UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

RECONSTITUTION DE LA COMPOSITION DES FORÊTS PRÉINDUSTRIELLES DU TÉMISCAMINGUE (QUÉBEC) À PARTIR DES ARCHIVES DE L'ARPENTAGE PRIMITIF

THÈSE
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AVANT-PROPOS

Cette thèse est rédigée sous forme d'articles scientifiques, qui représentent le cœur du document, et sont complétés d'une introduction et conclusion générale. Deux des articles sont déjà publiés ou soumis à des revues avec comité de lecture, et un article reste en préparation pour soumission.

Chapitre II. Danneyrolles V., Arseneault D., & Bergeron Y. (2016). Pre-industrial landscape composition patterns and post-industrial changes at the temperate-boreal forest interface in western Quebec, Canada. *Journal of Vegetation Science,* 27, 470–481.

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Les changements globaux modifient les écosystèmes forestiers à la fois de manière directe par l'usage des sols et l'exploitation des ressources forestières, et de manière indirecte avec les changements climatiques. La connaissance des dynamiques historiques des paysages forestiers est donc essentielle pour la conservation des écosystèmes et pour mieux anticiper leur évolution future.

Dans le but de maintenir les écosystèmes et la biodiversité, l'aménagement écosystémique vise à reproduire les patrons écologiques créés par la dynamique naturelle des forêts. Aussi, dans les régions qui ont été largement impactées par les activités humaines dans le passé, comme ceci a été le cas au Témiscamingue, l'aménagement écosystémique peut s'inspirer d'états de référence historique; les forêts préindustrielles. Dans cette thèse, les archives de l'arpentage primitif du Témiscamingue ont été utilisées pour reconstituer la composition des forêts préindustrielles et les changements de composition survenus depuis cette époque, avec différentes approches répondant chacune à des questions spécifiques.

Une reconstitution de la composition des forêts préindustrielles et des changements de composition a premièrement été réalisée pour le domaine bioclimatique de la sapinière à bouleau jaune. Une approche cartographique (regroupements statistiques sous contrainte spatiale) a permis d'identifier des structures spatiales dans les paysages préindustriels, qui semblent principalement liées aux régimes de feux. Les épinettes noires (*Picea mariana*) et le sapin baumier (*Abies balsamea*) dominaient les coteaux affectés par des feux relativement anciens, alors que le peuplier faux-tremble (*Populus tremuloides*) dominait les plaines argileuses affectées par des feux récents. Par la suite, les feux liés à la colonisation et superposés aux coupes du début du siècle ont dans l'ensemble abouti à un remplacement des conifères par les feuillus de début de succession (*Populus tremuloides*, *Betula papyryfera*). Les changements post-industriels de composition doivent donc être perçus comme le résultat d'interactions entre la structure du paysage préindustriel et les perturbations naturelles et humaines.

Si les forêts très perturbées depuis l'époque préindustrielle ont enregistré une forte augmentation des feuillus de début de succession, les forêts ayant uniquement subi des perturbations de plus faible intensité (coupes partielles anciennes, épidémies de tordeuse des bourgeons de l'épinette) semblent avoir poursuivi des trajectoires distinctes. Pour caractériser ces trajectoires, 108 observations historiques localisées dans des forêts aujourd'hui matures ont été réarpentées. Les résultats indiquent une augmentation de taxons de milieux à fin de succession (*Acer saccharum, Betula alleghaniensis, Thuja occidentalis)* au détriment des conifères dominant cet échantillon de forêts à l'époque préindustrielle (*Abies balsamea, Pinus strobus*). En permettant la comparaison de sites appariés, le réarpentage d'observations historiques améliore remarquablement la compréhension des changements de composition survenus depuis l'époque préindustrielle.

Les relations entre les communautés et les gradients environnementaux représentent une question centrale en écologie. Un partitionnement de la diversité-β a permit de comparer l'influence des gradients environnementaux (latitude, altitude, pente, dépôt, drainage) sur la composition des forêts préindustrielles et modernes. Bien que l'histoire des feux ait été à l'origine d'une importante structuration spatiale des forêts préindustrielles, nos résultats montrent que les conifères dominants à cette époque (*Picea* spp., *Abies balsamea*, *Pinus* spp.) étaient très ubiquistes du point de vue des gradients environnementaux. Les perturbations du XXe siècle ont ensuite augmenté l'influence des gradients environnementaux sur la composition des forêts en favorisant des taxons plus spécialistes (*Populus* spp., *Acer* spp.) et en confinant les conifères dominant à l'époque préindustrielle vers les extrémités des gradients. Les perturbations représentent donc des facteurs clefs dans la diversité des paysages forestiers du nord de la zone tempérée et de la zone boréale. Non seulement les gradients de fréquence des perturbations génèrent des structures spatiales, mais les perturbations pourraient aussi augmenter l'influence des filtres environnementaux.

Finalement, cette thèse apporte plusieurs éléments pertinents pour l'aménagement écosystémique au Témiscamingue. Face à l'enfeuillement général des forêts, l'aménagement écosystémique doit avoir pour principal objectif de rétablir des forêts à dominance résineuse. Cet objectif peut être atteint par l'utilisation de coupes partielles qui permettrait de limiter l'envahissement par les feuillus de début de succession, tout permettant le développement de la régénération résineuse préétablie. Des plantations de réintroduction après coupes devraient aussi être envisagées quand l'abondance des conifères a trop diminué pour assurer une régénération naturelle efficