al., 2008)	(Carcaillet et al., 2001)	(Oris et al., 2014)	(Ali et al., 2009)	(Oris et al., 2014)

Pollen diagrams and CHARanalysis results for the study sites

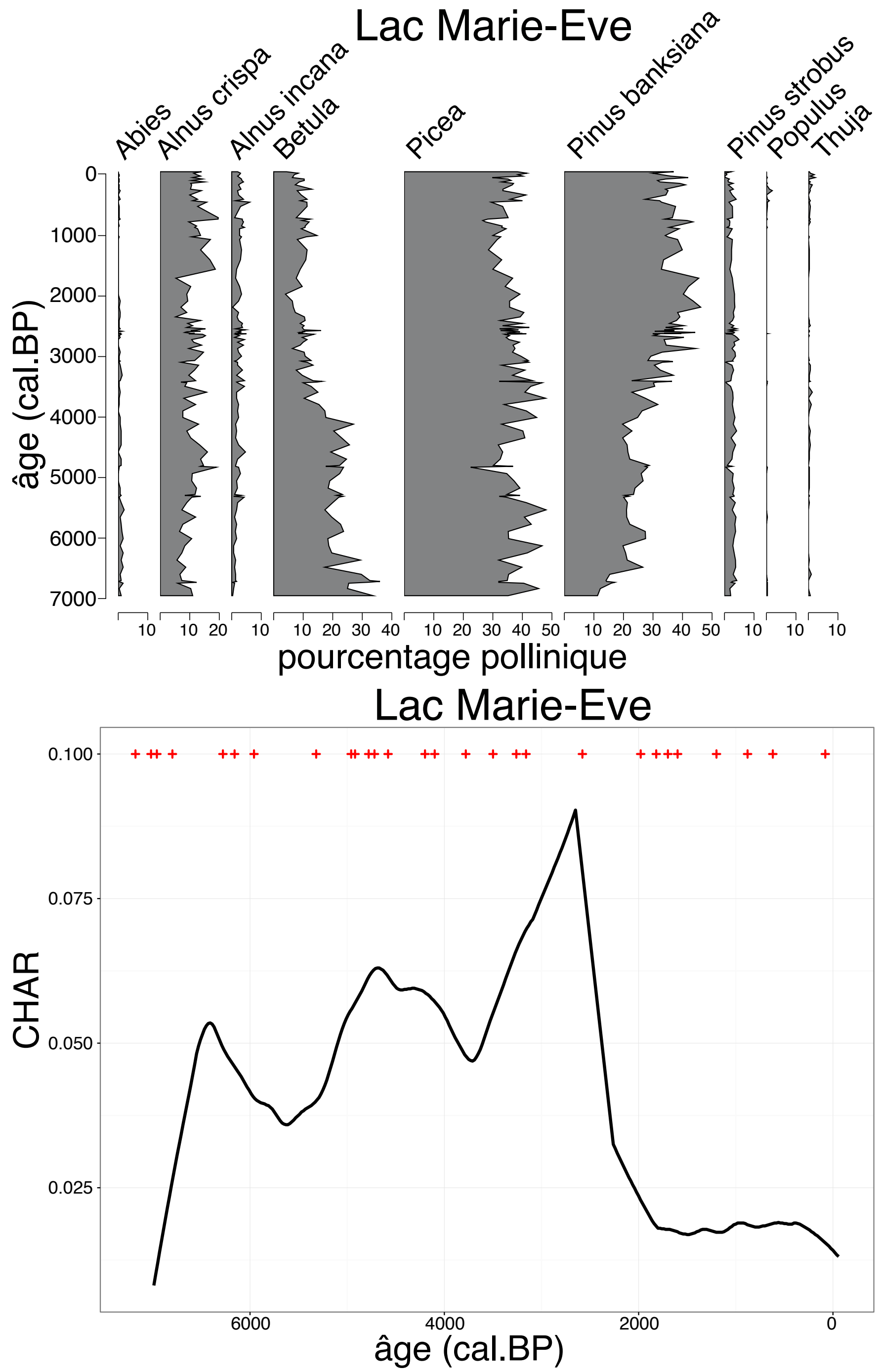

Figure S1.2. Zone 1 : Lake Marie-Eve

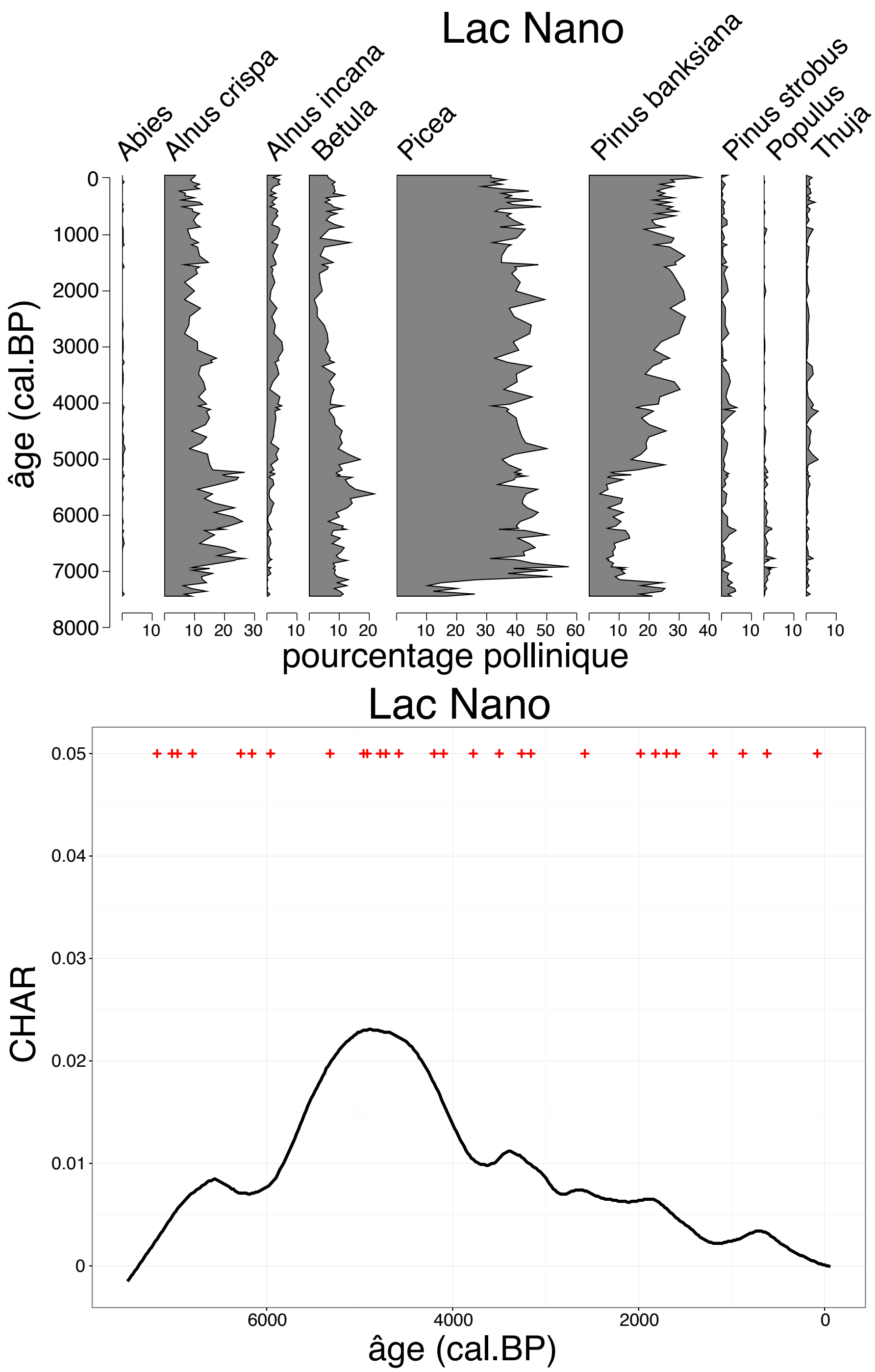

Figure S1.3. Zone 1 : Lake Nano

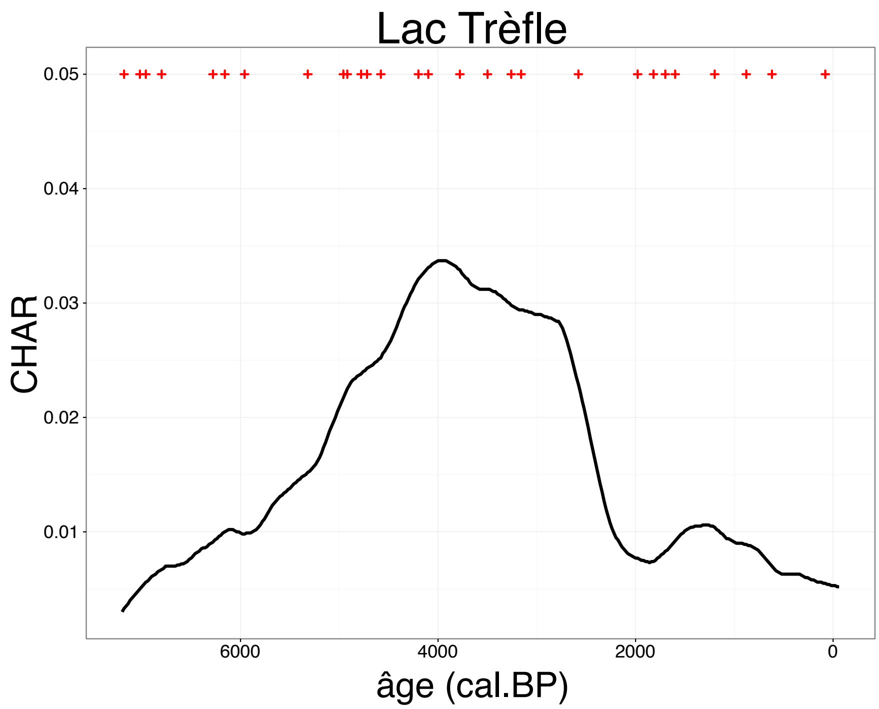

Figure S1.4. Zone 1 : Lake Trèfle

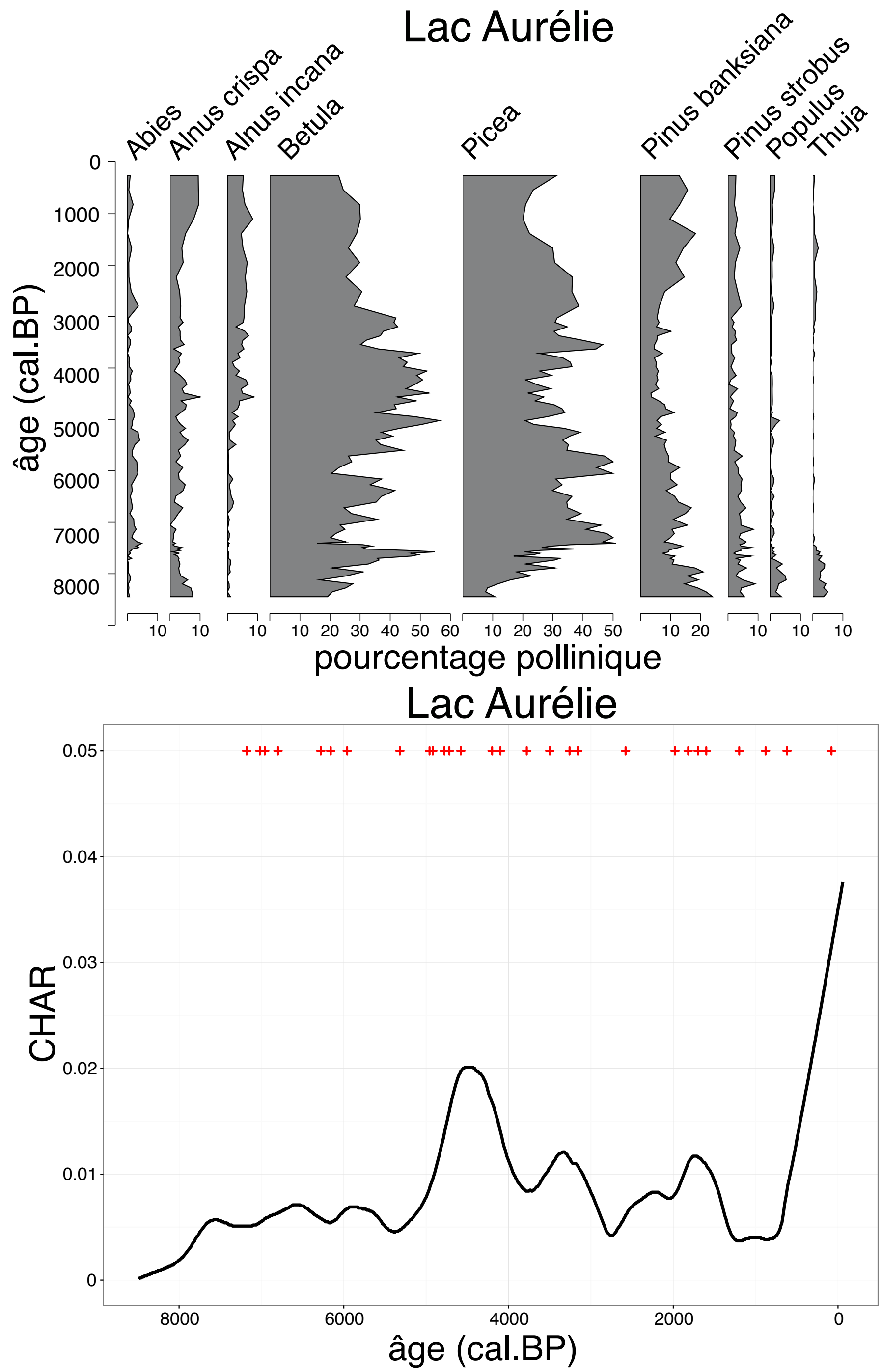

Figure S1.5. Zone 2 : Lake Aurélie

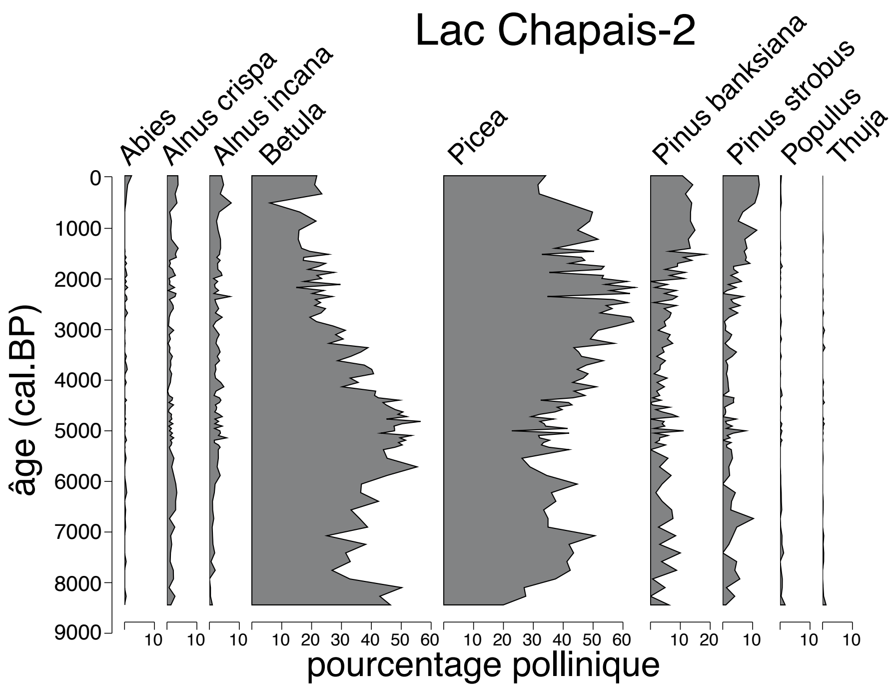

Figure S1.6. Zone 2 : Lake Chapais 2

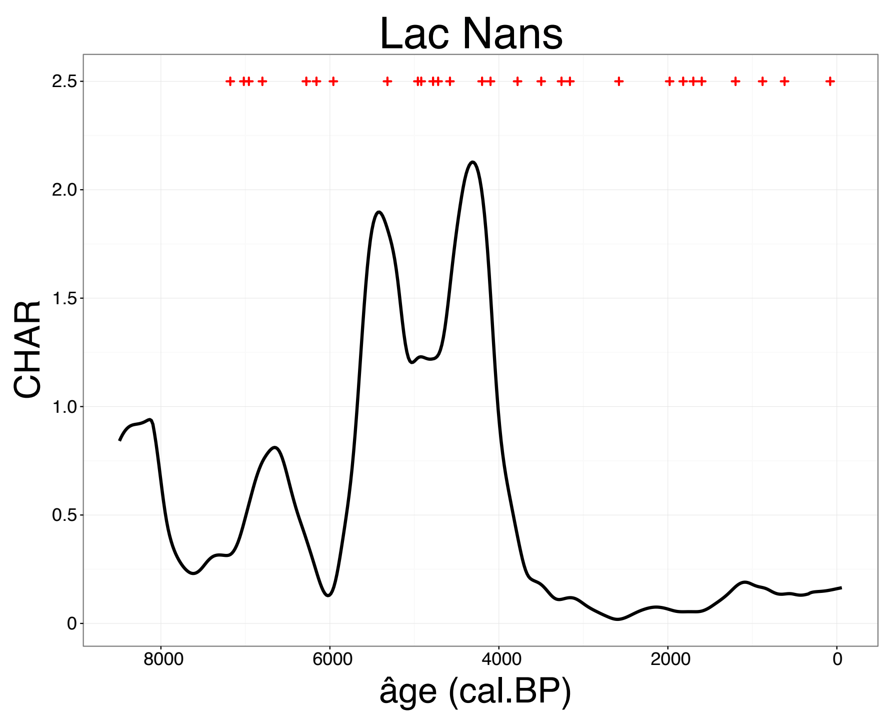

Figure S1.7. Zone 2 : Lake Nans

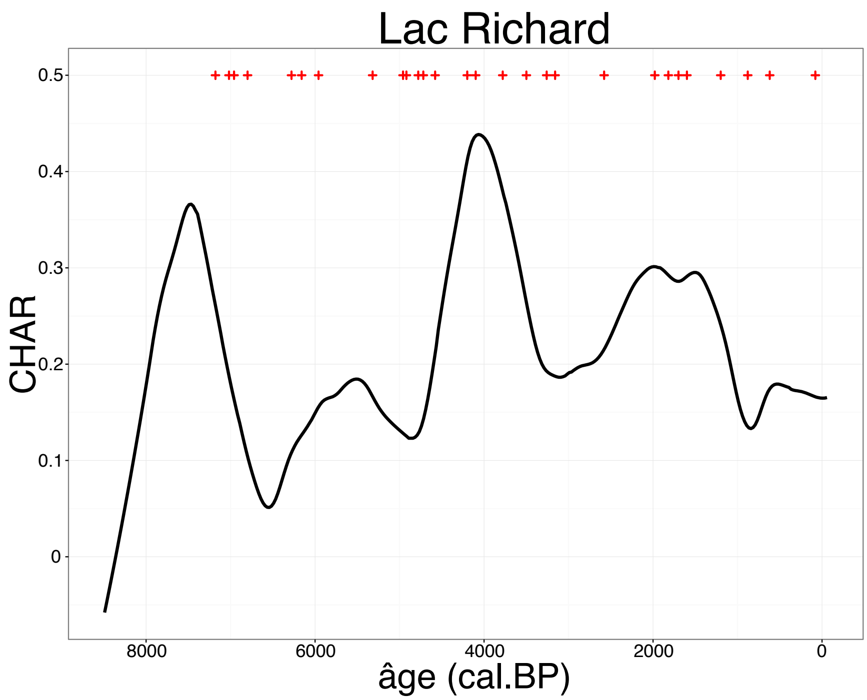

Figure S1.8. Zone 2 : Lake Richard

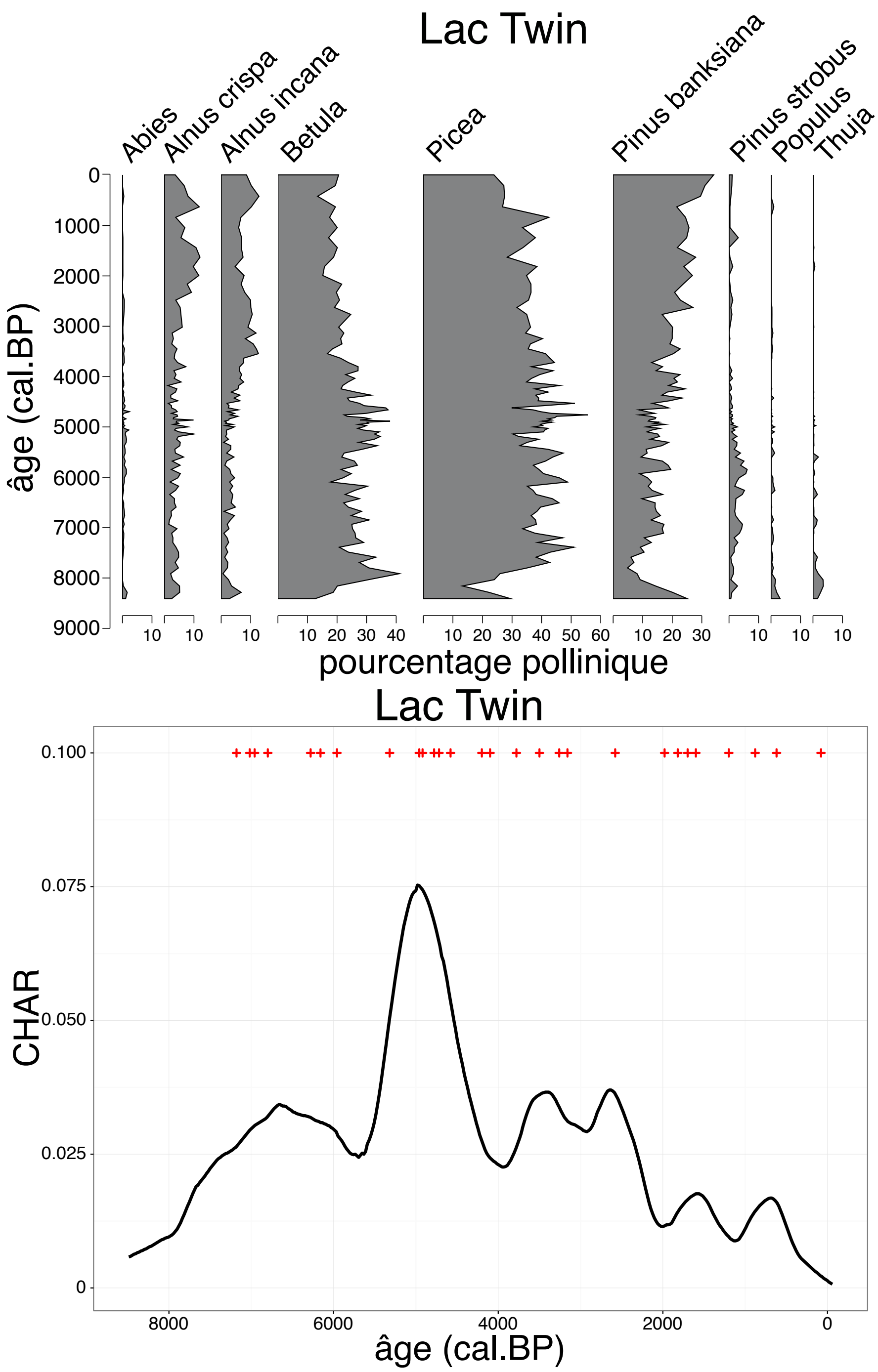

Figure S1.9. Zone 2 : Lake Twin

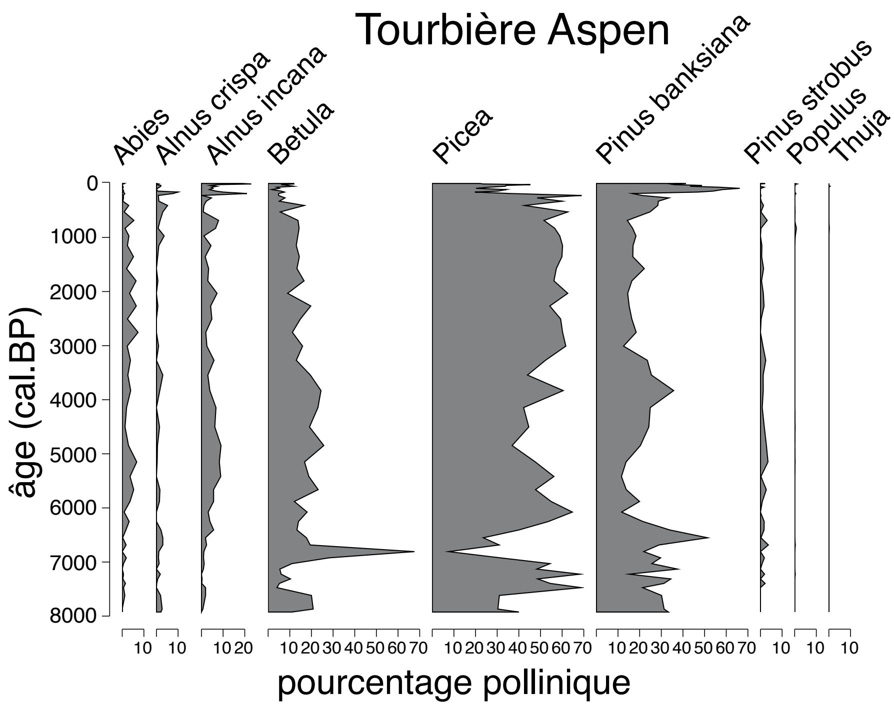

Figure S1.10. Zone 3 : Peatland Aspen

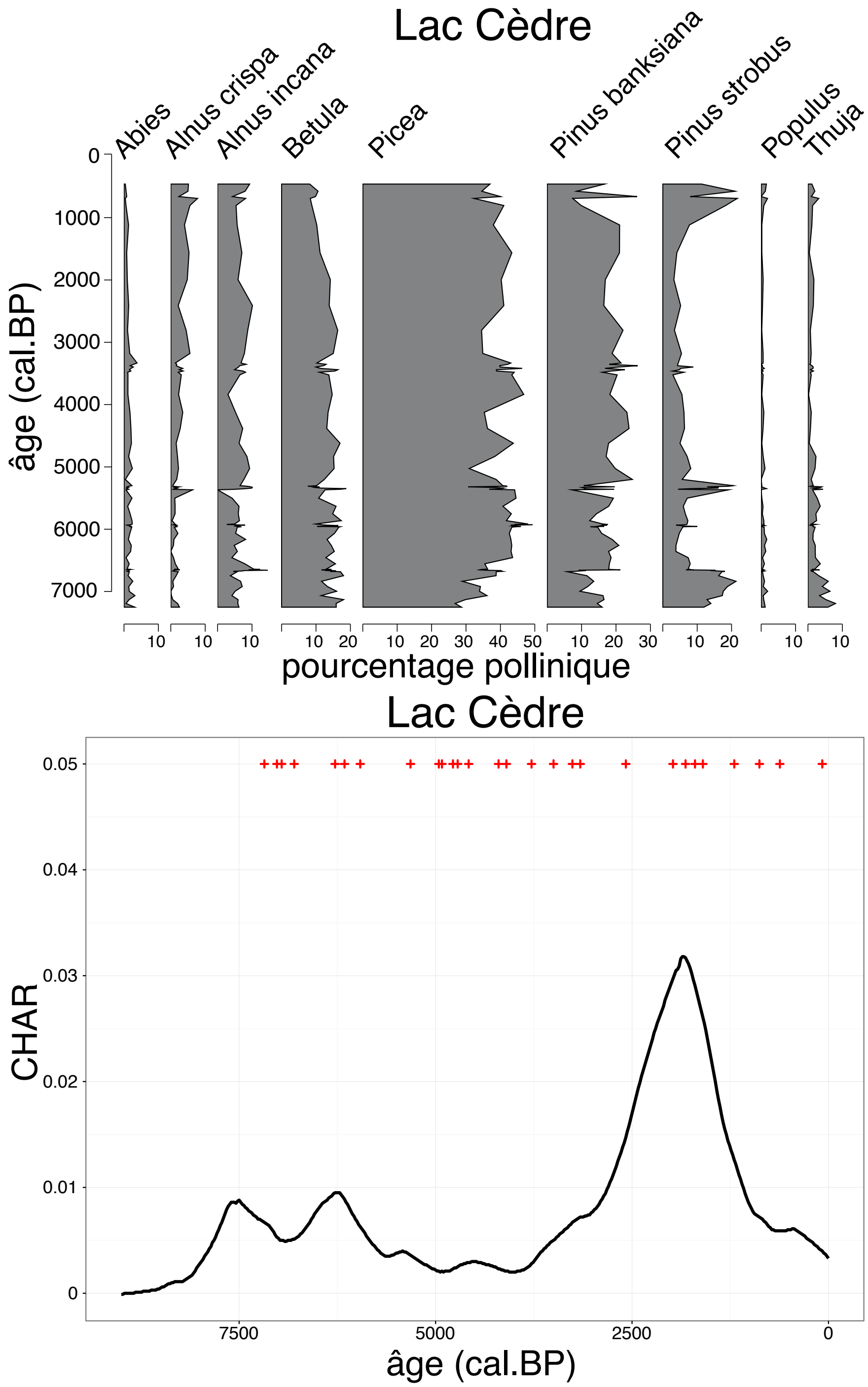

Figure S1.11. Zone 3 : Lake Cèdre

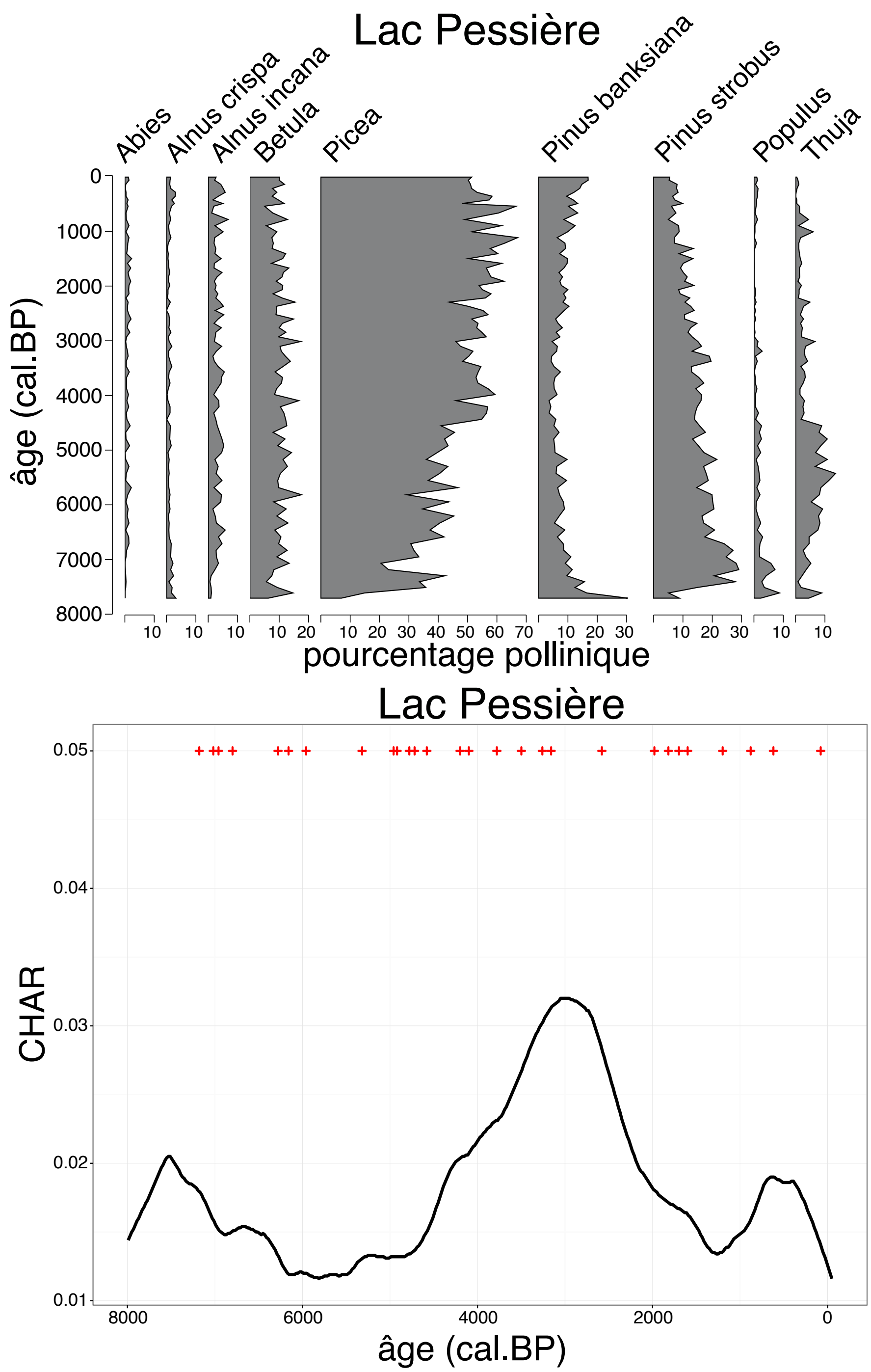

Figure S1.12. Zone 3 : Lake Pessière

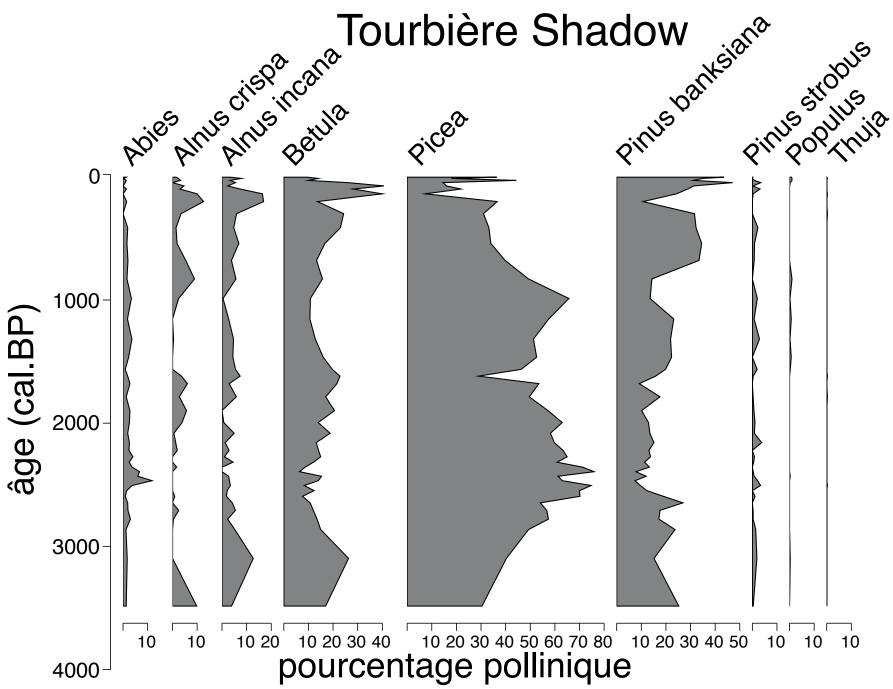

Figure S1.13. Zone 3 : Peatland Shadow

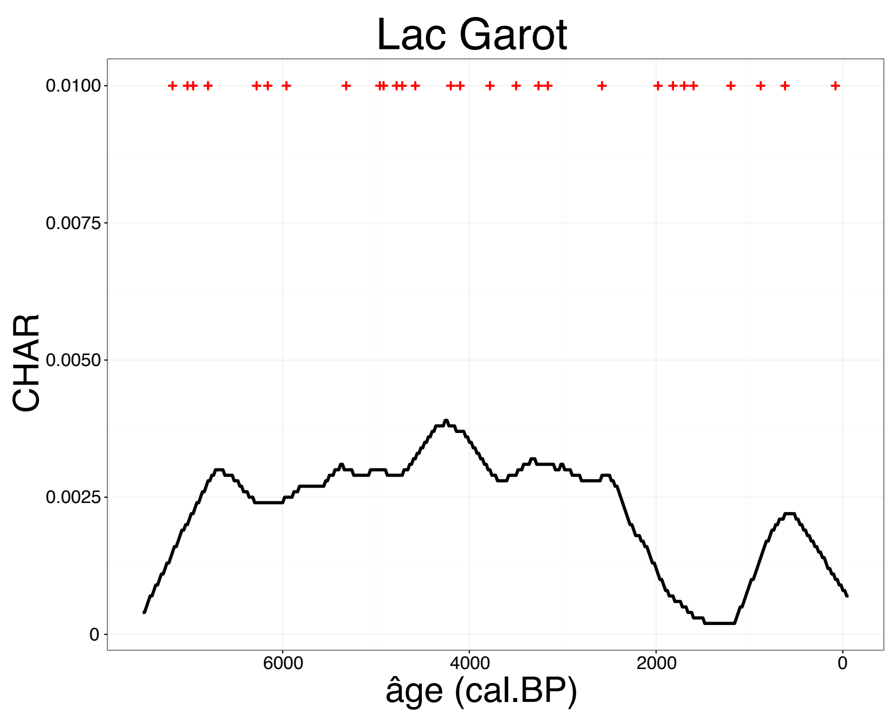

Figure S1.14. Zone 4 : Lake Garot

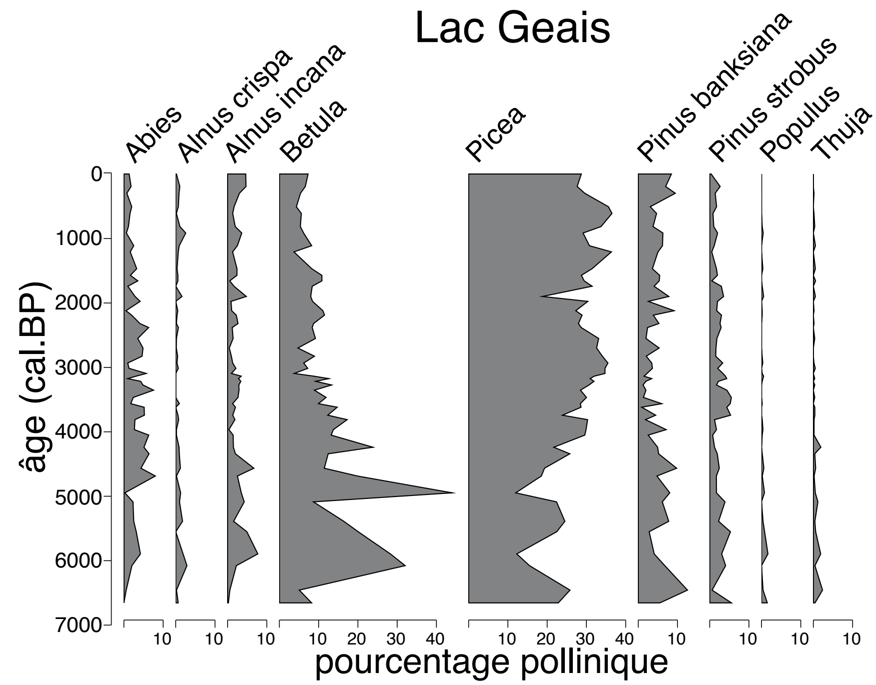

Figure S1.15. Zone 4 : Lake Geais

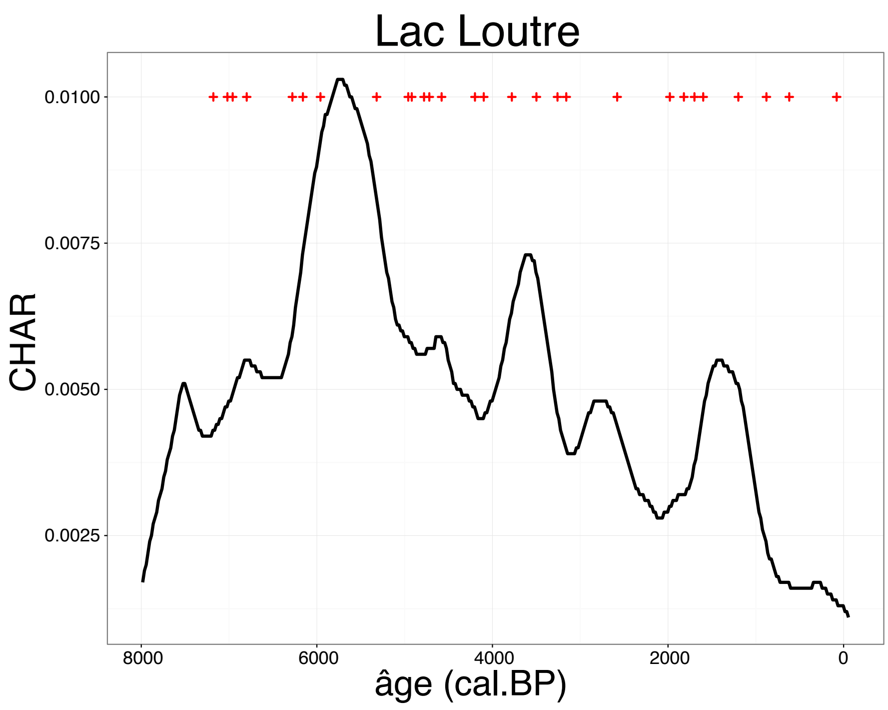

Figure S1.16. Zone 4 : Lake Loutre

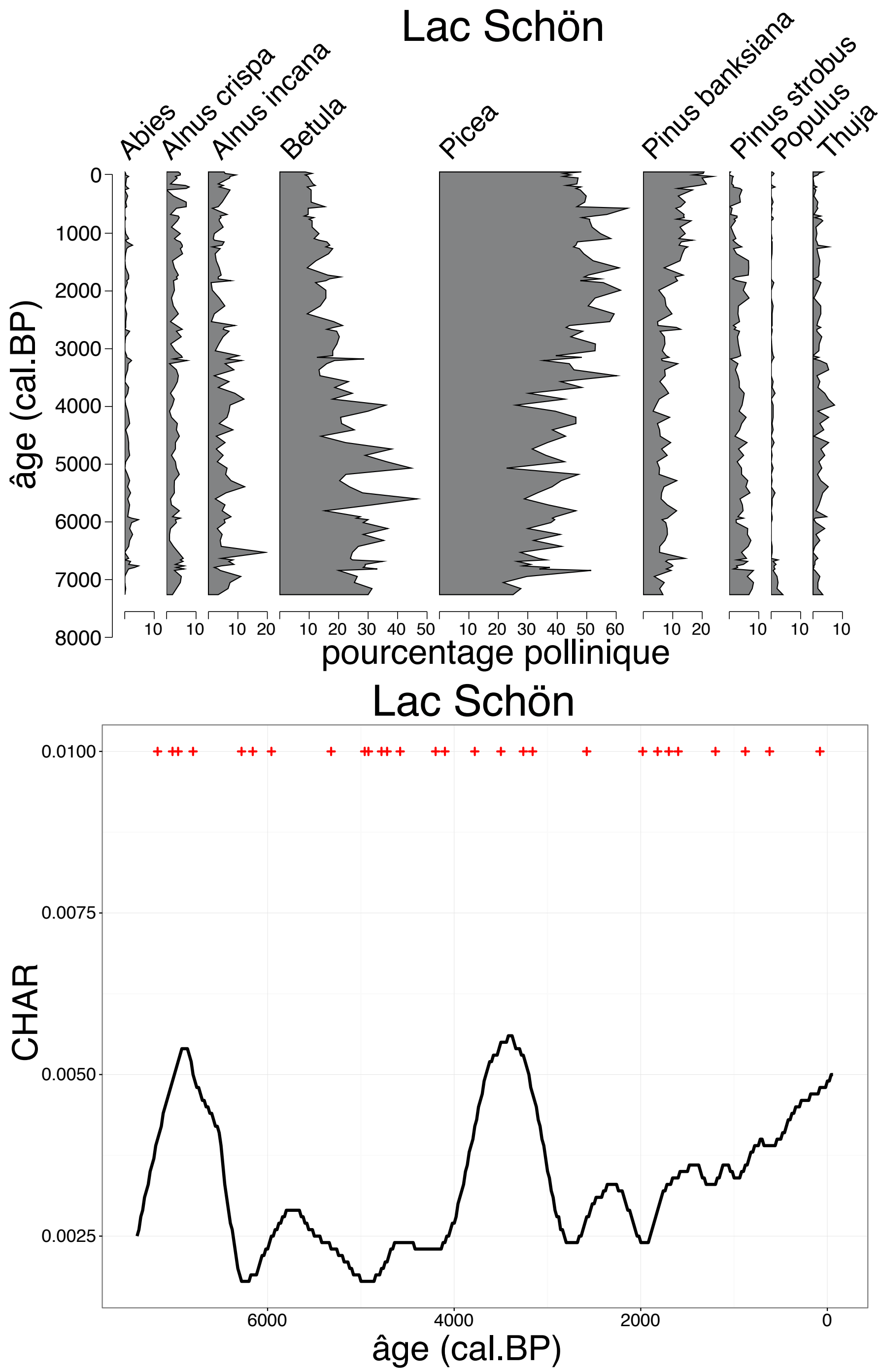

Figure S1.17. Zone 4 : Lake Schön

Chapitre 2

The reconstruction of burned area and fire severity using charcoal from boreal lake sediments

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Abstract

Although lacustrine sedimentary charcoal has long been used to infer paleofires, their quantitative reconstructions require improvements of the calibration of their links with fire regimes (i.e. occurrence, area and severity) and the taphonomic processes that affect charcoal particles between the production and the deposition in lake sediments. Charcoal particles >150 μm were monitored yearly from 2011 to 2016 using traps submerged in seven head lakes situated in flat-to-rolling boreal forest landscapes in eastern Canada. The burned area was measured, and the above-ground fire severity was assessed using the differentiated normalized burn ratio (dNBR) index, derived from LANDSAT images, and measurements taken within zones radiating 3, 15 and 30 km from the lakes. In order to evaluate potential lag effects in the charcoal record, fire metrics were assessed for the year of recorded charcoal recording (lag 0) and up to 5 years before charcoal deposition (lag 5). 92 variables were generated and sorted using a Random Forest-based methodology. The most explanatory variables for annual charcoal particle presence, expressed as the median surface area, were selected. Results show that, temporally, sedimentary charcoal accurately recorded fire events without a temporal lag ; spatially, fires were recorded up to 30 km from the lakes. Selected variables highlighted the importance of burned area and fire severity in explaining lacustrine charcoal. The charcoal influx was thus driven by fire area and severity during the production process. The dispersion process of particles resulted mostly of wind transportation within the regional (<30 km) source area. Overall, charcoal median surface area represents a reliable proxy for reconstructing past burned areas and fire severities.

KEYWORDS : calibration, fire, forest, charcoal, trap, lake, severity, dNBR, taphonomy

1. Introduction

In boreal forests, multi-millennial fire regimes and vegetation dynamics, inferred from sedimentary charcoal and pollen respectively, helped to characterize long-term natural range of ecosystem dynamics. This natural range of variability can in turn provide data for improving forest management (Cyr et al., 2009; Hennebelle et al., 2018). Even though large databases are available for reconstructing the fire history for a wide range of ecosystems (Global Charcoal Database, (Marlon et al., 2016), many studies have nevertheless highlighted the need for the calibration of charcoal-fire relationships (Clark and Royall, 1996; Aleman et al., 2018; Hawthorne and Mitchell, 2016). Calibration can enable the reconstruction of past fire characteristics on a quantitative basis Higuera et al. (2011) and improves our understanding of the taphonomic processes affecting the dispersal of charcoal particles, from the production source, via transportation by wind (primary) and water bodies (secondary) and deposition processes, to conservation in natural archives. Charcoal production (in terms of number and surface area of particles) during a fire has been linked to fire characteristics such as burned area, distance from fire, number of fires or fire intensity in a wide range of ecosystems, including grass-dominated ecosystems (Duffin et al., 2008; Aleman et al., 2013; Leys et al., 2015), temperate forests (Clark and Royall, 1995; Adolf et al., 2018a), boreal forests (Ohlson and Tryterud, 2000; Higuera et al., 2010; Oris et al., 2014) and mountain forests (Higuera et al., 2011; Adolf et al., 2018a). Dispersion and deposition of charcoal particles have also been studied using experimental fires in boreal ecosystems, with traps located at the fire edge, within and outside the fire perimeter to a distance of a few tens to hundreds of metres (Clark et al., 1998; Lynch et al., 2004; Ohlson et al., 2011). Sediment traps submerged in lakes were used to disentangle the potential time lag between charcoal production and deposition in lakes (Oris et al., 2014), while other studies used top-most sediment stratigraphy of charcoal compared to dataset of recent fires for reconstructions of local fire characteristics such as fire dates (Clark, 1990; Pitkänen et al., 1999; Higuera et al., 2005), burned area (Higuera et al., 2011) or fire severity (Higuera et al., 2005). Even though, by definition, fire severity can be referred to as the quantity of above-ground biomass burned (Keeley, 2009), the influence of fire severity at a landscape scale in controlling the charcoal record is still poorly documented (Clark and Royall, 1996).

Charcoal dispersion occurs primarily in the atmosphere via thermal buoyancy and wind, and has been the subject of theoretical modelling studies (Clark, 1988; Peters and Higuera, 2007). Theoretical models of deposition and incorporation of charcoal into lake sediments have been developed (Higuera et al., 2007) and used to identify peaks of charcoal accumulation that can be attributed to local fire events (Higuera et al., 2009). This method is widely used to determine past fire occurrences in ecosystems for which the temporal resolution of sediment samples is shorter than the likely fire return interval.
The aim of our study was to identify the most significant fire characteristics that help explain the taphonomic processes involved in charcoal deposition, in particular the variation in charcoal production and airborne transportation that modulates the quantity of charcoal deposited in lakes. The novelty of our approach is the consideration of fire severity at a landscape scale, and the distance between the lake and the source area for the charcoal. We hypothesized that the amount of charcoal deposited at the surface of a lake is directly related to the burned area and fire severity. We therefore : (1) measured the burned area and assessed the severity of fires that occurred around seven head lakes (lakes situated at the head of the catchment area for a river basin) that were monitored for charcoal deposition from 2011 to 2016 ; and (2) identified the most relevant fire characteristics that helped explain the charcoal influx into the lakes.

2. Material and Methods

2.1. Study sites

The seven lakes (Figure 2.1) are located along a 418-km north-south gradient, and ranged in size from 0.57 ha for Lake Nano to 5.6 ha for Lake Garot (see Table S2.1). All the lakes are situated in the western boreal forest of Québec (east Canada), and are characterized by a relatively short fire cycle of 150 years, as calculated for the last 300 years (Boucher et al., 2011). Five sites (lakes Pessière, Schön, Garot, Walt and Dave) are located within the spruce-feathermoss bioclimatic domain (Saucier et al., 2009). The lakes surrounding has a vegetation dominated by black spruce (*Picea mariana* [Mill.] BSP) and an understorey dominated by feathermoss on clay deposits. Two sites (lakes Loup and Nano) are located in the spruce-lichen bioclimatic domain (Saucier et al., 2009) on till deposits ; the vegetation are dominated by black spruce, except in sandy areas where jack pine (*Pinus banksiana* Lambert) dominates. The climate of the study area had a mean annual temperature of 0.2±3.7°C and annual precipitation of 995±29 mm (snow and rain ; (Environement Canada, 2011). The water bodies are head lakes or lakes with very limited input, within landscapes that are flat to hilly. Understanding these features is crucial to the quality of the records, because runoff is an important component of the sedimentary charcoal record when the catchment area is

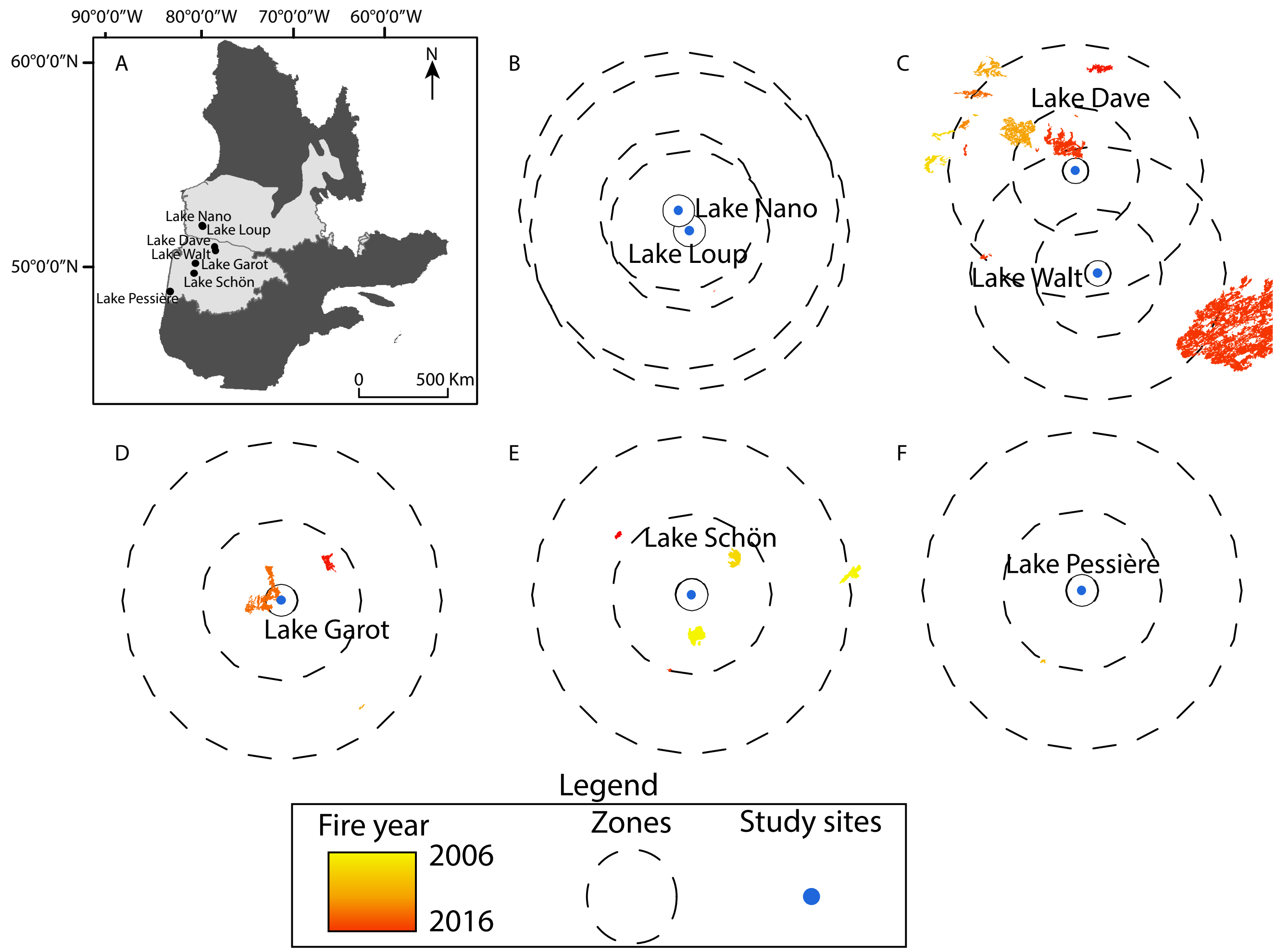

Figure 2.1. (A) Location of Québec in Canada. (B) Location of the seven study lakes in western boreal Québec forest, Canada, situated between spruce moss forest (southernmost light grey area) and spruce lichen woodlands (northernmost light grey area). (C-G) Detail of the three zone radii used (3, 15 and 30 km ; dashed circles) and fire location (colour gradient) around lakes Nano and Loup (C), Dave and Walt (D), Garot (E), Schön (F) and Pessière (G). The characteristics of the fires recorded (n=21) are presented in Table S2.1. For each lake, fire data were cumulated per year and per zone.

large with steep slopes and an extensive stream network (Meyer and Harmon, 1992; Earle et al., 1996; Carcaillet et al., 2007).

2.2. Charcoal data

Charcoal traps were placed vertically in the water column in the center part of the lake basin (Figure S2.1), more than 1 m under the water surface (to avoid to be disturbed or trapped by winter ice cover), and were emptied annually from 2011 to 2016 (6 years) for lakes Nano, Garot, Pessière, Schön and Loup, and from 2011 to 2014 (4 years) for lakes Dave and Walt, resulting in 36 charcoal-years. Data acquired between 2011 and 2013 have already been published (Oris et al., 2014) and are available via the Global Modern Charcoal Database (GMCD ; (Hawthorne et al., 2018)). Over the entire study period, we only considered those records taken during years when fires burned within the 30-km zones, resulting in 12 charcoal samples for analysis.
Traps contents were sieved using a 150 μm mesh, which is a size cut-off generally used in the literature, to retain charcoal particles associated with what were assumed to be mainly local fires (Clark and Royall, 1995; Carcaillet et al., 2001; Lynch et al., 2004; Vachula and Richter, 2018) but also some regional fires (Earle et al., 1996; Oris et al., 2014). In this study we also choose a 150 μm mesh to be consistent with Oris et al. (2014) and the recommended size fraction for the GMCD (Hawthorne et al., 2018). The sieved content was soaked in a 5% NaOH solution to deflocculate the particles, and then soaked in a 10% solution of NaOCl to bleach any uncharred organic particles. The charcoal particles were analysed under a stereomicroscope coupled with a digital camera, and image analysis software (WinSEEDLE 2016a, Regent Instruments Inc., Canada) was used to measure the surface area of the charcoal and the number of particles per sample. These two charcoal metrics are commonly used for paleofire analysis (Power et al., 2008; Leys et al., 2013). In order to analyse the charcoal particle size distribution, which is an important parameter for inferring fire characteristics (Clark et al., 1998; Asselin and Payette, 2005; Oris et al., 2014), we calculated their median surface area.

2.3. Fire characteristics

Six fires characteristics were considered around each studied lake : burned area, year of ignition, time lag, charcoal source (zone), severity and fire lake distance (Table S2.1).
The burned area and date of ignition were extracted from open data shapefiles compiled by the Ministry of Forest, Wildlife and Parks of Québec (`https://www.donneesquebec.ca/recherche/fr/dataset/feux-de-foret`) (Table S2.1). Some fire polygons delineating burned areas encompassed water bodies such as lakes or rivers, leading to an overestimation of this metric. To remove water bodies from fire polygons and LANDSAT images before calculating burned area and fire severity, we used hydrologic data from the National Topologic Data Base (NTDB ; `www.rncan.gc.ca/sciences-terre/geographie/information-topographique/donnees-gratuites-geogratis/repertoire-telechargement-documentation/17293`).
In order to consider the effect of distance between the fires (charcoal source) and lakes (charcoal sink), we used three zones, i.e. radii of 3, 15, and 30 km around the lakes (Figure 2.1). Fires can

encompass several zones thus leading to the 30 lines in Table S2.1. We assumed that the 3-km radius would represent a « local » source of charcoal particles and was selected to encompass the local source area defined in several studies (< 1 km (Clark, 1988; Lynch et al., 2004; Leys et al., 2015) and possibly < 2 km (Leys et al., 2017)). We selected a 30 km radius as the regional source area of charcoals. In our context we assumed this radius to be a good approximation of the maximal distance charcoal generally travel during boreal forest type fires (Clark, 1988; Oris et al., 2014). We defined an intermediate 15-km radius as the « semi-local » or intermediate source area. Several studies have provided evidence of a lagged (protracted) charcoal deposition after a fire of up to 5 years (Whitlock and Millspaugh, 1996; Oris et al., 2014). Consequently, we decided to consider that one fire can contribute to a charcoal deposition in the traps if it happened 5 years or less before the charcoal measurement, i.e. from 2006 (Table S2.1).

The effect of fire severity on above-ground biomass can be measured either in the field using the composite burn index (CBI ; (Key and Benson, 2006; Boucher et al., 2017)) or via remote sensing data using the differentiated normalized burn ratio index (dNBR ; (Lentile et al., 2006)). Because CBI and dNBR are highly correlated (Cocke et al., 2005), we used the dNBR to infer fire severity at a landscape scale. This index uses spectral bands 4 and 7 of LANDSAT images (30-m resolution). These two bands represent two contrasting responses to burning. Band 4 represents a positive outcome after burning (Key and Benson, 2006), with near infrared (NIR) wavelengths ranging from 636–673 nm indicating vegetation content in the area. Band 7 represents a negative outcome after burning, with short-wave infrared (SWIR) ranging from 2107–2294 nm indicating the presence of rocks and mineral deposits (Barsi et al., 2014). The difference between these two bands provides a measure of the quantity of above-ground vegetation (NBR ; eqn 1) and the difference of NBR before and after the fire provides a measure of the quantity of vegetation consumed during a fire, and thus the aerial severity of the fire (dNBR ; eqn 2). The calculation used is :

$$NBR = (NIR - SWIR)/(NIR + SWIR) \tag{2.1}$$

$$dNBR = NBR_{beforefire} - NBR_{afterfire} \tag{2.2}$$

where NIR (eqn 1) is band 4 near infrared, SWIR (eqn 1) is band 7 short-wave infrared, $NBR_{beforefire}$ (eqn 2) is the NBR value taken at the latest date before the fire, and $NBR_{afterfire}$ (eqn 2) is the NBR value 1 year after the fire event. NIR and SWIR were derived from images chosen from open access LANDSAT data either using LANDSAT-7 (available since April 1999) or LANDSAT-8 (available since February 2013). To minimize the effects of differing phenology phases or solar angle, the pre-fire scenes were selected as near as possible in date to the fire event, and the after-fire scenes 1 year after the fire event.

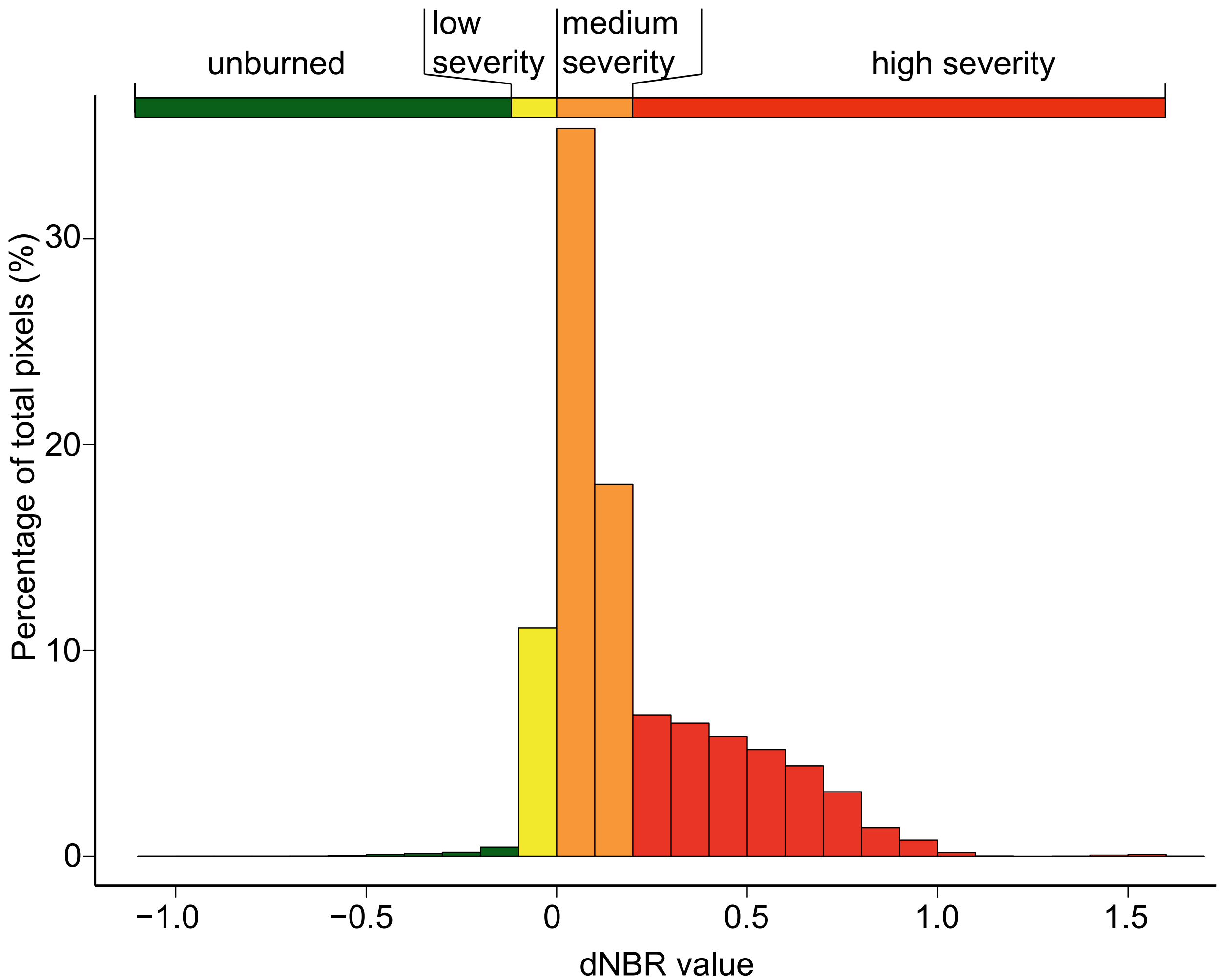

Figure 2.2. Distribution of dNBR values observed at the study sites ; green, unburned pixels (dNBR values of -0.1 and below) ; yellow, low severity (dNBR values ranging from -0.1 to 0) ; orange, medium severity (dNBR values ranging from 0 to 0.2) ; red, high severity (dNBR values of 0.2 and above).

2.4. Definition of severity classes

To analyse the influence of fire severity on the charcoal records, we created severity classes based on the distribution of dNBR values across pixels. Usually, dNBR values range between -0.10 and 0.10 in an unburned area and between 0.10 and 1.35 within a burned matrix (Key and Benson, 2006). Three classes of fire severity were therefore created (Figure 2.2), excluding an unburned area for dNBR that fell between the minimum value measured and -0.10. Low severity was represented by a value range of [-0.10, 0] (Figure 2.2 ; yellow) ; 0 represented the upper limit of the first quartile and corresponded to surface fires that only affected understorey plant species. Medium severity was represented by [0, 0.20] (Figure 2.2 ; orange) ; 0.20 represented the upper limit of the second quartile (=median) and corresponded to fires that consumed the leaves of trees and understorey vegetation (e.g., shrubs). The severely burned class was represented by dNBR values of 0.20 and above (Figure 2.2 ; red), and corresponded to stand-replacing fires that consumed a greater part of the aerial biomass (Ryan, 2002). The dNBR pixel data were classified using these categories and the corresponding surface area of the burned areas within each severity class was measured within the different zones. We also determined the cumulative severity as the sum of the dNBR values derived from a burned area. In order to remove unburned patches, we only considered pixel values above 0 before classification (Figure 2.2).

2.5. Database architecture

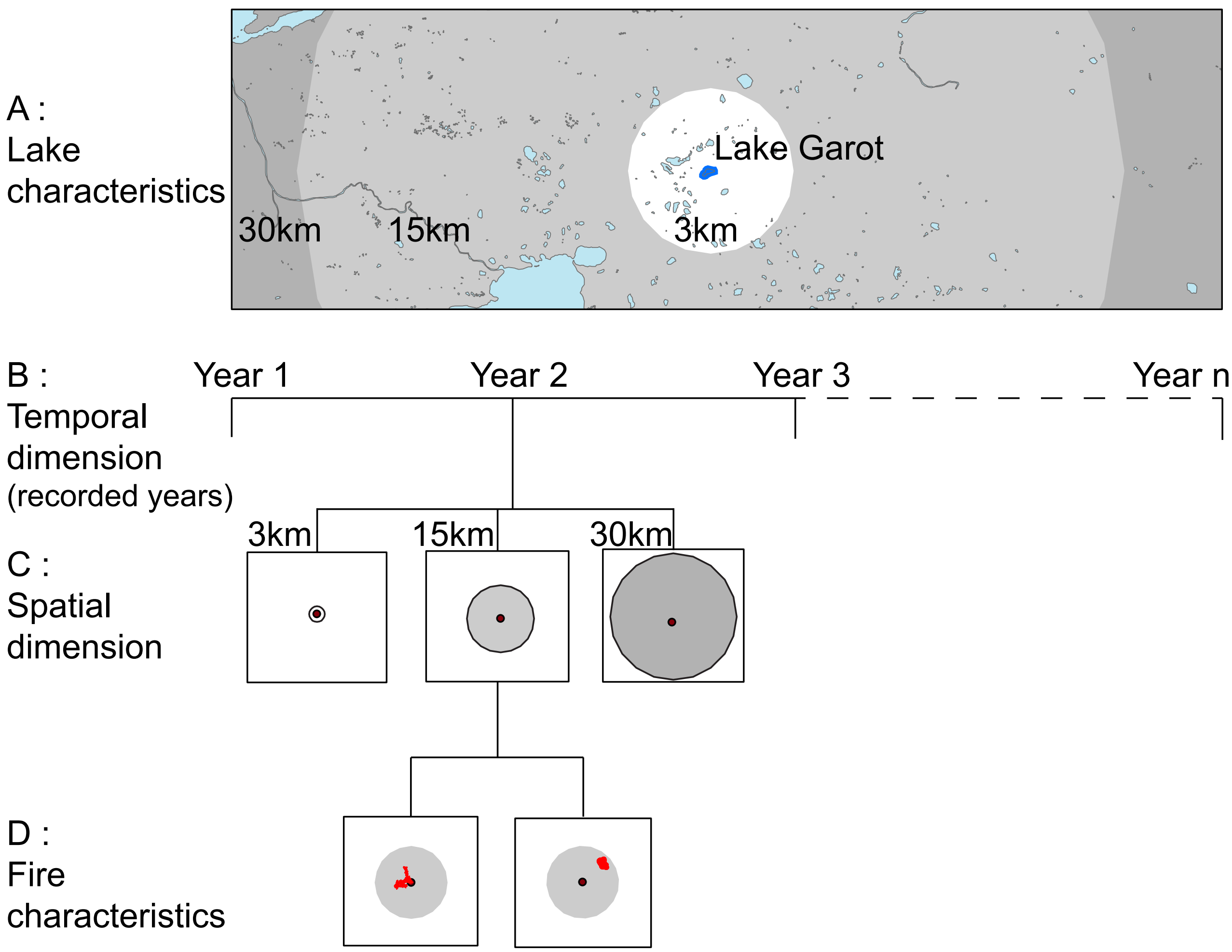

Figure 2.3. Experimental design used to analyse the effect of various taphonomic processes on charcoal production (fire characteristics), transportation and deposition-redeposition (lag-time) for the seven study lakes (A). The timing of deposition was assessed using fire characteristics measured up to 5 years before charcoal was recorded in a lake (B). The spatial dimension of charcoal transportation was assessed using three zones, with radii of 3, 15 and 30 km (C), within which the burned area and the fire severity were assessed for each fire (D).

The experiment was designed to link the charcoal measured in a lake (charcoal record) with fire severity, size and remoteness. We created a database containing the seven sites for which we had yearly recorded charcoal data (Figure 2.3 A and B, respectively) for a total of 38 individual charcoal records (forming the number of rows). From these, we selected the 12 samples that were recorded during a year with a known fire. For each sample (n=12), within the three zones (Figure 2.3 C) we calculated three parameters for each fire (Figure 2.3 D), namely cumulative severity (the summed severity of all fire pixels), burned area and a variable that measured the burned area for the three fire severity classes. These variables were used to isolate their relative importance in explaining the charcoal taphonomic processes. Likewise, we included lake surface area to assess the relative importance of the deposition process. Transportation of particles was studied using the distance between the lakes and the fire edge and the fire locations across the three zones (with radii of 3, 15, 30 km) within which the fire characteristics were assessed.

We summed the fire characteristics of the fire the year when the charcoal was recorded for lag = 0. Lag = 1 corresponds to fire events that can contribute to a charcoal record from zero to one year after it happened and repeated the process up to lag = 5. It resulted in 36 variables for the burned area and cumulative fire severity (six lag periods within the three zones), and 54 variables for the burned area for each fire severity class (three severity classes for six lag periods within the three zones), the distance between the burned area edge and the lake and the size of the lake. Overall, the database comprised 92 explanatory variables.

2.6. Selection of explanatory variables

The fire variables contained a plethora of zeros, as a result of dichotomies within the different criteria used and the relatively low sample size (charcoal-record years) ($n \ll p$). A Pearson correlation test revealed high correlations between variables (not reported here). Thus, we applied a methodology developed by Genuer et al. (2010) using random forest theory (Breiman, 2001) to the charcoal area, charcoal number and charcoal median surface area data separately. The procedure entailed creating a classification and regression tree (CART) for the complete dataset and then extracting increment of mean square error (IncMSE) values. IncMSE values describe the tree misclassification rate for a variable applied to a subset of samples excluded from the tree building by bootstrap resampling, the out-of-bag technique (OOB). The values for the variables were permuted randomly. The mean difference between the OOB-error of a particular variable and the OOB-error calculated from 50 tree building procedures is referred to as the variable importance index (VI).

We also used a complementary method (Genuer et al., 2015) to a pool of variables to identify those with a significant effect on charcoal metrics. Calculations were carried out using package VSURF (Genuer et al., 2015) in R 3.3.2 (R Core Team, 2018). Two methods can be used for interpretation or prediction of charcoal measurements, and both were used here. The variable retained in the interpretation pool can include some redundancies such that the second pool used for prediction is a subset of the first pool. For both methods, the variables were ranked based on the standard deviation (sd) of VI. A variable that is poorly linked to charcoal measurements will tend to have a lower VI sd. The minimum VI sd-value was set to define an interpretation threshold, to discriminate between explanatory and less explanatory variables for charcoal measurements. For the interpretation protocol, the first variable in the ranking was used to build a tree, and the OOB-error was then calculated. The remaining variables were added iteratively to build other trees for which the OOB-error was calculated, until the OOB-error stopped diminishing. The variables were then selected until the OOB-error reached its smallest value. The second model used to define the prediction threshold was based on the previous pool of selected variables and used the same method except that a variable was only added to the tree if the OOB-error decreased by more than the threshold value. This threshold value was calculated as the average variation of OOB-error when a noisy variable was added.

2.7. Linear regression on predictive variables

Linear regressions were performed on charcoal median surface area records using the pool of variables that were above the prediction threshold. The objective was to analyse the effect of predictors on charcoal accumulation. For each model, the r^2, P and Akaike Information Criterion (AIC ; (Akaike, 1974)) values were calculated to assess model performance.

3. Results

3.1. Modern fires around the study lakes

For the period 2006-2016, 21 fires occurred within the widest zone (30 km) around the seven lakes (Figure 2.1, Table S2.1 and S2.2). All fire events occurred between 24 May and 16 July ; 21 of the 24 were caused by lightning, and the last three fires were of anthropogenic origin. Two fires were limited to the 3-km zone for lakes Garot and Dave, while nine fires were within the 15-km zone for lakes Pessière, Schön, Garot and Dave, and 19 fires were within the 30-km zone of all seven lakes, with some encompassing several zones around one or more lakes. The accumulated burned area per lake within the 30-km zone was on average 812 ha. The smallest fire had a total burned area of only 1 ha, occurring near Lake Pessière in 2015, while the largest fire was 115 414 ha (5052 ha within the 30-km zone), occurring near Lake Walt in 2013. Fires that affected the lake surroundings were generally of medium to high severity (Figure 2.2). The lowest fire severity, with a dNBR of -0.32, occurred in 2007 near Lake Dave, representing a surface fire that had a low impact on the aerial biomass and was indistinguishable from the unburned area (Figure 2.2). The highest fire severity (dNBR of 0.66) occurred in 2011 near Lake Garot and was a crown fire.

3.2. Recorded charcoal

For the period 2011-2016, the average (±sd) charcoal median surface area was 0.0714±0.042 mm^2 (n=36). The smallest value was 0.00808 mm^2, found in Lake Nano (Figure 2.4B) in 2016, while the highest value was 0.17 mm^2, found in Lake Garot (Figure 2.4F) in 2011. Overall, the year with the

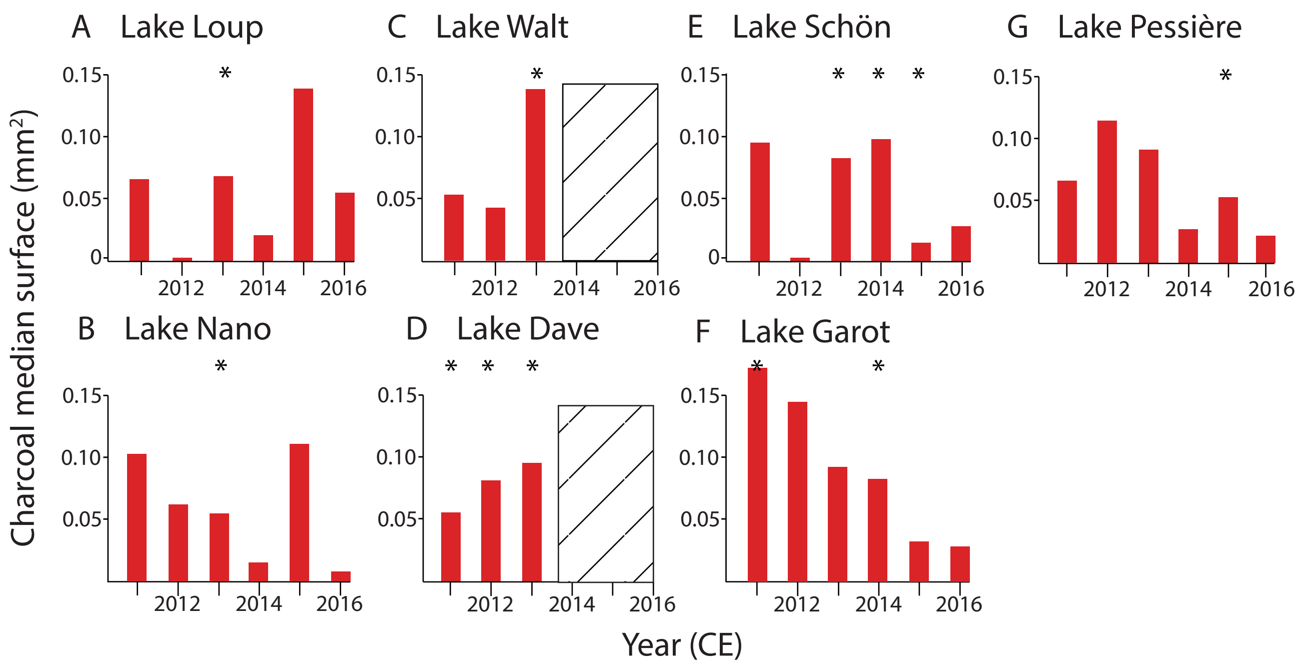

Figure 2.4. Charcoal median surface area for each site and for each year with records. Hatched boxes refer to years for which we do not have charcoal records. The asterisk corresponds to the charcoal records used for the linear regressions

smallest charcoal median surface area was 2016, with 0.0286 mm^2, and the year with the highest value was 2013, with 0.0895 mm^2.

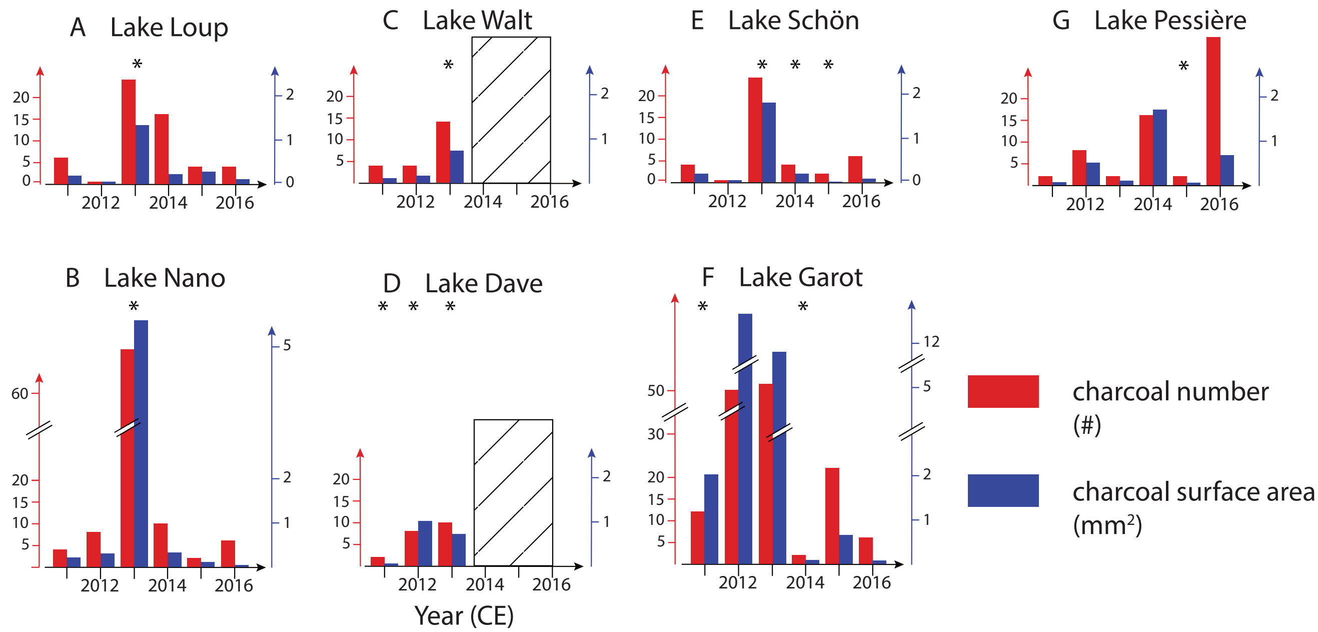

Figure 2.5. Distribution of charcoal number (red) and charcoal surface (blue) for each site and for every recorded year. The asterisk corresponds to the charcoal records used for the linear regressions.

For the recorded years, from 2011-2016, charcoal number varied from 1 to 65 particles for Nano (Figure 2.5B) in 2013 with a mean of 7.6±13.7 particles and charcoal surface varied from 0.41 to 12.8 mm^2 obtained by Garot (Figure 2.5F) in 2012 with a mean of 1±2.4 mm^2. On average, 2011 is the year with the less charcoal number and surface recorded and 2013 is the year with the most important values for both charcoal measurements (n=36).

3.3. Interpretation and prediction variables selected based on VI

The most significant variables explaining charcoal median surface area were fire characteristics within the 30-km zone (seven variables), and fire characteristics in the 15-km zone (three variables ; Figure 2.6). Four out of the 10 variables represented a lag interval of 0 year, two variables represented a lag of 1 year and four represented a lag of 2 years. All three categories of fire characteristics measured presented in Figure 6 were among the predictive pool of variables, and those variables were measured within the 30-km zone with a lag interval of 0. Considering the variables above the prediction threshold, variable selection for charcoal median surface area shared two variables with the selection for charcoal surface area (see Figure S2.2), namely « medium severity area 30-0 » and « total burn area 30-0 ». The latter variable also fell within the selection for charcoal surface area. Lake surface area fell within the two most significant and predictive variables for charcoal surface area and number (Figure S2.2).

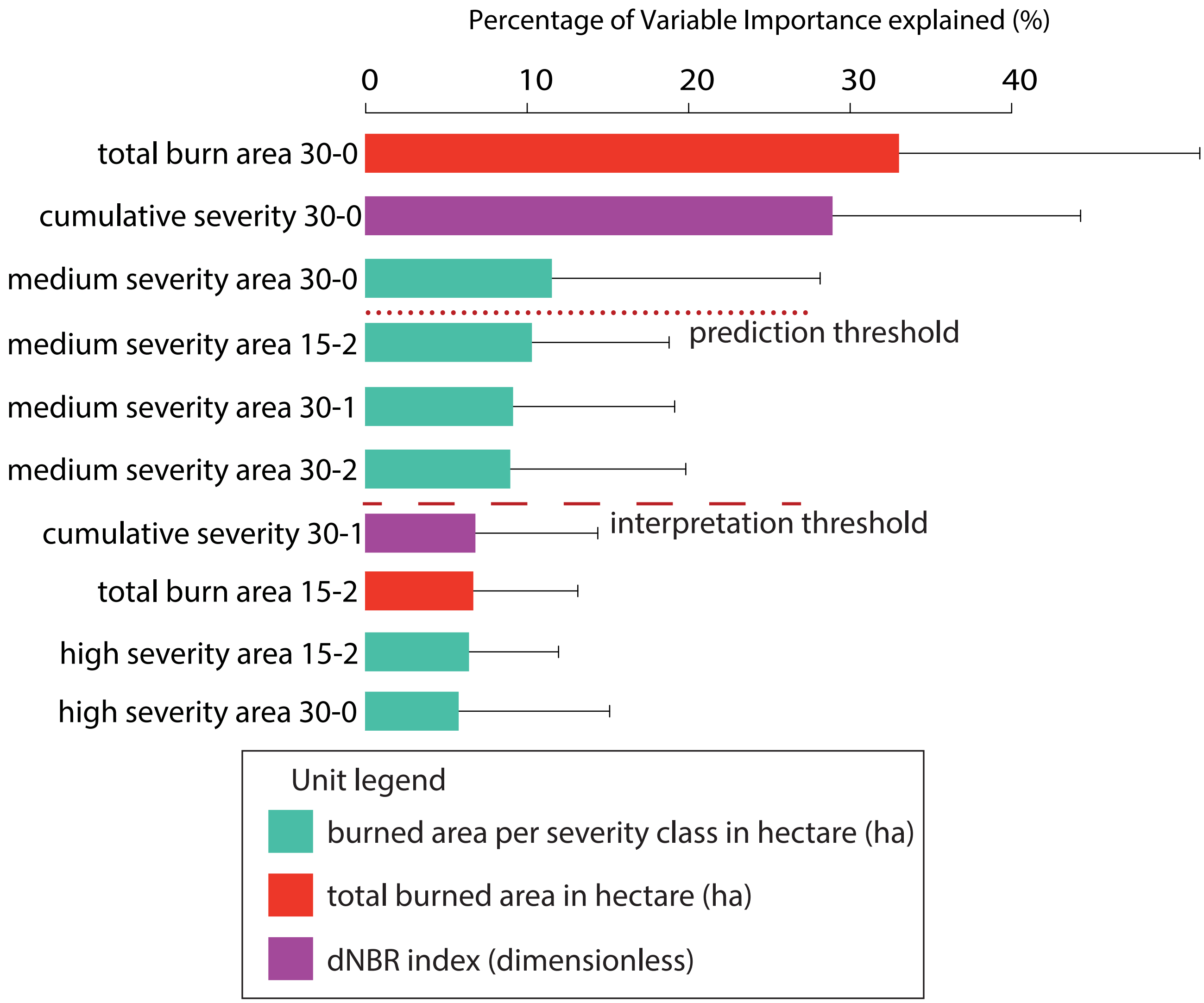

Figure 2.6. The 10 first explanatory variables for charcoal median surface area. Colours refer to the categories of environmental variables linked to the charcoal : cumulative fire severity (purple), burned area per fire severity class (green), and total burned area (red). Dotted lines refer to the prediction threshold and dashed lines refer to the interpretation threshold. The naming convention for the variable code is : first the type of variable, then the zone in which it was measured and the delay (lag) interval between the fire trait measurements and the charcoal record.

3.4. Linear regressions linking charcoal median surface area CHAR_{ms} to fire severity and burned area

We estimated the parameters of the linear regressions linking charcoal median surface area to each variable above the prediction threshold (Figure 2.6) but tests showed significant parameters only for cumulative fire severity and burned area measured within the 30-km zone with no time lag between the fire event and the charcoal record (Figure 2.7). When applied to the variable « medium severity area 30-0 » , the model characteristics ($r^2 = 0.01$, $p = 0.71$ and AIC $= 62.1$)

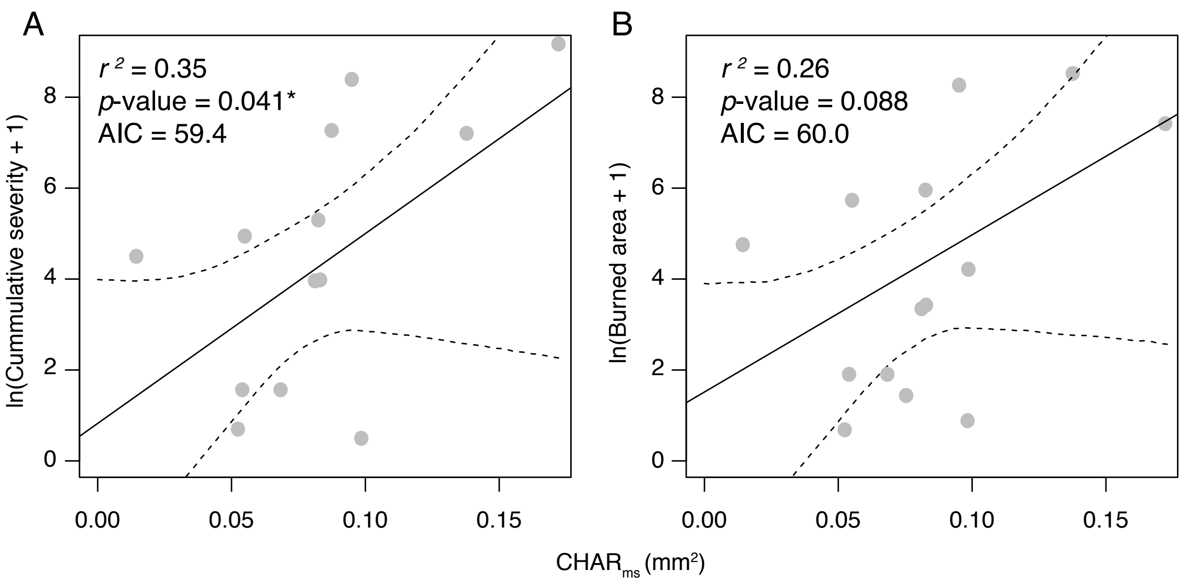

Figure 2.7. Linear regression between charcoal median surface area (CHAR$_{ms}$) and (A) cumulative severity measured within the 30-km zone with no time lag between the fire and charcoal measurement, and (B) linear regression between burned area in the 30-km zone with no time lag and charcoal median surface area. Dotted lines correspond to 95% confidence intervals obtained with bootstrap resampling (1000 iterations).

revealed an inaccurate model. The model for cumulative severity was significant (r^2 = 0.35, p = 0.041, AIC = 59.4), and for burned area marginally significant (r^2 = 0.26, p = 0.088, AIC = 60). The resulting equations for these 30-km radius models are :

$$Cumulative\ severity = exp(41.75 CHAR_{ms} + 0.82) - 1 \tag{2.3}$$

$$Burned\ area = exp(34.57 CHAR_{ms} + 1.51) - 1 \tag{2.4}$$

where exp(x) refers to the natural exponential function.

Discussion

The results show that the median surface area of charcoal particles in boreal forest is explained by cumulative fire severity and burned area within a 30-km zone during the year (with no time lag), while charcoal number and total surface area are mostly influenced by both lake surface area and medium fire severity (30-km zone, no time lag, Figure S2.2). It appears that taphonomic processes involving charcoal production during a fire, *i.e.* area, severity and transportation by wind (30 km), are the main drivers influencing the charcoal deposition in boreal lake sediments.

Time-lag between fire and cumulating year affects charcoal deposition

By considering a lag between fires and charcoal measurements, we analysed the relative influence of primary transportation by buoyancy and wind, and secondary transportation as a result of multiple processes, such as runoff and disturbance caused by wind eddies or biota. The delay between a fire and a charcoal peak can be up to 5 years after the actual fire event (Whitlock and Millspaugh, 1996; Oris et al., 2014), potentially because of wind-caused eddies (Bradbury, 1996), runoff sustaining a flux of charcoal even a few centuries after a fire within a mountain relief landscape with an extensive stream network (Carcaillet et al., 2007), or bioturbation by moose (Bump et al., 2017), beavers or diving ducks foraging in shallow waters (Bakker et al., 2016) that can cause reworking of sediments which has been documented for pollens (Davis, 1973). However, the study lakes were head lakes situated in a flat-to-rolling landscape, thus reducing partially or completely the run-off effect (e.g. Lake Pessière, with a totally flat topography). The size of the selected lakes was too small to support disturbance by eddies, but bioturbation by moose or beaver in shallow waters could still offer a potential explanation for a protracted charcoal record. However, our results suggest that, even if a delay of up to 5 years could eventually happen, charcoal deposition in fact usually occurred during the year of the fire event (lag 0) or the year after (lag 1, Figure2.6 and Figure S2.2), which suggests a transportation mode dominated by wind during the fire (a primary process) rather than runoff or bioturbation (secondary processes) (Anderson, 2014).

Charcoal source area

One of the first parameter that should impact charcoal source area is lake size. The relative importance of lake surface area in capturing charcoal in the water column was shown in this study (charcoal number and area, see Figure S2.2) echoes the results of studies on surface sediments (Gardner and Whitlock, 2001) and highlights the need to transform data to exclude the effect of lake bodies on charcoal time series (Carcaillet et al., 2002; Power et al., 2008).
Studies have tried to empirically differentiate between local and regional fires using the slope of charcoal size distribution (SCD method) for sedimentary charcoal (Asselin and Payette, 2005; Remy et al., 2018), or charcoal in traps ((Oris et al., 2014) from which we used the experimental design to calibrate charcoal-fire relationships with yearly records from traps. Some studies have attempted to linearly link charcoal number with local fire characteristics such as burned area and fire occurrence. No significant relationship has been found within grassland ecosystems (Duffin et al., 2008; Leys et al., 2015), but charcoal number has been shown to be linearly correlated with more regional events (Asselin and Payette, 2005; Adolf et al., 2018a). Using the variable classification, we found that no local variables (within the smallest zone) explained the median surface area of charcoal particles but only semi-regional (15-km zone) and regional (30-km zone) scale variables. The distance between the charcoal source and the depositional environment has long been known to explain variation in charcoal samples, through theoretical (Clark, 1988; Higuera et al., 2007), experimental (Clark et al., 1998; Ohlson and Tryterud, 2000; Lynch et al.,

2004) and empirical studies (Clark and Royall, 1995; Duffin et al., 2008; Aleman et al., 2013). However, in our experimentation, the distance measured between fires and lakes (column 10 TableS2.1) was not a significant variable (Figure 2.6 and S2.2) which have also been noticed by Oris et al. (2014). The structure of boreal forest fires compared with temperate grassland fires (Leys et al., 2017), the landscape physiognomy or the wind speed might explain these differences. We thus considered in this study that charcoal median surface area of charcoals can be a better indicator of fire severity and burned area than of fire edge-lake distance.

We have therefore shown that in boreal ecosystems characterized by a flat-to-rolling landscape and large and severe fires (Figure S2.3), charcoal particles > 150 μm in lakes can originate from long distance transportation over at least 30 km (regional). Under boreal forests conditions, primary transportation of particles during a fire can be greater than 15 km, as shown using a particle dispersion model (Peters and Higuera, 2007) based on equations that simulate the behaviour of charcoal deposition (Clark, 1988), or via monitoring experiments (Oris et al., 2014). The charcoal signal indicated by particles on pollen slides can sometimes be related to even more distant fires, the smallest particles (with a minimum of 10 μm) can be occasionally transported above 100 km from the source (MacDonald et al., 1991; Clark and Royall, 1996; Vachula and Richter, 2018).

The variable selection for median surface area shows some peculiarities compared to charcoal number and charcoal surface area. We decided to use charcoal median surface area since it depends on both charcoal number and surface, thus it is a better representative of charcoal distribution. This metric seems to be less sensitive to lake surface area (Figure 2.6) but more sensitive to fire severity and burned area (Figure 2.6 and 2.7). The later result show that the more a fire is severe and burns a large surface, the bigger the charcoal median surface area will be. This can be attributed to the number of charcoal particles that tends to increase when fire severity or size increases (Pitkänen et al., 1999; Duffin et al., 2008; Higuera et al., 2005). Charcoal particle size is often considered an indicator of proximity (Clark et al., 1998; Higuera et al., 2007) with bigger charcoal particles attributed to local fires. In our case this characteristic didn't seem to be significant since all variables above the interpretation threshold (Figure S2.2) were associated with regional fire characteristics (measured within the 30-km zone). This could be attributed to the small number of local fire, measured within the 3-km zone. But it could also be attributed to the transportation mode, since our methodology mostly allowed us to measure charcoal influx from wind transportation which can prevent charcoal particles from being broken up by secondary transport via water bodies.

Burned area and severity affect charcoal production

Using a non-parametric technique based on random forest theory (Leys et al., 2017), we found that burned area is always among the most significant variables (prediction threshold) in explaining total and median charcoal areas (Figure 2.6 and Figure S2.2). We also found that fire severity at a landscape scale (30-km radius) is a significant predictor explaining the amplitude of charcoal influx. This observation supports studies that have only measured local fire severity (Higuera et al., 2005).

High severity fires can produce more ashes than charred particles, but the high thermal buoyancy above the fire lifts the fragments high above the forest (Clark, 1988; Val Martin et al., 2010; Vachula and Richter, 2018), facilitating the suspension of charred particles in the air and their transportation far outside the region, depending on the wind speed (Clark, 1988). Conversely, low severity fires produce few charred particles relative to burned biomass, and the energy released by the fire front is too low to allow their suspension and thus their transportation away from the burned area (Ohlson and Tryterud, 2000). Studies have only considered burned area or fire occurrence when investigating the role of fire components on charcoal measurements (Leys et al., 2015; Adolf et al., 2018b). The present study thus highlights the importance of fire severity in understanding the charcoal time series (Figure 2.6). As the dNBR index refers to the amount of biomass burned (Cocke et al., 2005), it should be considered in subsequent calibration studies. The dNBR index is particularly relevant for methods attempting to distinguish between charcoal peaks in lake sediments generated by surface fires (low severity) and crown fires (high severity).

Quantitative reconstruction of burned area and fire severity using charcoal median surface area

Attempts have been made to reconstruct past fire characteristics using charcoal influx without any consensus on the characteristics being reconstructed, nor experimental verification of the strength of the reconstruction, *i.e.* the burned area (Ali et al., 2012) and fire severity (Colombaroli and Gavin, 2010; Kelly et al., 2013). One statistical relationship correlating fire severity and sedimentary charcoal is based on comparisons between recent sedimentary charcoal in eastern Canada and northeast USA and the Canadian fire severity database of recent fires (Clark and Royall, 1996). In our study, the linear regressions showed a marginally significant and significant relationship between the median area of charcoal particles and the burned area, respectively, and fire severity. The positive linear regression between $\ln(\textit{Burned area})$ and $\ln(\textit{Cumulative severity}$; Figure S2.3) shows that fire severity (above-ground biomass burned) and burned area are probably linked in boreal ecosystems (Flannigan et al., 2009). Future attempts at quantitative reconstruction of fire regime parameters using transfer functions applied to sedimentary charcoal records would benefit from study of the relationships highlighted here. The significant linear regressions revealed here could serve as a basis for assessing past fire severity and burned area for paleoecological sites located within boreal forest.

Conclusion

We have demonstrated the importance of considering fire severity at a landscape scale as well as the burned area when calibrating charcoal deposition. This is unsurprising, given that fire severity is strongly linked with the amount of biomass burned during a fire (Boucher et al., 2017) ; however, until now the relationship between fire severity and charcoal load in sediments has only been demonstrated locally (Higuera et al., 2005). We suggest that subsequent studies should include fire severity in the set of variables used to explain charcoal metrics. We have also shown that the median surface area of charcoal particles is linearly related to the severity of the fire and the burned area. The use of charcoal median surface area allows consideration of charcoal particle distribution and appears to be more independent of lake surface area than number of charcoal particles or total surface area. Applying these transfer functions on long-term sequences will probably enable the reconstruction of past fire severity and burned area as well as fire frequency. These fire characteristics provide more insight into past fire-vegetation history and can help answer complex ecological questions concerning long-term fire-vegetation interactions.

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Supplementary material

Tableau S2.1. Raw data of fire event characteristics (n=24) sorted by site, year and zone. The two last columns refer to respectively distance between fire and site, and lake surface area. Burned areas and lake surface area are expressed in hectares ; distances are expressed in meter and cumulated severity is dimensionless. This table has then been modified as explained in the methodology (see section Database architecture). Fire characteristics (columns 4 to 8) were accumulated according to the year (column 2) considering the lag of up to five years with charcoal records and within each zone (column 3).

Name	Year	Buffer area	Burned area	Unburned area	Low severity area	Medium severity area	High severity area	Cumulated severity	Fire-lake distance	Lake surface
Dave	2006	30	4.01	0	0	0.59	3.42	25.91	29.3	5.26
	2007	30	40.54	40.54	0	0	0	0	26.1	5.26
	2009	30	3043.11	3.06	22.29	463.91	2553.86	12281.53	11.6	5.26
		15	793.81	0.87	3.65	112.97	676.31	5854.58	11.6	5.26
	2010	30	269.64	0	0.63	21.78	247.23	1520.34	27.1	5.26
	2011	30	306.44	6.95	4.27	29.3	265.92	141.02	26.2	5.26
	2012	30	27.7	0.09	1.44	17	9.17	51.38	12.6	5.26
		15	27.7	0.09	1.44	17	9.17	51.38	12.6	5.26
	2013	30	3819.75	0.21	24.74	3629.86	164.93	4412.96	27.7	5.26
		15	3601.8	0.21	21.26	3413.54	166.78	4197.19	27.7	5.26
		3	12.13	0	0	12.13	0	10.34	27.7	5.26
Garot	2009	30	31.94	0.63	8.19	18.26	4.86	33.52	24.8	5.62
	2011	30	1675.37	38.6	0	2.09	1634.69	9616.38	0	5.62
		15	1675.37	38.6	0	2.09	1634.69	9616.38	0	5.62
		3	615.78	13.53	0	0.6	601.65	4029.81	0	5.62
	2014	30	388.99	26.45	53.53	309.02	0	199.43	10.2	5.62
		15	388.99	26.45	53.53	309.02	0	199.43	10.2	5.62
Loup	2013	30	5.8	0	0.26	5.54	0	3.78	16.3	1.66
Nano	2013	30	5.8	0	0.26	5.54	0	3.78	12	0.57
		15	5.8	0	0.26	5.54	0	3.78	12	0.57
Pessière	2007	30	45.11	36.25	1.88	2.6	4.39	18.23	14.6	5.29
		15	12.63	12.01	0.31	0.1	0.21	1.33	14.6	5.29
	2015	30	1	0	0	1	0	1	15.3	5.29
Schön	2006	30	560.19	2.7	12.79	50.25	494.44	3350.35	8.8	3.04
		15	560.19	2.7	12.79	50.25	494.44	3350.35	8.8	3.04
	2013	30	29.63	0	0	22.41	7.22	52.88	14.4	3.04
		15	18.9	0	0	13.66	5.24	37.75	14.4	3.04
	2014	30	1.44	0	0	1.44	0	0.65	17.1	3.04
	2015	30	116.35	0	8.72	107.16	0.47	87.33	15.6	3.04
Walt	2013	30	5052.32	0.18	1396.29	3655.76	0.09	1358.54	24.1	2.12

Tableau S2.2. Lakes coordinates

Name	Longitude	Latitude
Pessière	-79.240	49.509
Schön	-77.568	50.595
Garot	-77.554	51.100
Nano	-77.364	53.024
Loup	-77.401	53.055
Dave	-76.152	52.062
Walt	-76.043	51.852

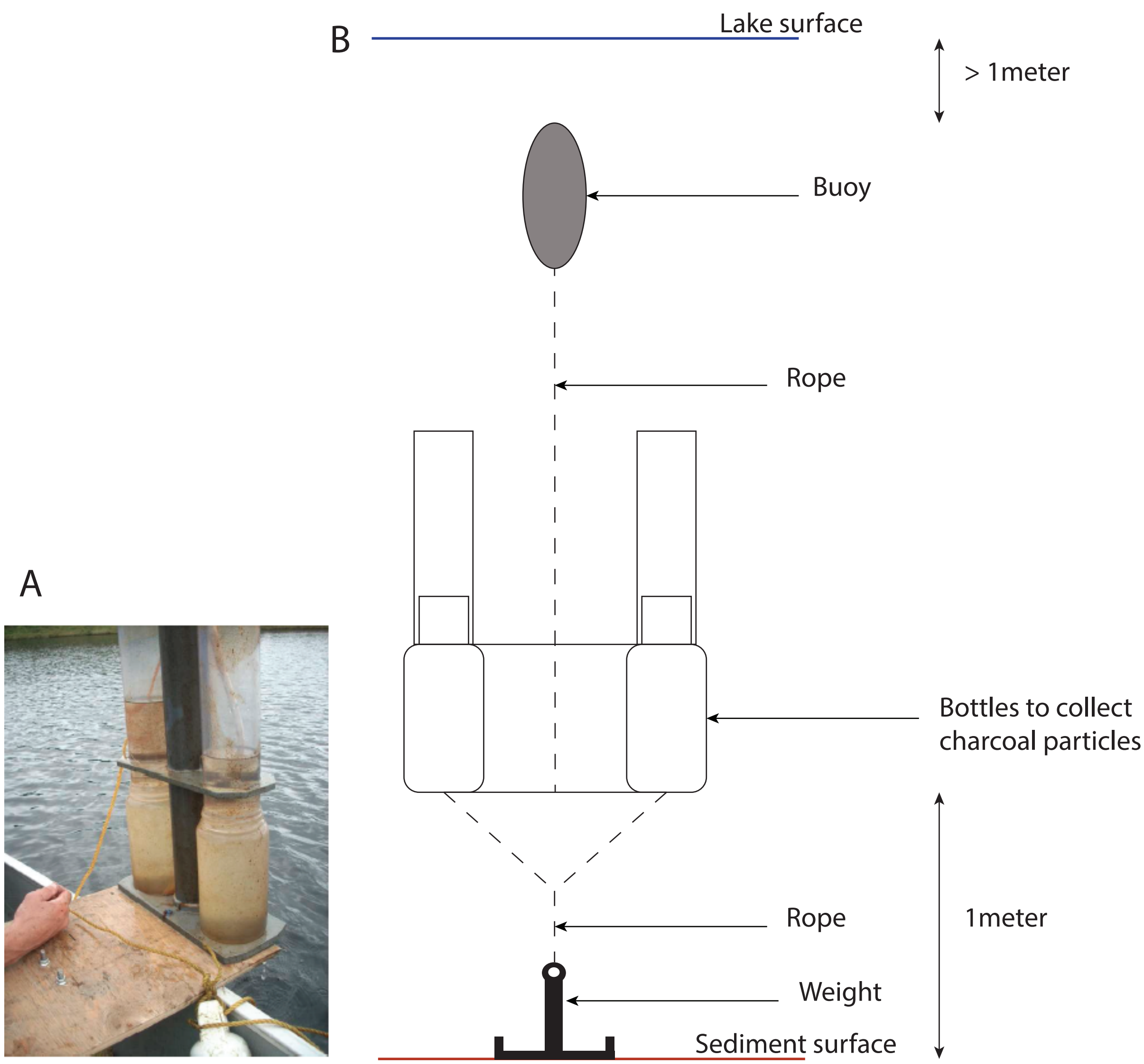

Figure S2.1. (A) Picture of the actual trap device used to collect charcoal particles and (B) the corresponding design schema of the trap device.

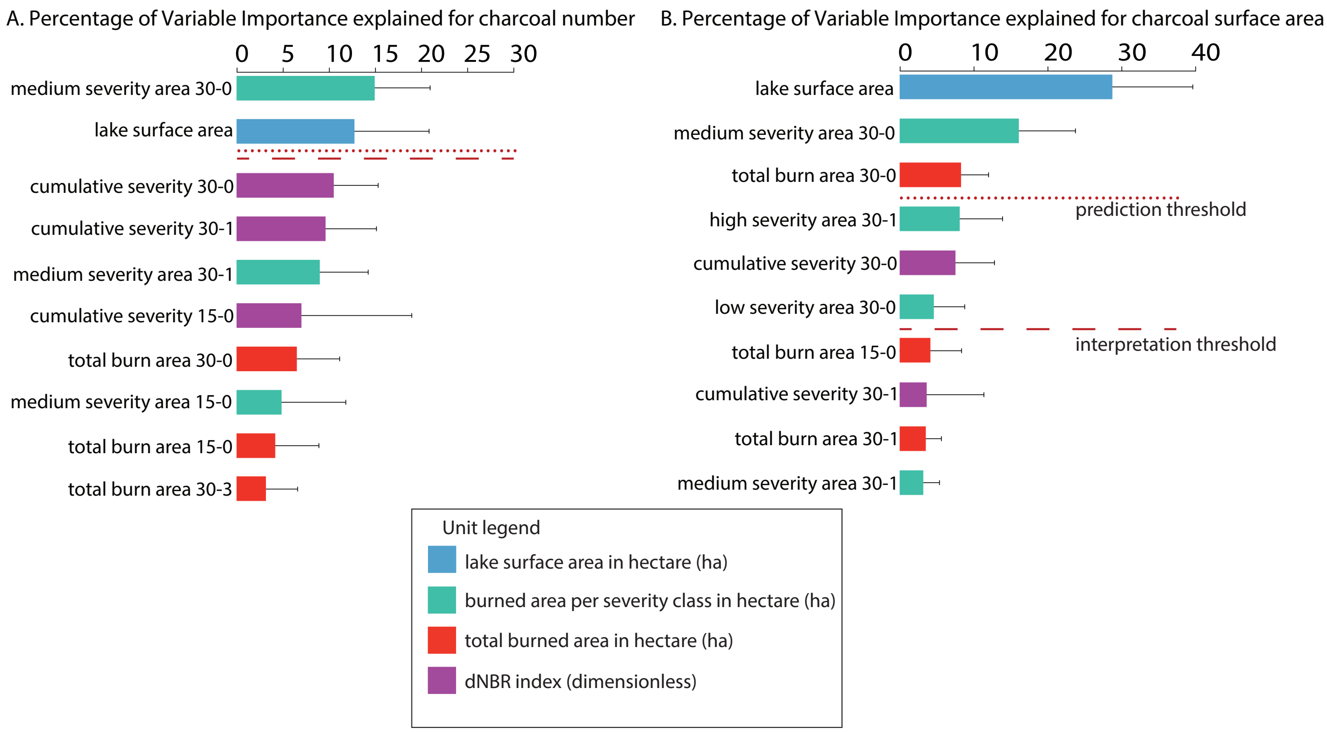

Figure S2.2. Ten first explanatory variables of charcoal number (A) and charcoal surface (B) expressed in percentage ; the variables were selected based on the method of Genuer et al. (2010). Colors refer to the categories of environmental variables linked to charcoal : fire severity (purple), burned area per fire severity class (green), total burned area (red), and lake size (blue). Dotted lines refer to the prediction threshold and dashed lines refer to the interpretation threshold (see Material and Methods, Genuer et al. 2015). In panel (A), both thresholds are identical. Nomenclature of variable shows in first the type of variable, then the zone in which it has been measured and the delay (lag) between the fire trait measurements and the charcoal record.

Both for charcoal number (Figure S2.2A) and surface (Figure S2.2B), all types of variable are among the most explanatory variables of the dataset. Seven out of ten variables are common for the two charcoal measurements. Respectively 3 and 1 variables out of ten describe fire characteristics within the 15 km zone for charcoal number and surface, as they are 6 and 8 out of ten for fire characteristics within the 30 km zone. Likewise, variables that describe a lag of 0 year between the fire events and the charcoal record represent 6 and 5 variables out of ten for charcoal number and area, as lag 1 variables represent 2 and 4 variables out of ten. Yet, only two variables were significant in terms of both interpretation and prediction for charcoal number : the medium severity area within the 30-km zone and the lake size (Figure S2.2A). In the case of charcoal surface, three and six variables were significant respectively to the prediction and the interpretation thresholds (Figure S2.2B). Lake size is the second and the first variable selected for charcoal number and surface, respectively, thus stressing the function of lake size characteristics in explaining those two indices. The medium severity area within the 30 km zone is the other most important variable for explaining both charcoal number and surface, highlighting the role of fire severity relative to burned area to explain charcoal pattern. Concerning charcoal surface solely, total burned area within the 30 km zone during the year of charcoal record is one out of the three most significant variables contributing to predict the charcoal pattern.

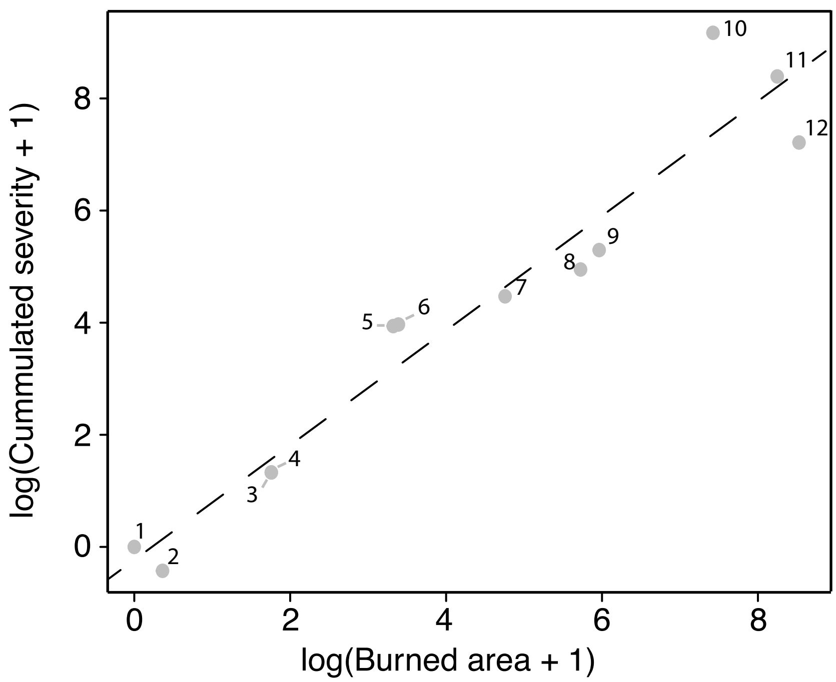

Figure S2.3. Linear regression between fire cumulative severity and burned area (dotted line). Each of the twelve dots corresponds to one fire characteristics (burned area and cumulated severity) measured in one year. Large and severe fires will tend to be on the upper right part of the graph as small and not severe fires, that can be classified as surface fires, will be in the lower left part of the graph. Fire events above the dotted line will tend to be more severe than large as fires below the dotted line will tend to be larger than severe.

Chapitre 3

Sedimentary charcoal calibration with surrounding fire characteristics : challenges and new opportunities

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Hennebelle A, Grondin P, Aleman JC, Bergeron Y and Blarquez O. (*accepted with revision*). Sedimentary charcoal calibration with surrounding fire characteristics : challenges and new opportunities. *PLoS ONE.*

Abstract

Paleoecology enables the reconstruction of ecosystem dynamics in various types of ecosystems. In the western part of the boreal forest of Québec (Canada), we have a good understanding of pluri-millennary vegetation composition dynamics and fire regimes during the Holocene. These descriptions are however mainly qualitative and recent studies are trying to establish more quantitative reconstructions of vegetation composition and fire regime dynamics. In this study, we extracted short sediment cores at the transition between water and sediments for 6 lakes located in the western spruce feathermoss subdomain in Québec. We established the history of fire events that occurred up to 30 km around the lakes from 1976 to 2015. Burned areas were measured using freely available data from the Ministry of Forest, Wildlife and Parks of Québec and fire severity were calculated via the dNBR index using LANDSAT images. We combined the charcoal records from the 6 lakes to establish a semi-regional composite reconstruction of charcoal number, charcoal surface area and charcoal median surface area. We used linear regressions between the charcoal composite record and the fire characteristics and found marginally significant parameters between

charcoal number and fire severity ($r^2 = 0.18$, P-value = 0.058) and with burned area ($r^2 = 0.16$, P-value = 0.076). The limited performances of these models highlight the taphonomic processes that affect charcoal signal and that blur the relationships with the fire characteristics. Finally, we will discuss our results with regard to the current knowledge on the different taphonomic processes that affect charcoal particles between the production, the transportation and the deposition. We will propose an interpretation of the results and the insights they bring for the analysis of charcoal signals.

KEYWORDS : calibration, fire, forest, charcoal, short cores, lake, severity, dNBR, taphonomy

1. Introduction

In the boreal biome, fire is a major driver of ecosystem dynamics (Stocks et al., 2003). With ongoing climate change, the eastern part of Québec's boreal forest is expected to experience more fire prone conditions compared to the preindustrial period (Girardin and Mudelsee, 2008). This preindustrial period is used as a baseline for defining ecosystem based management targets in Québec's managed forests. This type of management aims at reducing the gap that exists between today's managed lands and the preindustrial forests (Boucher et al., 2011). However, if the future fire regime exceeds the regime experienced during the preindustrial period, this will result in a loss of reference for setting sustainable management targets, with a risk of driving forest ecosystems out of their natural boundaries (Cyr et al., 2009). Thus, there is a need to explore wider time scales for defining sustainable reference period by using, for example, paleoecology which is a discipline that analyses bioproxies stored in natural archives for inferring multi-millennial ecosystem dynamics (Gillson and Marchant, 2014). Past fire regimes can be reconstructed using charcoal accumulated in various stratigraphic archives (Remy et al., 2018). For lake sediments, a very common method for reconstructing past fire regimes is the calculation of the time separating two consecutive detected peaks in charcoal accumulation for determining the FRI (Fire Return Interval) (Higuera et al., 2010). Various statistical methods were subsequently developed in order to improve the strength of FRI calculation (Itter et al., 2017; Blarquez et al., 2013; Higuera et al., 2009, 2007). FRI is well suited for the description of key periods of history characterized by greater or fewer fire episodes, and can be monitored at various scales (Marlon et al., 2008; Power et al., 2010). However, in terms of ecology, FRI is not always accurate for explaining the post-disturbance resilience of ecosystems (Hennebelle et al., 2018). Since when it comes to isolated events, fire size (often seen via burned area) and fire severity are key characteristics explaining ecosystem post-fire recovery (Greene et al., 2004). Indeed, a large and severe fire will be associated with stand replacement of the dominant tree species as surface fires will not induce a major change in the pre-fire forest composition or the canopy structure. Only a handful of studies have tried to reconstruct such characteristics in long sequences (Asselin et al., 2016; Kelly et al., 2013; Ali et al., 2012). But without appropriate calibration studies, quantitative reconstructions of such phenomenon is impossible (Hawthorne et al., 2018). Indeed, studies have tried to quantitatively link charcoal particle counts, surface area, volume or median surface area with fire characteristics such as burned area, fire frequency or fire severity in various ecosystems such as these of boreal forests (Hennebelle et al, *in rev*; Brossier et al. (2014)), temperate forests (Adolf et al., 2018; Higuera et al., 2005), and grasslands (Leys et al., 2015; Aleman et al., 2013). However, these reconstructions based on charcoal measurements are not successful in fully reconstructing fire characteristics. Charcoal particles pass through several filters that blur the final charcoal signal, including their production, transportation by the wind or water bodies, to the lake deposition and conservation in the lacustrine archive (Conedera et al., 2009). A theoretical knowledge of particle motion in the air and transport by wind (Clark, 1988) helped to reconstruct the potential source area of particles (Vachula and Richter, 2018; Peters and Higuera, 2007). Other studies attempted to unveil the magnitude of remobilization that affects charcoal particles when being incorporated into the lacustrine sediments (Higuera et al., 2007). In this article we propose a case study of calibration between charcoal extracted from surficial sediments that have recorded recent fire events for which the burned area and the fire severity have been measured around 6 lakes. Based on our results and a review of calibration papers we will discuss the current shortcomings and pitfalls of charcoal based reconstructions of fire characteristics and the discussion that results about the taphonomic processes affecting charcoal particles between the production site to the depositional archive.

2. Material and Methods

2.1. Study sites

The sites are located in the western spruce-feathermoss subdomain of Québec (Figure 3.1), in eastern Canada (Saucier et al., 2009). They are head-water lakes (without inlet streams), (except for Lake Gitans), and of a relatively small size, spanning from 0.18 to 4.5 ha. Among the sites, 2 groups can be distinguished, one being composed of Lakes Galinette and Bécasse and located in the south of the study area. The other group is located in the northern part of the study area and comprise the four other lakes, namely Lakes Cacahuète, Gitans, Syrah and Ténia. On till deposits the vegetation is dominated by black spruce (*Picea mariana* [Mill.] BSP) with feathermoss in the understorey. On sandy deposits, the stands are dominated by jack pine (*Pinus banksiana* Lambert). The climate is characterized by mean annual temperatures of 0.2±3.7°C and annual precipitation of 995±29 mm as snow and rain (Environement Canada, 2011). The topography is flat for the southern sites and hilly for the northern ones (Couillard et al., 2016).

2.2. Core dating

The lakes were cored during fieldwork in 2016. We used a Kajak-Brinkhurst gravity corer (Glew, 1991) to retrieve the sediments at the gyttja/water transition. The cores were about 40 cm in length and were subsampled on the field at 0.5 cm for the 10 first centimeters and at 1 cm for the rest of the cores. For this analysis, only the 10 first were used. The sediments were dated using the levels 0-0.5, 2-2.5, 5-5.5 and 10-11 cm using ^{210}Pb, and age-depth models were established using the

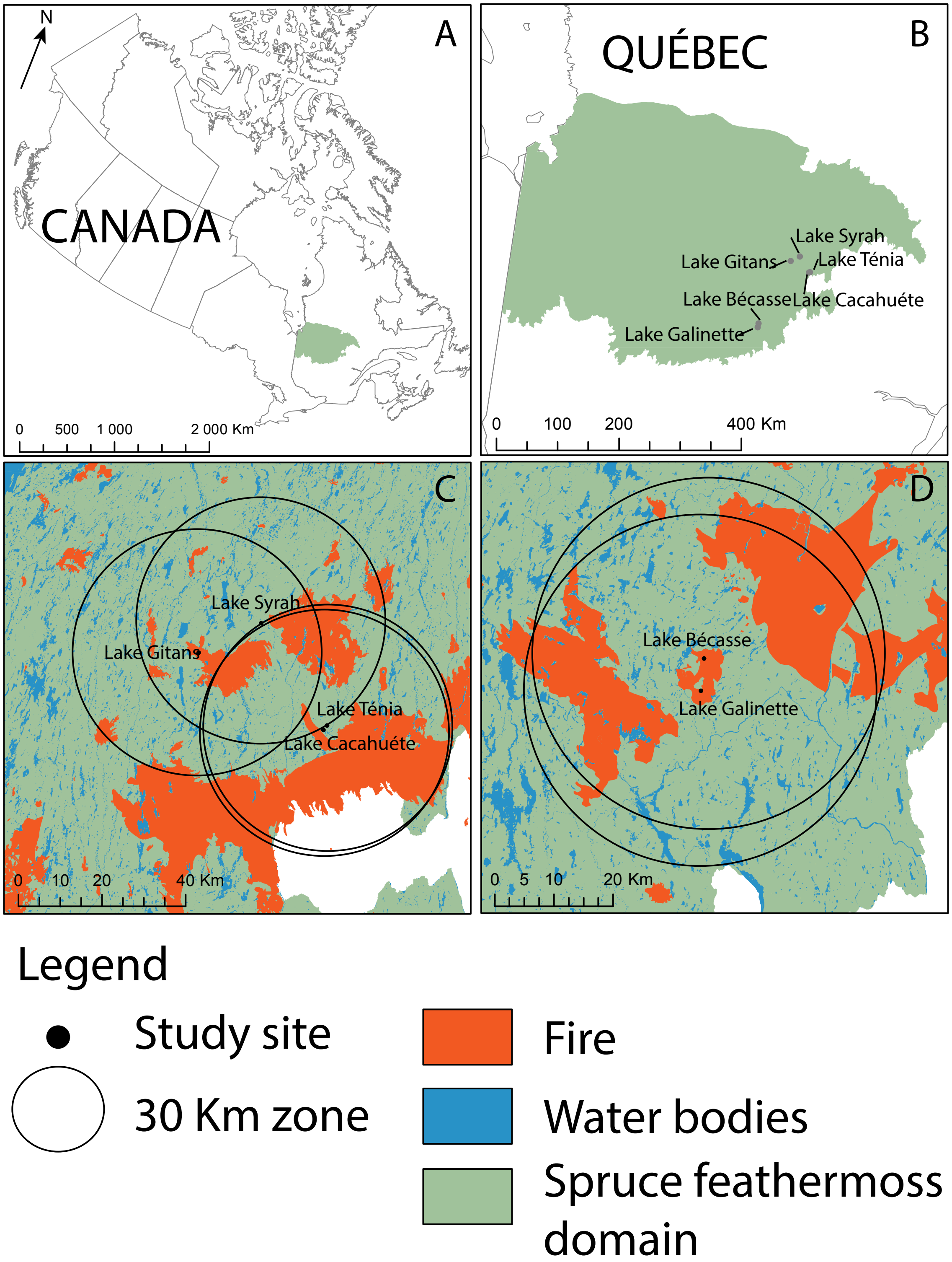

Figure 3.1. (A) Location of the Québec western spruce feathermoss domain in Canada. (B) Location of the six study lakes (non-official names) in the spruce feathermoss domain. (C) Details of the four northernmost lakes, the circles represent a 30 km diameter zone used for extraction of fires that occurred between 1977 and 2016 (shown in red). (D) Details of the two southernmost lakes.

constant rate of supply (CRS) model (Oldfield and Appleby, 1984; Binford, 1990). By convention, 1950 AD (Anno Domini) = 0 BP (Before Present) and hereafter years BP will be used.

2.3. Charcoal data

Charcoal particles were extracted from a 1 cm^3 volume of sediment (gyttja) by soaking overnight in a 10% solution of NaClO to deflocculate the sediments and to bleach uncharred organic particles. The samples were then sieved at 150 μm in order to discard the smallest particles and organic matter. Charcoal particles were identified under a stereomicroscope coupled to a digital camera and then counted and measured using an image analysis software (WinSEEDLE, 2016). For each 0.5 cm subsample, charcoal particles were counted and the surface area measured, which allowed the calculation of particles median surface.

2.4. Fire data

(Hennebelle et al., 2020) have previously shown that the most important fire characteristics in explaining charcoal accumulation in lakes are fire surface area (burned area) and fire severity measured in a zone of 30 km radius around the lakes. Burned areas were extracted from open data of the Ministry of Forests, Wildlife and Parks of Québec (`https://www.donneesquebec.ca/recherche/fr/dataset/feux-de-foret`). Fire severities were calculated using LANDSAT images at 30 m resolution to calculate the dNBR index (differentiated Normalized Burn Ratio) (Lentile et al., 2006) which is linked to the quantity of above-ground biomass burned by a fire event (Cocke et al., 2005). The dNBR index is calculated using the following equations :

$$NBR = (NIR - SWIR)/(NIR + SWIR) \tag{3.1}$$

$$dNBR = NBR_{beforefire} - NBR_{afterfire} \tag{3.2}$$

where NIR is band 4 of the LANDSAT images and SWIR is band 7. $\text{NBR}_{beforefire}$ was measured as close as possible to the fire date and $\text{NBR}_{afterfire}$ was measured 1 year after the fire date. The sum of only the strictly positive (>0) dNBR value of the fire pixels that composed the fire severity variable was also used for calibration with charcoal metrics, (for further explanation on the fire data see Hennebelle et al., (2020)). We constrained the analysis of fire characteristics to the period 1977-2016 since no LANDSAT images were available before 1977 for the study area. We stopped the acquisition of fire data in 2015 since our field work started in early summer 2016 when the fire season had not started yet (Table S2.1).

2.5. Statistical analysis

2.5.1. *Individual site analysis*

As the six lakes we studied have different age-depth models, the charcoal records need to be interpolated at the same time scale in order to be able to compare charcoal accumulation between sites following the procedure described in Higuera et al. (2009) and Long et al. (1998). The interpolation was done using the pretreatment function of the paleofire package (Blarquez et al., 2014) in R 3.3.2 (R Core Team, 2018).

2.5.2. *Regional data analysis*

In order to analyze the regional charcoal signal in response to the fire events, we pooled the charcoal data of the six lakes. Before performing the analysis, charcoal data needed to be transformed since charcoal metrics can vary greatly from site to site (Power et al., 2008). This transformation is three-fold and comprised (1) a minmax transformation for rescaling the values, (2) a Box-Cox transformation to homogeneize site records variance and then (3) a rescaling transformation using Z-scores. Then the six charcoal records were combined using a bootstrap resampling procedure and a LOESS curve fitted to create the composite series. All these steps were performed using the *paleofire* R package and the procedure described in Blarquez et al. (2014). To investigate the links between fire characteristics and charcoal median surface area, charcoal number and surface area, linear regressions were performed. In order to evaluate the performance of the models, we used r^2 and P-values of the linear regressions.

2.6. Results

2.6.1. *Single lakes' links between charcoal accumulation and fire characteristics*

Records of the individual lake charcoal number influx are different in terms of amplitude (green lines in Figure 3.2) ; and the variations in amplitude are different from lake to lake even after interpolation (red lines). Similar observations are shown for charcoal surface area and median surface area influx (see Figure S3.1). Close sites such as Lakes Cacahuète and Ténia or Lakes Bécasse and Galinette respectively show different charcoal accumulation patterns (the red lines) as we could expect these to be similar. This shows the importance of a regional reconstruction of charcoal accumulation and fire characteristics. There is a general trend however that can be observed as an increase in charcoal number influx, regardless of the individual amplitudes, for Lakes Bécasse, Gitans and Ténia from 1970 to 2015.

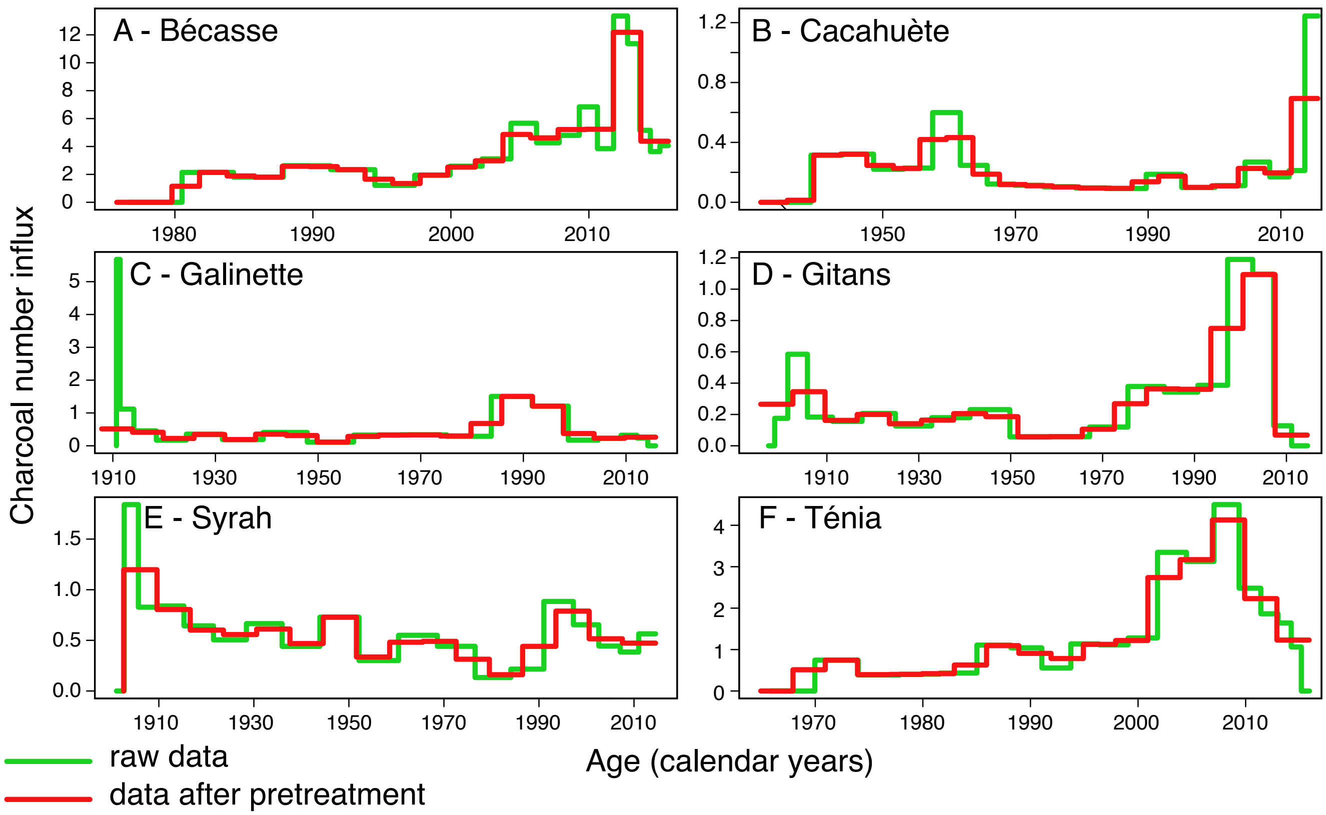

Figure 3.2. Charcoal number influx for the six lakes, raw data are shown in green and interpolated data are shown in red (interpolation = 2 years).

2.6.2. *Regional synthesis of charcoal accumulation and fire characteristics*

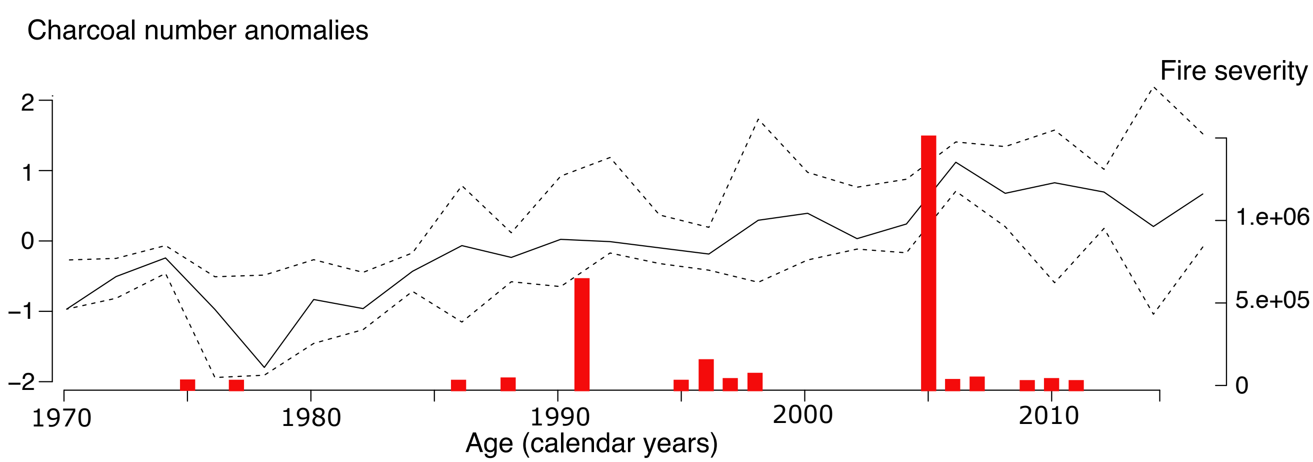

Figure 3.3. Charcoal number anomalies is showed as solid line, the dashed lines represent the 95% confidence interval calculated by a bootstrap resampling (1000 iterations). The vertical bars refer to the fire severity measured within the 30 km zone of all the lakes. Time is on the horizontal axis and years increase from left to right with 0 BP corresponding to 1950 calendar years by convention.

Charcoal number anomalies (Figure 3.3) show an increasing trend that seems coherent with the increase in fire severity (and number of fires) recorded during the 45 year study period. The maximal fire severity at -55 BP is quasi-synchronous with a maximum in charcoal number anomaly occurring in -56 with a 1-year time lag. This lag is in agreement with the 0 year time lag of Hennebelle et al., (2020) if the dating error is considered. The anomalies for charcoal median surface area and charcoal surface area are shown in (Figure S3.2) and followed the same trend. Although visually coherent, the results shown in (Figure S3.2) were only marginally significant when evaluated using linear regressions, likely owing to the low number of observations. Linear regression parameters were only marginally significant for charcoal number anomalies, respectively with fire severity (r^2=0.14, P-value=0.058) and with burned area (r^2=0.12, P-value=0.077). Linear regressions with charcoal median surface area and charcoal surface area showed no significant parameters.

Discussion

In this study we examined linear regressions between 1) charcoal measurements (number, surface area and median surface area) and fire characteristics. We also 2) explored the uncertainties on the links between sedimentary charcoal and fire characteristics due to the different taphonomic processes that affect charcoal particles from their production to their final storage in lake sediments. In boreal forest ecosystems, several authors have shown that charcoal accumulation can be statistically linked to fire events occurring within a 30 km radius zone around the lakes Hennebelle et al., 2020 , (Itter et al., 2017; Oris et al., 2014; Pisaric, 2002). For example, Hennebelle et al., (2020) were able to link charcoal median surface area with burned area and fire severity using charcoal traps. In the present study on sedimentary charcoal data, we only found marginally significant relationships, although the trends in charcoal accumulation and fire severity and burned area appeared coherent. We discuss below this apparent discrepancy in regard to the statistical pitfalls involved in this evaluation such as the low number of observations and the inherent variability associated with charcoal accumulation. We will thus focus our discussion on the taphonomic processes that blur the relationships between charcoal particles accumulated in sediments and fires due to production of charcoal particles, their transportation, the deposition and the conservation in the lacustrine archive.

The calibration of bioproxies demands a good understanding of particles taphonomy

As outlined by Figure 3.4, charcoal accumulation is well suited for the detection of individual fire events for three of our six study sites. Multi-site analysis is crucial for robust reconstructions of regional fire regimes in order to minimize the impact of site related taphonomic processes (Higuera et al., 2009; Long et al., 1998). The taphonomy of lacustrine charcoal particles is a multi-processes mechanism (Conedera et al., 2009) and until now calibration studies did not consider a comprehensive overview of all the processes involved in charcoal taphonomy. Adolf et al. (2018) studied temperate forests in Europe and showed that charcoal accumulation is primarily related to fire number then fire intensity and lastly burned area. On the other hand, Duffin et al. (2008) in their study of grass-dominated ecosystems located in South Africa showed that burned area and fire intensity controlled charcoal accumulation. The source area of charcoal particles has been evaluated based on particle motion models (Peters and Higuera, 2007; Clark, 1988), but uncertainties remain in the way particles are transported by wind or by water bodies. Carcaillet et al. (2007) showed, for example, a sequence of charcoal accumulated in cave sediments located in France that could only be transported by water bodies. On the contrary in flat boreal landscapes and with head-water lake sediments, transport should be dominated by wind (Hennebelle et al., 2020). These examples show that understanding the taphonomy of bioproxies from production to storage is not easily done nor trivial and that multiple sources of variation and uncertainties must be considered to better understand the between-site variability recorded in the present study.

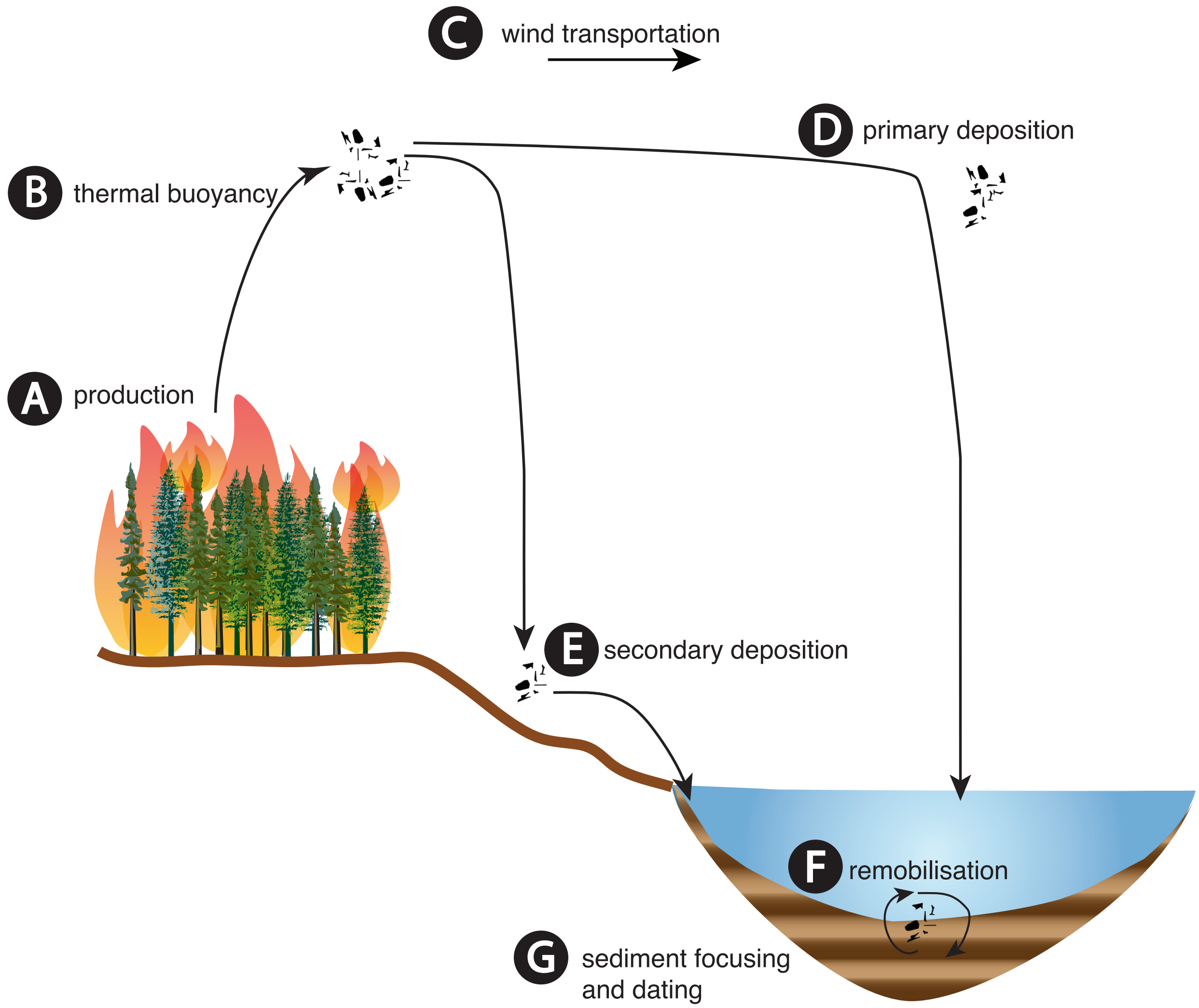

Figure 3.4. Block-diagram of charcoal taphonomic processes from production site to final deposition in a lacustrine sedimentary archive : (A) The quantity of charcoal produced by a fire depends on the quantity of biomass burned, thus the surface area of the fire (Higuera et al., 2010) and also its severity (Higuera et al., 2005). (B) The thermal buoyancy depends on the fire intensity and determines the height of injection of particles into the fire plume (Val Martin et al., 2010; Clark, 1988). (C) The wind speed, as well as the injection height, will determine the potential distance of transportation of the particles (Peters and Higuera, 2007; Clark, 1988). (D) and (E) The primary transportation is mostly due to wind. Particles from the lake littoral can also be washed in with a potential lag after the fire event (Whitlock and Millspaugh, 1996). (F) The reworking of sediments at the sediment-water interface is due water circulation (Bradbury, 1996) and to bioturbation and can generate mixing between the upper layers of sediments (Carcaillet et al., 2002). (G) Sediment focussing (Giesecke and Fontana, 2008) and conservation will determine the stratigraphy of the sediments and thus influence the dating precision. The establishment of core age-depth models relies on ^{210}Pb detection (Appleby, 1997) with its own taphonomic issues.

Charcoal production and particles uplift

To calculate fire severity we used the dNBR index that measures the quantity of above-ground biomass lost during a fire event (Key and Benson, 2006). It is thus reasonable to assume that above-ground biomass loss is proportional to the amount of charcoal produced (Figure 3.4A). In boreal

ecosystems this assumption has been verified using trapped charcoal surveys (Hennebelle et al., 2020), sedimentary charcoal and remote sensing (Adolf et al., 2018; Duffin et al., 2008). However, our regression results show that burned area and fire severity are only weakly related to the number of charcoal particles found in lake sediments while the trends appear coherent (Figure 3.3). These weak statistical relationships may be caused by several factors. Firstly, the number of observations is relatively small (38 fires) for the study period, possibly obscuring a real relationship that would be apparent for a larger set of fires and sites. Secondly, the charcoal production process might be modified by other taphonomic processes, namely : transport, capacity to capture particles, with various experiment devices, and most likely charcoal focusing and conservation in sediment (Conedera et al., 2009; Higuera et al., 2007).
Figure 3.2 shows that for relatively close sites (Figure 3.1) within similar physical environments, the charcoal signals are quite different, thus showing that we cannot ignore the processes that happen within the nearby lakes edges or within the water column and at the sediment-water interface (Conedera et al., 2009). Indeed, Courtney Mustaphi et al. (2015); Whitlock and Millspaugh (1996) noticed that sediment focusing (Figure 3.4F) can transport sediments, and thus charcoal particles, from shallower to the deepest part of lakes. This transportation induces a time lag between the fire event and the deposition of charcoal particles in the sediments. Sediment reworking has also been observed via water circulation between the lake surface and the sediment-water transition (Hostetler and Bartlein, 1990) or via bioturbation (Bump et al., 2017). Charcoal focusing and conservation remain difficult to evaluate quantitatively for individual sites and we cannot directly attribute a portion of the observed sites' variability to these processes. On the other hand, the capacity of capturing particles should be directly related to lake size, a mechanism demonstrated for pollen (Sugita, 1993; Hjelle and Sugita, 2011). In our study, the lake size varied by a factor of 25, ranging from 0.18 to 4.5 ha, which likely explains the tenfold absolute variation in charcoal influx ranging from 1.2 $\#.cm^{-2}.yr^{-1}$ at Lakes Cacahuète and Gitans to 12 $\#.cm^{-2}.yr^{-1}$ at Lake Bécasse.

Charcoal particles transportation by wind

Figures 3.2, S3.2A and S3.2B, respectively, charcoal number, charcoal surface area and charcoal median surface area anomalies, show relatively dissimilar anomalies for closely located lakes contrary to what would have been expected. This could be due to the relatively weak relationship between fires happening close to a lake and charcoal accumulation that could be related to these fires. In that case, the detection of a close fire can rely on the secondary deposition (Figure 3.4E). Fire intensity has been proved to be linked to charcoal size (Adolf et al., 2018), but also refers to the energy released by the fire line (Keeley, 2009), that in turn influences the thermal buoyancy of charcoal particles (Figure 3.4B) and the height of plume (Vachula and Richter, 2018). Charcoal particles will then be transported and diffused by the wind (Figure 3.4C). Depending on the particle size, the plume height and the wind speed, particle deposition (Figure 3.4D) can start between 50 to 10, 000 meters from the fire edge (Peters and Higuera, 2007). Based on the particle motion equations developed by Clark (1988) and Peters and Higuera (2007) (see equations in SI), we modeled charcoal transportation (Figure 3.4B, C and D) and deposition from a hypothetical fire of 1 × 1 pixel (Figure 3.5) that could occur in a boreal ecosystem.

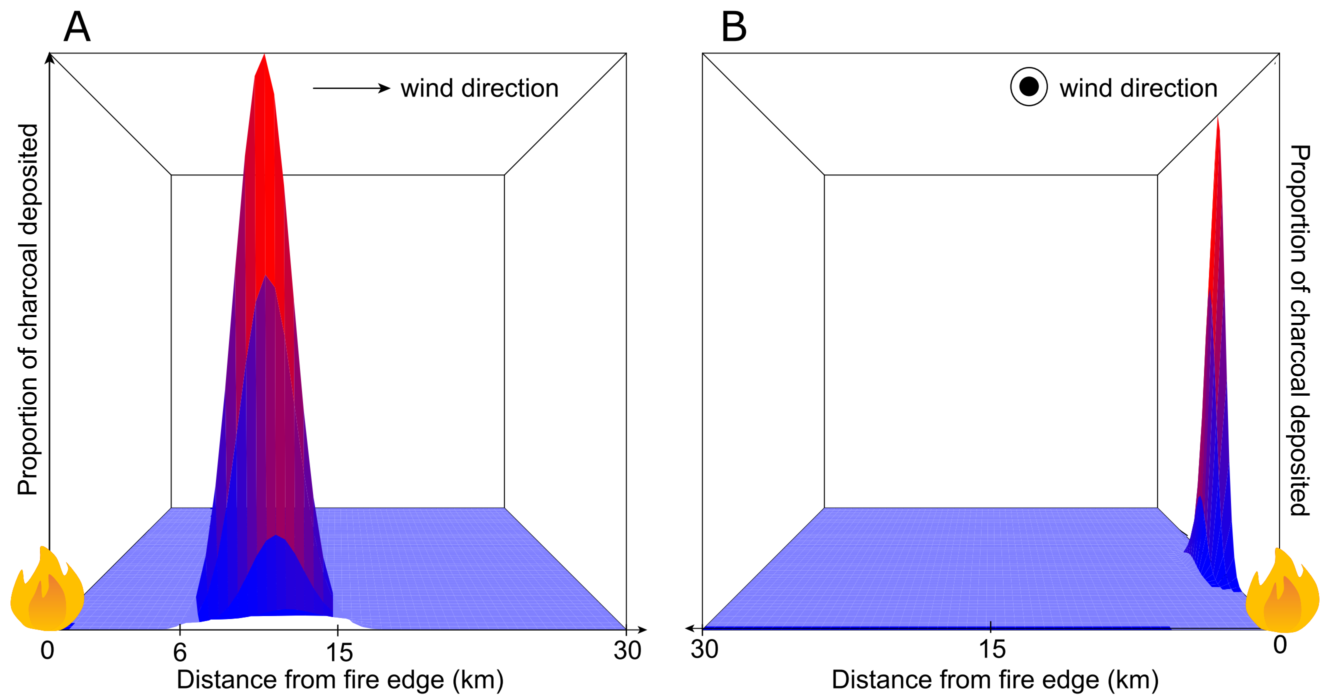

Figure 3.5. (A) Downwind transportation (horizontal axis) and deposition (vertical axis) of charcoal particles. (B) Perpendicular to wind direction transportation (horizontal axis) and deposition (vertical axis) of charcoal particles. Blue to red color gradient refers to the relative quantity of charcoal deposited.

The modelling experiment shows that downwind charcoal deposition begins around 6 km from the fire edge and ends around 15 km from the fire edge with a maximum around 10 km (Figure 3.5A). This experiment also shows that crosswind deposition is contained within 2 km from the main downwind direction (Figure 3.5B). These results agree with those of Peters and Higuera (2007). This modelling experiment is nonetheless a simplification of the mechanisms responsible for charcoal transportation by wind and does not include for example, changes in wind direction during fire events. Although wind direction may be estimated based on the prevailing winds in the region that are from the North to North-East, this direction is not necessarily accurate for the past fire events, since wind direction depends on the concurrent atmospheric conditions during the fire events. Other landscape features such as valley orientation are known to affect fire attributes such as size, shape and orientation, which in turn are also likely to affect charcoal particle transport (Mansuy et al., 2014). Finally during extreme fire-weather conditions, large and severe fires may create their own weather, that thus sustains high winds, which is a process that is also likely to affect in an unquantifiable way the charcoal transportation and thus sedimentary influx.

Uncertainties on ^{210}Pb dating of sediments

Dating sediment cores (Figure 3.4G) can result in uncertainties in fire event chronologies and lags with charcoal measurements in core sections. Dating is based on the decay of ^{210}Pb that has been used since the 1960's (Robbins and Herche, 1993). The CRS Model is also widespread for building age-depths models out of ^{210}Pb sediment dating but has some uncertainties (Binford, 1990).

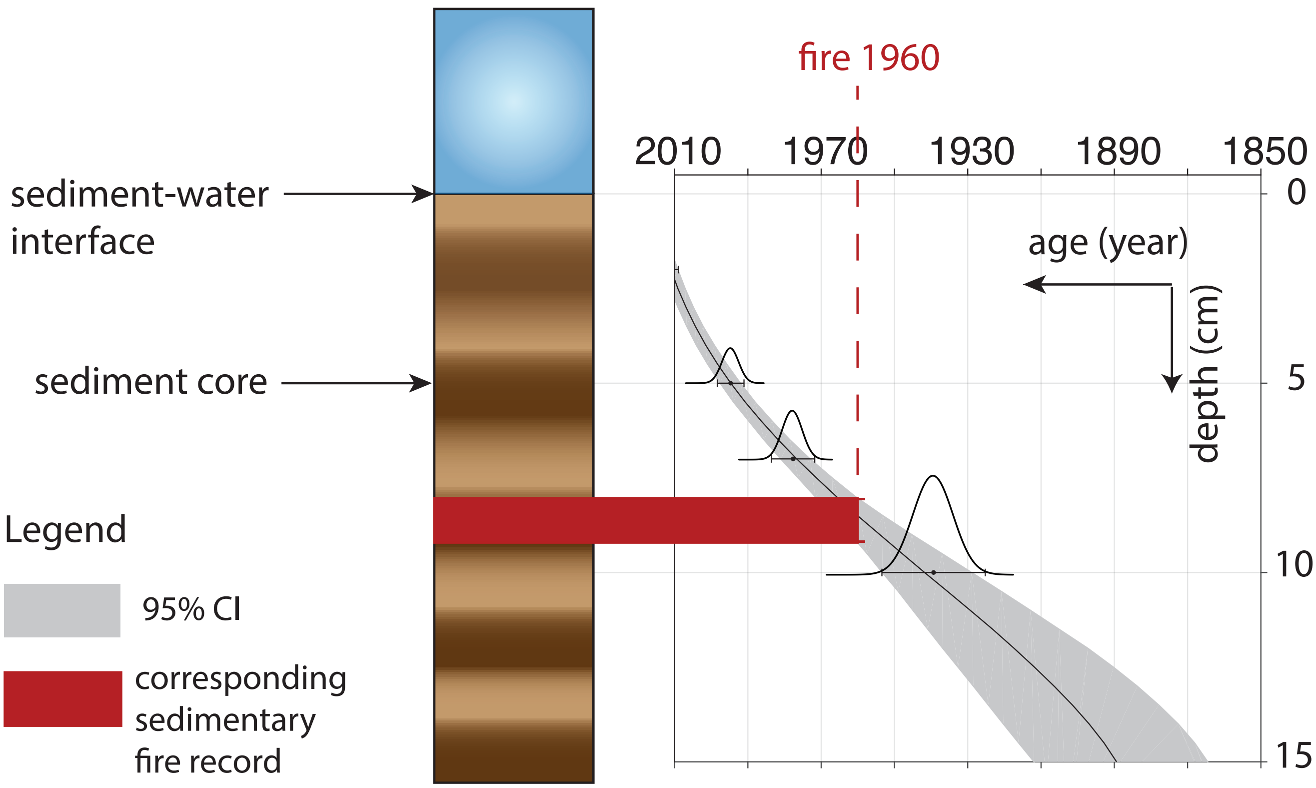

Figure 3.6. Representation of ^{210}Pb dating uncertainties with the example of one of our sediment short cores. We used a theoretical fire which would have occurred in 1960 to show the corresponding core section in which the charcoal particles would be buried in according to the uncertainties of the age-depth model.

Due to these uncertainties in ^{210}Pb dating, the recording of charcoal influx generated by a fire event can overlap several sub-samples of the sediment core (Figure 3.6). Blaauw (2012) suggested a manual fitting, called tuning, between, for example, the charcoal archives and a time series of fire characteristics either by smearing out (considering as synchronous a fire event and a peak of charcoal accumulation that seems asynchronous) or sucking (separating a fire event and a peak of charcoal accumulation that seemed synchronous) of events observed in the two sequences that can be useful when one knows that the age-depth model, based on ^{14}C dating, is not entirely reliable. Nevertheless, this method must be used carefully since it is based on an author's expertise on the synchrony of the phenomena and should thus be based on multi-proxy reconstructions to avoid any misleading conclusions due to single proxy analysis (Blaauw, 2010).

Conclusion

Reconstructing burned area and fire severity and understanding their respective influence on vegetation is of interest for studying, planing or managing ecosystems under the influence of ongoing changing climate. Paleoecology can help to reconstruct past dynamics of ecosystems under various climate conditions. But multi-proxy and multi-site reconstructions are still challenging in the quest of a consistent ecosystem dynamic history at a regional scale due to the taphonomic processes that affect the proxies. Calibration studies should help to better understand these taphonomic processes based on current environment-proxy interactions. This study explored fire characteristic-sedimentary charcoal relationships for six lakes in the Québec western spruce feathermoss domain. We found promising linear regressions linking charcoal number and fire severity and burned area that should be used to quantitatively reconstruct long-term fire characteristics based on sedimentary charcoal. We highlighted the shortcomings and pitfalls of calibration due to taphonomic processes affecting charcoal particles and discussed them using our methodology developed in this paper and various key papers that were previously not considered as a whole for a more complete understanding of charcoal particles' taphonomy. Subsequent studies should consider these outcomes in order to strengthen long term ecosystem dynamic reconstructions.

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Supplementary material

Tableau S3.1. Description of fire characteristics (fire severity and burned area) that occurred around the lakes

Lake name	Year	Fire severity	Burned area
Bécasse	1988	946.8	5406270.2
	1991	166.4	780858.6
	1998	18397	51249737.7
	2005	243136.4	548539306.7
	2006	3519	6469636.5
Cacahuète	1977	585.5	7447911.3
	1988	2232.7	4613175.2
	1991	257769.7	555263625.4
	1995	5	302974.8
	1996	32836.7	83967185
	2005	340486	571490334.3
	2006	5.8	956637.3
	2009	109.9	175030.4
	2010	3150.8	11656366.3
Galinette	1988	946.8	5406270.2
	1991	25.4	174072
	1998	18397	51138404
	2005	232884	477636833.7
	2006	179.1	242090.2
Gitans	1991	46792.8	108814794.7
	1996	18044.5	44341906.5
	1997	3920.3	9051758.1
	2005	141960.4	194353132.1
	2007	311.8	610270.2
	2010	2541.8	9796699.7
	2011	1307.9	4544874
	2014	0	44308.3
Syrah	1986	1260.6	3081058.6
	1991	47071.5	109795311.6
	1995	111.3	1048569.7
	1996	39607	107536529.8
	1997	3891.1	8579359.6
	2005	168891.2	284142192.1
	2007	16714.9	31293450.5
	2010	2541.8	9796699.7
	2014	0	44308.3
Ténia	1975	0	10768.3
	1977	585.5	7447911.3
	1988	1721.3	997897.8
	1991	257922.9	561322334.2
	1995	4.9	302974.8
	1996	32789.9	82548843.1
	2005	352411.3	566638106.7
	2006	5.8	956637.3
	2009	109.9	175030.4
	2010	3150.9	11656366.3

Individual lake charcoal measurements influx

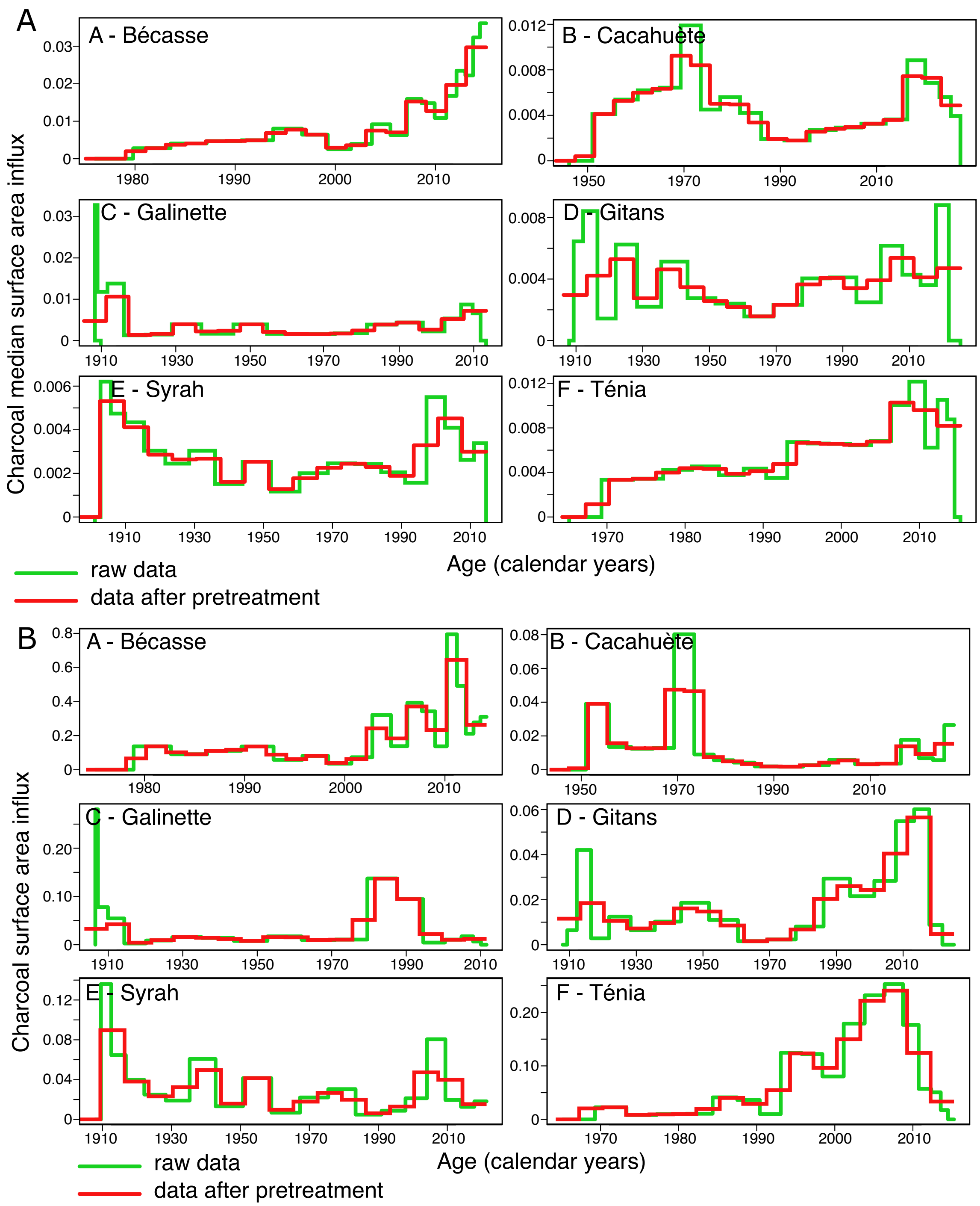

Figure S3.1. (A) Charcoal median surface area influx and (B) charcoal surface area influx for the six lakes, raw data are shown in green and interpolated data are shown in red (interpolation = 2 years).

Charcoal median surface area influx amplitudes (Figure S3.1A) show less variation than charcoal number influx (Figure 3.2 2) and for charcoal surface area (Figure S3.1B). Unlike for charcoal median surface area, charcoal surface area influx shows a similar trend to charcoal number influx with an increase from -20 BP to -65 BP.

Regional synthesis of charcoal anomalies and fire characteristics

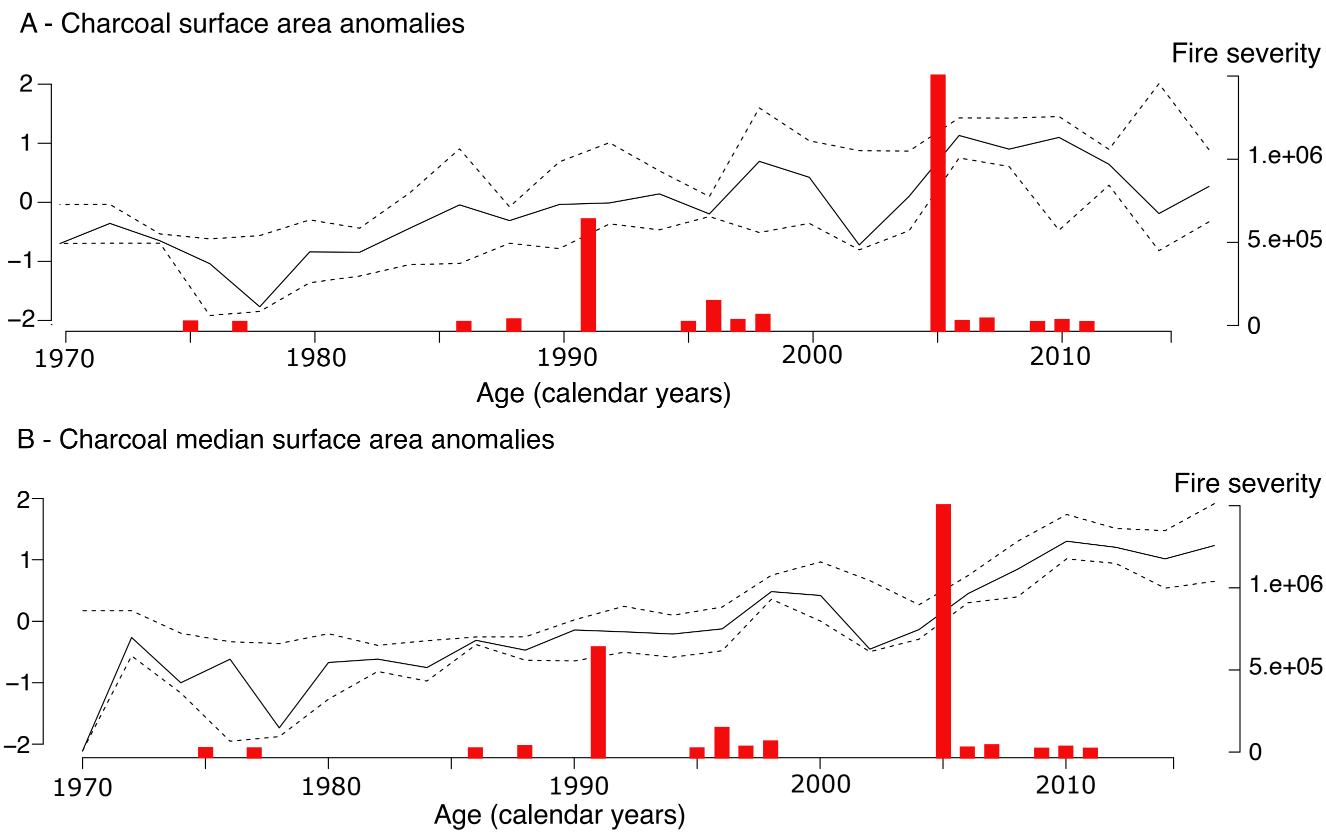

Figure S3.2. (A) Charcoal surface area anomalies and (B) charcoal median surface area anomalies are shown as solid line, the dashed lines represent the 95% confidence interval calculated by a bootstrap resampling (1000 iterations). Vertical bars refer to the fire severity measured in the 30-km zone of all the lakes.

Uncertainties on ^{210}Pb dating of sediments

In order to improve the links between charcoal particles' measurements and fire characteristics we suggest a method that aims at correcting the overlapping of fire events

The CRSModel developed in Matlab calculates unsupported Pb by averaging the Pb activities on selected dated levels (usually all levels but essentially the two last) in order to identify where in the core the activity of ^{210}Pb is too low to be measured. Knowing the date of extraction of the core, we are able to attribute an average age to this section. Based on the Pb activity measured at the top of the core and at the limit of detection, we are able to attribute a date to the intermediate sub-samples for which the ^{210}Pb activity has been measured. Between those dated sub-samples, the model interpolates the age in order to build the age-depth model. To do so, the intermediate ages are determined using a pool of 1000 age depth-models and a Monte-Carlo method is used to interpolate to calculate the 95% confidence interval following a normal distribution. The CRS Model developed in Matlab has been modified to consider all dated levels but the last, thus including the penultimate one as it was not with the original code. We used the same Monte Carlo method to calculate, not only the 95% CI but also the interval that corresponds to a 1σ distance from the median age-depth model. Knowing that, we calculated for each sub-sample of the core its average age and its standard deviation based on the mathematical theorem that says that the average of two normal distributions is the average of the parameters (mean and standard deviation) of the two initial normal distributions.

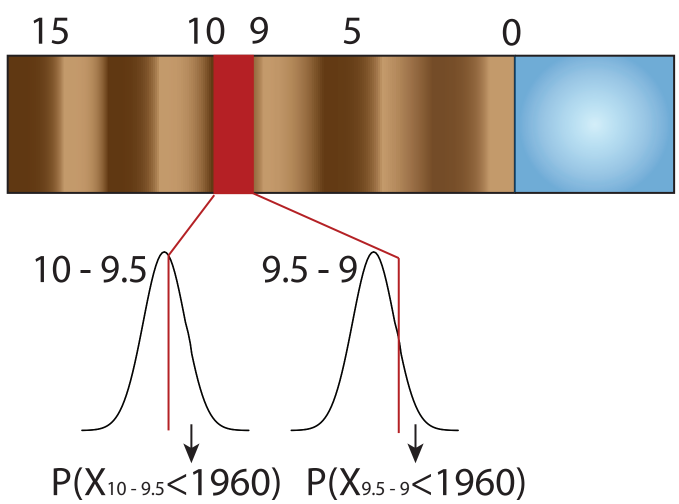

Figure S3.3. Illustration of the calculation of (P(X<YOF)) to be used as an age-depth model correction for charcoal metrics.

Thus, we were able to calculate the probability for the year of a fire (YOF) to be included in each sub-sample (P(X<YOF)) considering that the age follow a normal distribution for which we know the parameters to calculate the probability (Figure S3.3). We then multiplied the charcoal metric by the coefficient given by the calculated probability divided by the sum of all the probability obtained for a given fire year.

Equation of airborne transport adapted to boreal forest ecosystems

Equations of transportation and diffusion of charcoal sized particles

$$\chi(x,y) = \frac{2v_g Q(x)}{u\pi C_y C_z x^{2-n}} exp\left(\frac{-y^2}{C_y^2 x^{2-n}}\right) exp\left(\frac{-h^2}{C_z^2 x^{2-n}}\right) \tag{3.3}$$

$$Q(x) = Q_0 exp\left\{\frac{4v_g}{nuC_z\sqrt{\pi}}\left[-x^{n/2}e^{-\xi} + \left(\frac{h}{C_z}\right)^{2m} \times (\Gamma(-m+1) - \Gamma_\xi(-m+1))\right]\right\} \tag{3.4}$$

$$m = \frac{n}{(4-2n)} \tag{3.5}$$

$$\xi = \frac{h^2}{x^{2-n}C_z^2} \tag{3.6}$$

$$(\Gamma(-m+1) - \Gamma_\xi(-m+1)) = -m\int_\xi^\infty e^{-t}t^{-m-1}dt \tag{3.7}$$

List of equation components

χ represents the quantity of charcoal particles deposited in the coordinates (x,y)

x = downwind distance (m)

y= crosswind distance (m)

v_g = deposition velocity of particles ($m.s^{-1}$) = 1.56 (Lynch et al., 2004)

Q(x) represents the relative quantity of particles that are trasported beyond x

Q_0 represents the initial quantity of particle emitted = 1

u = wind speed ($m.s^{-1}$) = 5 (Sutton, 1947) usualy comprised between 5-10 $m.s^{-1}$ (Taylor et al., 2004)

C_y = diffusion constant equals to 0.21 $m^{\frac{1}{8}}$ (Sutton, 1947)

C_z = diffusion constant equals to 0.12 $m^{\frac{1}{8}}$ (Clark, 1988; Sutton, 1947)

n=1/4 n represents the measurement of the turbulence near the ground (Sutton, 1947)

h= height of injection of charcoal particles is 879 m (Val Martin et al., 2010)

Conclusions et discussions

Bilan général des apports des chapitres

Chapitre 1

Le premier chapitre de la thèse visait à explorer et démontrer le potentiel d'utilisation des études paléoécologiques pour l'aménagement écosystémique des forêts du sous-domaine bioclimatique de la pessière à mousses de l'Ouest (PMO). Il s'agissait de montrer que les outils actuellement utilisés par les aménagistes pour établir les plans d'aménagement, comme le cycle de feu et le pourcentage de vieilles forêts, pouvaient être reconstruits sur plusieurs millénaires via des méthodes de paléo-écologie. L'intérêt d'utiliser des données paléoécologiques est qu'elles permettent de reconstruire les dynamiques de ces écosystèmes sur plusieurs millénaires et de porter un regard critique sur les cibles d'aménagement écosystémiques établies sur la base de données récentes (Figure C.1).

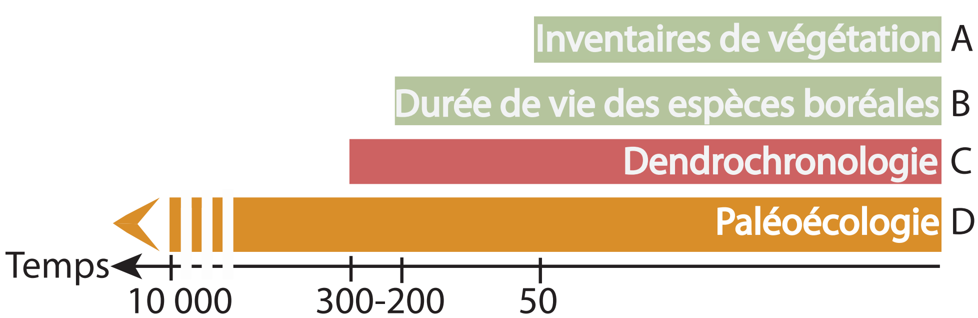

Figure C.1. Représentation graphique de la profondeur temporelle relative des différents types de données utilisées pour l'établissement des cibles d'aménagement écosystémique. En vert sont représentées les données de végétation avec (A) les inventaires de végétation décennaux qui ont débuté dans les années 1970 et (B) la durée de vie moyenne de certaines espèces boréales parmi les plus longévives. En (C) est représentée la profondeur temporelle des données dendrochronologiques qui permettent de reconstruire le cycle de feu et en (D) la profondeur temporelle des données paléoécologiques.

1- L'hétérogénéité paysagère contemporaine s'est implantée dès le début de l'Holocène

Nous avons montré que la végétation que l'on observe actuellement dans la PMO est hétérogène. L'action combinée du climat, des variables du milieu physique ainsi que des perturbations naturelles et anthropiques ont favorisé la distinction de territoires aux caractéristiques similaires. Ainsi, la portion Nord (zone 1 de la Figure 1.1) se caractérise par une dominance de pinèdes grises. Dans l'Est (zone 2), la répartition de la végétation est fortement conditionnée par un gradient altitudinal. La toposéquence de ce territoire se compose des platières de sable couvertes de pin gris, des bas-versants constitués de pessières noires à pin gris, des mi-versants dominés par les pessières à sapin puis des sommets de sapinières à bouleau blanc. Dans la plaine argileuse de l'Abitibi (zone 3), les forêts sont principalement constituées de peuplier faux-tremble, de pin gris et d'épinette noire. Dans la partie Ouest (zone 4), là où les tourbières dominent, l'épinette noire abonde et les processus de paludifications primaire et secondaire sont actifs. Chacuns de ces territoires ainsi que les divers segments de la toposéquence ont évolué d'une manière spécifique au cours de l'Holocène. Cette hétérogénéité doit être prise en compte en aménagement pour respecter la diversité écosystémique. Des modalités spécifiques d'aménagement forestier doivent être définies pour chacune de ces entités afin d'assurer leur durabilité.

2- Une dynamique spécifique à chaque territoire

Nous avons montré que des périodes spécifiques de végétation s'étaient succédées durant l'Holocène, ce qui a mené à la détermination de trois types de dynamiques de végétation. Le premier type, découlant principalement de l'analyse des lacs Pessière et Cèdre, met en évidence les périodes suivantes : 1) un début de l'Holocène caractérisé par une afforestation dominée par les espèces de début de succession, notamment de pin gris et de peuplier faux-tremble 2) une période subséquente dans laquelle les espèces tempérées étaient bien représentées (Hypsithermique : 7000-3500 BP) et 3) une période plus récente (Néoglaciaire : depuis 3500 BP) où la végétation boréale telle qu'on la connaît aujourd'hui s'est mise en place. Le second type de dynamique se distingue du premier type principalement par l'absence de la période d'espèces tempérées. Néanmoins, une augmentation du pin gris est visoble dans les derniers millénaires et notamment depuis environ 1800 BP, cette période est appelée la Boréalisation. Le troisième type montre une abondance initiale de pin gris qui se poursuivra et s'amplifiera jusqu'à nos jours. Chaque type de dynamique forestière est associé aux différents territoires définis dans la section précédente. En d'autres termes l'hétérogénéité observée aujourd'hui s'est mise en place tôt dès les premières phases de l'afforestation. Des liens entre les divers territoires, leur dynamique holocène et la gestion forestière ont été définis.

3- Une proportion élevée de vieilles forêts s'est maintenue tout au long de l'Holocène

Nos résultats montrent qu'avec une cible de maintien de 49% de vieilles forêts (forêts de plus de 100 ans), la cible fixée par le MFFP respecte la variabilité pluri-millénaire moyenne des écosystèmes. Cependant par le passé et en fonction des territoires, la proportion de vieilles forêts dans le paysage a pu être plus importante. L'une des améliorations possibles de ces cibles serait de prendre en compte les variations plus régionales (4 territoires) et locales (échelle de la toposéquence) des écosystèmes pour l'établissement des cibles d'aménagement.

4- Les interrogations soulevées par ce chapitre

Ce premier chapitre a aussi permis de soulever des interrogations relativement à l'interprétation des principaux bio-indicateurs retrouvés dans les sédiments lacustres, soient le pollen et les charbons. Ces indicateurs ont été à la base des réflexions de la suite du doctorat. En effet, nous avons pu observer que durant plusieurs périodes, le signal de charbons montrait des feux rares (FRI long) alors que le signal de pollen indiquait quant à lui une plus grande abondance de taxa correspondants à des espèces de début de succession, et inversement (Figure C.2, voir les diagrammes polliniques et les données sur les charbons de bois de chacun des lacs en annexe du ***Chapitre 1***). Il y a donc des inadéquations entre les interprétations de ces deux bio-indicateurs (pollen et charbons) ce qui nous amène à nous questionner sur la production, le transport et le dépôt des charbons de bois : est ce que les signaux de charbons et de pollen enregistrés dans les sédiments lacustres proviennent des alentours du lac (origine locale) ou de plusieurs kilomètres ou dizaines de kilomètres (origine régionale) ? Y a-t-il un lien entre la sévérité et la surface des feux et la quantité de charbons de bois déposée dans les lacs ?

Chapitre 2

L'ensemble des phénomènes qui affectent les bio-indicateurs entre le moment où ils sont produits et le moment où ils sont stockés dans une archive, y compris le transport, constitue ce que l'on appelle la taphonomie. Le second chapitre de la thèse a ainsi exploré les processus taphonomiques qui affectent les particules de charbons de bois que l'on retrouve au niveau des lacs. Plus précisément, il s'agissait de comprendre l'origine des particules de charbons qui se déposent dans les sédiments lacustres. Nous avons pu montrer que le principal mode de transport des particules de charbons dans notre contexte géographique de l'Ouest de la PMO est le vent. Ces particules, déposées en une année à la surface des lacs, ont été décrites en fonction de leur nombre, de leur surface et de leur surface médiane. Dans ce chapitre nous avons démontré que cette dernière variable est liée aux feux ayant eu lieu jusqu'à 30 km autour des lacs lors de l'année en cours. Nous avons pu démontrer que les modulations du signal de charbons observées sont statistiquement associées à la surface brûlée par un feu ainsi qu'à sa sévérité. En résumé, plus un feu est étendu et plus il brûle de la végétation (sévère), plus il va émettre des particules de surface médiane élevée qui pourront se déposer sur un lac qui peut se situer jusqu'à 30 km de distance.
Ensuite, pour poursuivre dans notre objectif de mieux comprendre comment les processus taphonomiques affectent le signal de charbons, nous avons voulu étudier les biais taphonomiques induits par la sédimentation des particules et leur incorporation au sédiment.

Chapitre 3

En nous basant sur les résultats du second chapitre, nous avons donc cherché à comprendre à quel point le processus d'incorporation des particules de charbons dans les sédiments est en lien avec les feux contemporains. Pour ce faire, nous avons comparé 1) l'accumulation de particules de charbons dans les sédiments récents avec 2) les feux pour lesquels la surface et la sévérité ont été calculées pour les 40 dernières années dans l'Est de la PMO. Les résultats confirment les liens que nous avions obtenus dans le ***Chapitre 2***, à la différence que ces liens statistiques ne sont que marginalement significatifs entre, d'une part, le nombre de particules mesurées dans les sédiments de surface et, d'autre part, la surface et la sévérité des feux récents. Ainsi, au regard de la littérature qui porte sur la calibration en paléoécologie, nous avons mis en évidence les difficultés auxquelles sont confrontées de telles études tout en soulignant les connaissances qu'elles ont déjà apportées à la compréhension de la taphonomie des particules de charbons. Les résultats ainsi que leur analyse soulignent le potentiel de l'utilisation des outils de la paléoécologie pour établir des reconstructions toujours plus précises des écosystèmes du passé afin de mieux comprendre les écosystèmes actuels et leur devenir.

Discussion

L'ensemble de ces résultats (***Chapitres 1 à 3***) ainsi que l'expérience de mon doctorat m'ont permis de développer une expertise dans l'analyse de données paléoécologiques de plusieurs natures (données sédimentaires, pièges à particules) qui correspondent à plusieurs échelles temporelles (de l'échelle plurimillénaire à annuelle), sur plusieurs territoires qui composent la zone d'étude. Chaque territoire possédant ses spécificités en terme de composition, de climat, de milieu physique et de perturbations.

La section qui suit aborde des éléments de méthodologie, de résultats et des points de discussions soulevés dans mes trois chapitres afin de les replacer dans un contexte plus général.
Le premier objectif de ce doctorat était de mettre en évidence la pertinence des études paléoécologiques pour la compréhension des écosystèmes actuels principalement dans un objectif d'amélioration de la gestion. Cet objectif peut être résumé sous la forme : **Joindre le passé et le présent**.

Le second objectif s'est développé suite à l'observation d'incohérences dans les signaux de bio-indicateurs sur de longues séquences temporelles. Il s'agissait de mieux comprendre les processus taphonomiques qui influencent les particules de charbon de la production, au transport et jusqu'au dépôt dans les sédiments lacustres. Cet objectif peut être résumé sous la forme : **Joindre le spatial et le temporel**.

Réconciler le passé et le présent

Discontinuité entre les reconstructions paléoécologiques et l'état actuel des écosytèmes...

...dans la compréhension de la végétation :

Trois principaux messages peuvent être tirés des divers types de dynamique forestière définis dans la PMO au regard de l'aménagement forestier.

Le premier porte sur la régionalisation des écosystèmes : Cette démarche de régionalisation fait écho à l'établissement des différents niveaux de perception de la végétation du Québec dont fait partie la PMO (Saucier et al., 2009). La considération des interactions entre végétation et milieu physique, climat, perturbations avait permis de mettre en évidence des découpages encore plus fins (Grondin et al., 2007). Cette méthode, reprise dans la ***Chapitre 1***, a permis de définir 4 zones et de montrer leur stabilité à long terme. L'intérêt de reprendre une telle zonation est de souligner l'existence d'une diversité écosystémique locale à laquelle nous avons donné une profondeur temporelle (voir la section bilan sur les chapitres). L'efficacité à long terme et la pertinence des mesures mises en place pour la préservation des écosystèmes sont tributaires de ces connaissances (Gillson, 2009). Cette démarche de lier le passé et le présent dans un but d'amélioration de l'aménagement est peu commune dans la littérature, mais son potentiel a été souligné à plusieurs reprises (Gillson and Marchant, 2014; Birks, 2012; Gillson, 2009; Gauthier et al., 2008).

Le second message est que dans le contexte des changements climatiques, les espèces tempérées (pin blanc, thuya...), aujourd'hui retrouvées plus au Sud, auraient le potentiel de s'étendre plus au Nord soit jusque dans la portion Sud du la PMO. Ces espèces coloniseraient donc à nouveau des territoires où elles ont déjà été présentes au cours de l'Holocène ce qui soulève des questions en terme d'aménagement (Périé and de Blois, 2016). On peut notamment se demander si des stratégies facilitant la migration des espèces tempérées ne devraient pas être développées.

Le troisième message est que pour la majorité du territoire de la PMO, la progression du pin gris risque de se poursuivre si l'augmentation des feux estimée se produit (Boulanger et al., 2014; Girardin and Mudelsee, 2008). Dans les territoires les plus affectés, comme la zone 1, et possiblement ailleurs sur le territoire, ce sont les processus d'ouverture des forêts qui pourraient se mettre en place. Ces processus sont déjà en cours (Girard et al., 2011) et ils pourraient s'intensifier. Dans plusieurs paysages, les espèces de début de succession (peuplier faux-tremble, bouleau à papier, pin gris) pourraient devenir encore plus abondantes.

Ainsi, chaque dynamique forestière que nous avons identifiées nous informe sur les processus qui ont marqué l'évolution des paysages au cours de l'Holocène. Et chacuns de ces types est en lien avec des éléments relatifs à la gestion forestière et les changements climatiques à venir.

...pour la reconstruction des feux :

Qui a révélé des périodes aux régimes de feu distincts mais dont les comparaisons entre régions ne montrent pas de différence notable.
Problème 1 :
La reconstruction des FRI pour les 4 zones identifiées dans le ***Chapitre 1*** (Figure 1.1) ne montrait pas de différence significative entre les zones. Or nous savons qu'à l'actuel la zone 1, au Nord de la PAMO, est appelée « triangle de feu » et est marquée par des cycles de feux courts par rapport à la moyenne de la PMO (Portier et al., 2016; Gauthier et al., 2015). Au contraire, la zone 4 (abondance de tourbières) est actuellement caractérisée par des cycles de feux très longs. Ainsi, le pourcentage de vieilles forêts aurait dû être plus élevé dans la zone des tourbières et plus court dans le triangle de feu.

Problème 2 :
Lorsqu'on analyse conjointement plusieurs indicateurs, comme par exemple dans le ***Chapitre 1*** le pollen et les charbons, il peut y avoir des incohérences entre les reconstructions de la dynamique de végétation et du régime de feu. En effet, les reconstructions peuvent associer des signaux polliniques pouvant être interprétés comme des forêts de début de succession avec des signaux de charbons qui révèlent des périodes aux FRI longs (feu peu fréquents).
Sur la Figure C.2 nous voyons que depuis les 1000 BP dernières années l'occurrence de feu tend à diminuer (B). Or le graphique (D) montre que depuis la même période, l'abondance de *Pinus banksiana*, considéré comme un taxon de début de succession, a augmenté (Payette, 1993). Les reconstructions (C) permises par les travaux de calibration réalisés dans le ***Chapitre 2*** montrent quant à elles une augmentation de la sévérité. La sévérité et la surface brûlée étant liées (Figure S2.3) cela suggère un changement dans le régime des feux jusqu'alors non visibles uniquement par l'analyse du FRI. Cette hypothèse serait plausible, mais elle suppose que le FRI demeure relativement court ce qui favoriserait le renouvellement des cohortes de pin gris. Mais deux éléments viennent mettre à mal cette hypothèse. Le premier est que les analyses réalisées en considérant les charbons dans les sols minéraux suggèrent une augmentation des feux dans les derniers millénaires. Il y a donc ici des réponses contradictoires selon le type d'archive. Le second élément est que d'autres études que la nôtre (Remy et al., 2017) portant sur les sédiments lacustres montrent que des feux peu fréquents mais sévères pourraient caractériser la PMO. Or cette même étude montre des fréquences, surfaces et sévérité de feux globalement plus importantes dans la Pessière à mousses de l'Est que dans la section Ouest. Cette conclusion ne correspond pas à l'état actuel des écosystèmes caractérisés par relativement peu de pin gris dans l'Est comparativement à l'Ouest où il abonde. Ce deuxième élément montre possiblement que les processus taphonomiques des sédiments lacustres sont encore trop méconnus pour définir un régime de feu basé uniquement sur le FRI reconstruit à l'aide du logiciel CHARanalysis.

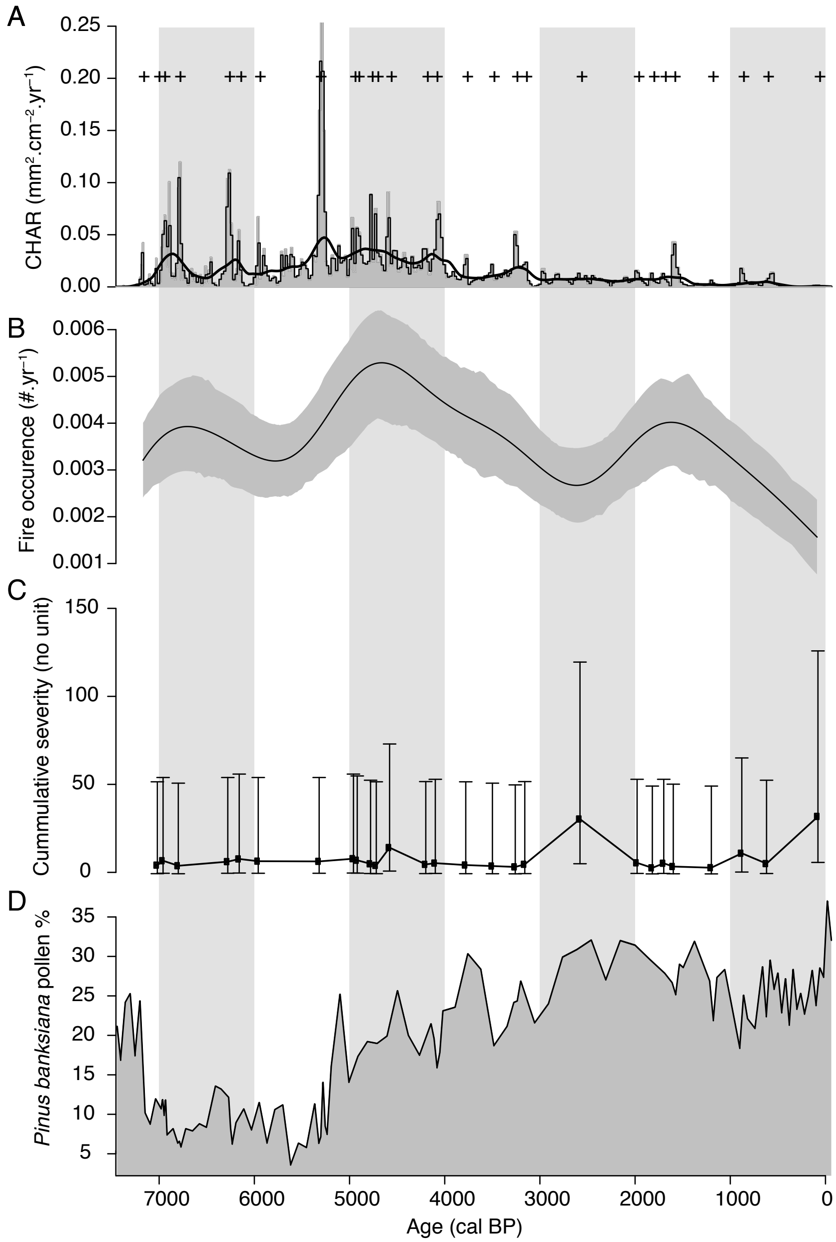

Figure C.2. Exemple du lac Nano montrant une augmentation du pin gris depuis 3000 BP, accompagnée d'une baisse dans le FRI. Il y a ici une inadéquation entre la représentation pollinique du pin gris et un FRI qui augmente. Notre étude a soulevé ce problème, mais n'a pu le résoudre. Nous avons cependant cherché à comprendre les processus de production, de transport et de sédimentation de charbons dans les sédiments lacustres selon la superficie et la sévérité des feux.

Plusieurs hypothèses peuvent être formulées afin d'expliquer ces résultats contradictoires entre le régime des feux et l'écologie des paysages et des espèces forestières.

H1- les lacs ne sont pas représentatifs de la zone :

Des travaux menés dans la section Nord de la zone 2 ont montré une grande variabilité locale du cycle de feu en lien avec les types de dépôts (Mansuy et al., 2010) ce qui vient appuyer la seconde hypothèse. Ainsi, il s'agit de savoir si l'environnement direct des lacs est représentatif de la zone dans laquelle il se trouve. Dans cette optique, nous avions étudié dans le ***Chapitre 1*** la distance statistique entre lacs et les zones que nous avions définies (Figure S1.1). Il en résultait que les lacs d'une même zones étaient regroupés autour de caractéristiques qui correspondaient à celles de leur zone. La combinaison d'analyses menées sur plusieurs sites doit ainsi bien rendre compte de la dynamique régionale de la végétation et des feux.

H2- le FRI des lacs ne permet pas de rendre compte du clycle de feu régional :
Ainsi, il semble que la description de la dynamique pluri-millénaire des feux basée uniquement sur le FRI ne serait pas suffisante pour décrire l'écologie des paysages forestiers. Dans la suite du doctorat, nous avons donc cherché à reconstruire d'autres caractéristiques de feu, telles que la surface brûlée et la sévérité, à partir des charbons enregistrés dans les lacs. Ce sont ces travaux de calibrations menés sur les écosystèmes contemporains qui ont permis de montrer dans les ***Chapitre 2 et 3*** qu'il est effectivement possible de reconstruire ces caractéristiques à partir des charbons déposés annuellement (***Chapitre 2***) et dans les sédiments de surface (***Chapitre 3***). L'une des hypothèses qui pourrait expliquer cela est que plus les feux sont sévères, plus la végétation a été consumée au point de ne produire que très peu de particules de charbon en faveur d'une production plus importante de cendres (Girardin et al., 2019; Santín et al., 2015). Or ces cendres ne sont pas mesurables avec les dispositifs actuels et par conséquent les feux qui en sont à l'origine sont difficilement détectables lors de l'analyse des charbons lacustres. Cela expliquerait partiellement les incohérences entre l'augmentation de l'abondance de *Pinus banksiana* (Figure S2.3D) et la diminution de l'occurrence des feux (B). La combinaison de plusieurs archives permettrait d'obtenir une image plus cohérente de l'histoire holocène des feux, surtout lorsqu'on considère que les charbons des sols minéraux sous-estiment les feux anciens (Dietze and Dietze, 2019; Remy et al., 2018). Ce dernier phénomène serait notamment causé par le rebrulage des charbons forestiers à chaque fois que survient un feu. Plus spécifiquement, les charbons de bois sont intégrés au sol minéral par chabilisation. Par conséquent, les charbons datés ne permettent pas de reconstuire de manière fiable le régime à long terme des feux. De cette manière, l'analyse conjointe de ces deux archives pourrait permettre de reconstruire plus fidèlement le régime des feux d'un territoire donné.

Réconcilier le spatial et le temporel

La paléoécologie se base sur des bio-indicateurs issus de l'environnement des lacs, mais la provenance de ces bio-indicateurs est méconnue. En effet, nous ne connaissons que très peu les liens qui existent entre les caractéristiques des feux (superficie et sévérité) et le dépôt des charbons de bois dans les lacs. Cette méconnaissance représente l'une des limites principales à l'utilisation de la paléoécologie en aménagement.

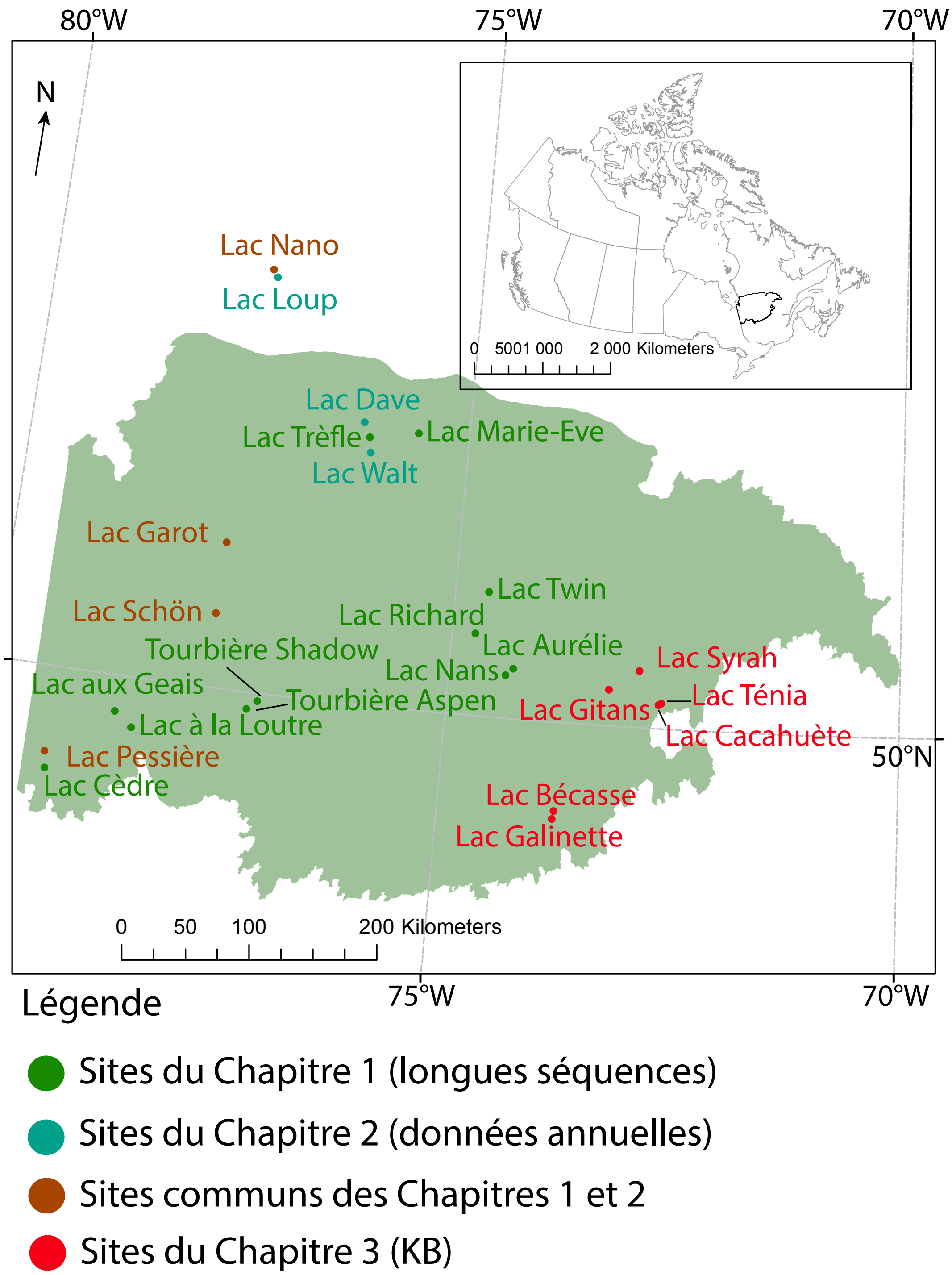

Figure C.3. Localisation des sites (n=24) utilisés dans les différents chapitres qui composent ce doctorat au sein de la PMO (territoire vert)

Nous avons voulu montrer l'importance des analyses multi-sites (Figure C.3) pour s'affranchir des processus taphonomiques de plus ou moins grande échelle qu'il est impossible de contourner. Néanmoins, il est nécessaire de les considérer pour des reconstructions régionales, donc spatialement plus explicites, de la dynamique pluri-millénaire des écosystèmes. Les analyses multi-sites et méta-analyses sont essentielles pour confronter et unifier les histoires écosystémiques reconstruites au niveau de chaque site. Celà permet de réaliser des synthèses à plus grande échelle, de comprendre l'état actuel du territoire, et de définir des zones aux histoires similaires (***Chapitre 1, 2 et 3***) (Figure 1.1). Les études multi-sites ont aussi l'avantage de mettre en évidence l'importance des phénomènes taphonomiques dans la diversification des signaux de bio-indicateurs observés pour chaque site comme le montrent les résultats des (***Chapitre 2 et 3***). Les intervalles d'erreur sont importants ce qui limite la possibilité de réaliser des reconstructions quantitative solides sur le long terme comme nous avons pu l'observer pour les reconstructions effectuées sur la séquence du lac Nano (Figure C.2). L'intérêt des études multi-sites apparaît donc ici accru couplé à des prises de données annuelles afin de poursuivre ces études de calibration. Le ***Chapitre 2*** s'inscrit dans cette optique puisqu'il se base sur les données prises entre 2011 et 2013 publiées par Oris et al. (2014) avec en plus les données acquises entre 2014-2016. Dans le ***Chapitre 3***, les processus taphonomiques liés à la concentration des sédiments au centre du lacs, à leur remobilisation ou les erreurs de datation rendent les liens statistiques entre les charbons et les feux encore plus fragiles (Adolf et al., 2018; Giesecke and Fontana, 2008). Ces phénomènes limitent d'autant plus les reconstructions pluri-millénaires des caractéristiques des feux.

La caractérisation des feux à l'aide des charbons lacustres nécessite plus d'investigations

Les résultats des ***Chapitres 2 et 3*** ont nécessité de regrouper tous les enregistrements des lacs. Les relations ainsi obtenues permettraient de reconstruire des caractéristiques de feu à l'échelle régionale (Adolf et al., 2018).

La Figure C.4 montre que, de manière générale, plus les feux sont sévères et de vaste superficie, plus les influx de charbons sont importants. Par exemple, G-2011 est un feu sévère et vaste (1675 ha) dont la surface médiane des charbons est élevée. Cependant, plusieurs feux étudiés dérogent à cette affirmation, à l'exemple de S-2014 (Schön 2014) qui est un feu de faible superficie (1 ha) qui a produit un faible nombre de charbons (Figure 2.5) mais dont la surface médiane est proche de 0.10 mm^2. À l'opposé, S-2015 (Schön 2015) qui possède une superficie relativement importante (116 ha) a produit des charbons de faible diamètre et en très faible nombre.

Il serait possible de dresser un portrait type de "bon" site paléoécologique à échantillonner pour un territoire donné. En effet, il semble sur la Figure C.4 que des sites comme Garot, Nao ou Walt répondent bien à la relation alors que des sites comme Pessière ou Loup montrent de mauvaises relations puisqu'ils sont situés en dehors des lignes en pointillés qui symbolisent un intervalle de confiance à 95% autour de la droite de régression. Avec plus d'années d'enregistrement, il serait éventuellement possible d'affiner ces affirmations. Au contraire, d'autres sites présentent des propensions à capter des influx de charbons issus de transports secondaires comme les enregistrements du lac Pessière en 2012 (P-2012), du lac Nano (N-2015) et Loup en 2015 (L-2015)

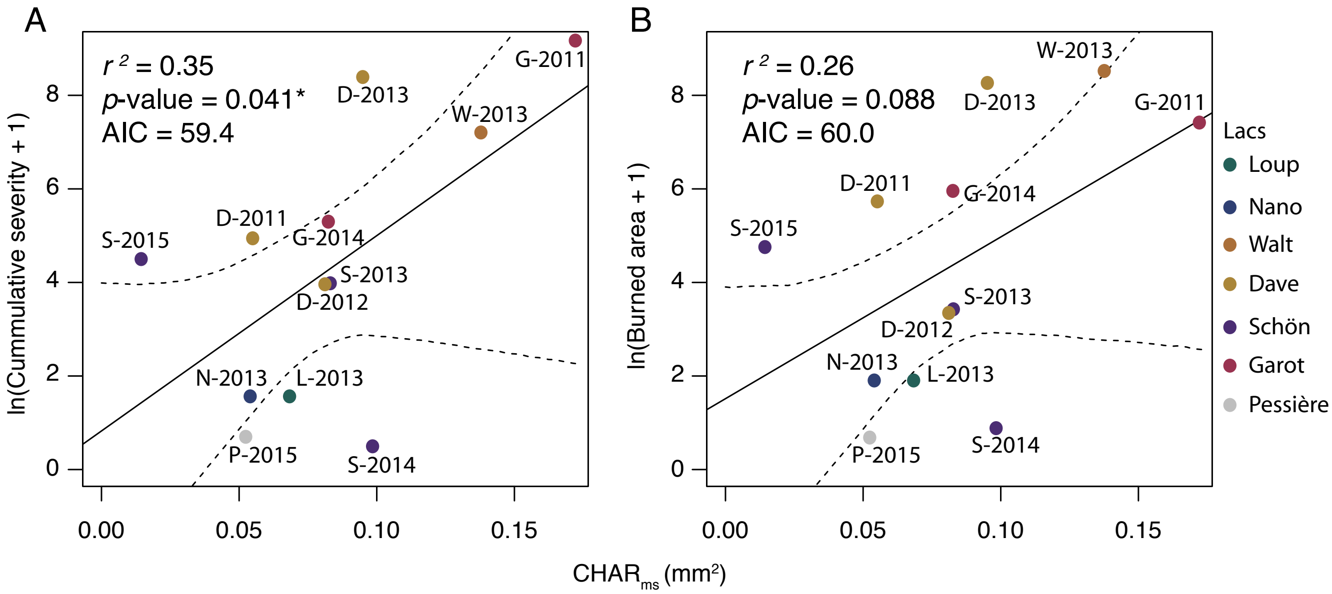

Figure C.4. Reinterprétation de la figure 2.7 avec l'identification des lacs (points de couleurs) d'où proviennent les enregistrements de charbons. La nomenclature d'identification des points se base sur la première lettre du nom du lac et sur l'année de l'enregistrement, e.g. : G-2011 correspond à l'enregistrement de Garot en 2011.

(Figure 2.5). Ces divers éléments montrent que toutes les interprétations qui impliquent, d'une part, la surface et le nombre des charbons et, d'autre part, le nombre de feux, leur superficie et leur sévérité, doivent être avancées avec beaucoup de prudence.

Au même titre que pour l'interprétation de l'importante abondance du sapin baumier dans des périodes aux FRI courts, la sévérité des feux semble être un élément explicatif non négligeable pour les études paléoécologiques (Ali et al., 2008). Cependant, la réelle valeur explicative de cette variable restait à être démontrée. Il est donc important de reconstruire des caractéristiques de feux autres que le FRI car il ne suffit plus pour expliquer certaines observations écologiques. Des études ont permis de reconstruire ces caractéristiques telles que (Remy et al., 2017; Ali et al., 2012) mais de manière relative car seuls des indices ou des anomalies basées sur des fréquences de pics d'accumulation charbons (FRI) et des superficies (BB, biomasse burning) ont pu être étudiés. De plus, l'ensemble de ces indices et anomalies se base sur le CHAR qui est calculé à partir de la surface des charbons mesurée dans chaque échantillon de carotte sédimentaire. Or les résultats contrastés des ***Chapitres 2 et 3*** montrent que le nombre, la surface et la surface médiane sont des mesures faillibles et ne permettent pas de rendre compte de manière absolue de la surface brûlée et de la sévérité des feux. Il semble donc que lL'étude des liens holocènes entre les feux et la végétation nécessitent plus d'approfondissement et que de nouveaux développements méthodologiques devront être mis en place afin d'établir des relations plus précises.

La paléoécologie ne permet pas encore de reconstruire des cycles de feu

En effet, les ***Chapitres 2 et 3*** ont permis d'appréhender la provenance minimale des particules de charbons à 30 km autour des lacs (Peters and Higuera, 2007). Cependant, des travaux similaires suggèrent une provenance encore plus éloignée pouvant atteindre 100 à 150 km (Adolf et al., 2018; Vachula et al., 2018). Des analyses plus fines devraient ainsi être menées dans le contexte de la forêt boréale afin de mieux établir la source d'origine des charbons. Ceci permettrait d'unifier la dimension temporelle de la paléoécologie avec la dimension spatiale des aménagistes dans l'objectif de faire converger le FRI paléoécologique avec le cycle de feu des aménagistes. Il est ainsi important de maintenir et d'émuler les dialogues entre aménagistes et chercheurs afin de co-construire et développer des indices de mesures communs.

Combiner les connaissances du passé et du présent pour assurer la pérennité des écosystèmes

Le premier objectif de mon doctorat était de montrer aux aménagistes qu'il est possible maintenant de prendre en compte les dynamiques pluri-millénaires des écosystèmes pour l'établissement de cibles d'aménagement forestier plus durables en utilisant la paléoécologie (***Chapitre 1***). À l'échelle plus globale, des scientifiques s'unissent et travaillent à faire valoir la pertinence de l'utilisation de la paléoécologie comme outil d'aide à la décision. Le GPWG (Global Paleofire Working Group) vise à valoriser les connaissances apportées par l'étude des paléofeux. À l'issue d'un Workshop tenu à Montréal en 2017, plusieurs d'entre eux ont voulu souligner le fait que la paléoécologie est arrivée à un point de maturité (Aleman et al., 2018; Marcisz et al., 2018) et qu'il était possible de donner une nouvelle interprétation aux données de paléofeux. Ces nouvelles interprétations devraient appuyer la prise de décision en terme d'exploitation, de conservation ou de gestion des écosystèmes dont le feu représente un élément de dynamique (Hennebelle et al., *en préparation*). Ce même groupe cherche à mettre en relation les scientifiques avec les professionnels gestionnaires (aménagistes, ministères, parcs naturels) afin de développer et valoriser les divers savoirs que ces acteurs peuvent apporter ((Colombaroli et al., 2019), Workshop de Londres en 2018). Les orientations futures du GPWG sont en accord avec les innovations les plus récentes en paléofeux/paléoécologie notamment en valorisant et encourageant les études de calibration ainsi que les études portant sur plusieurs archives.

En nous basant sur l'adage *pour comprendre le présent il faut regarder le passé*, nous avons aussi pu démontrer que *pour comprendre les enregistrements des témoins du passé il faut comprendre comment ces témoins sont enregistrés dans le présent*, et qu'il reste encore des zones d'ombre.

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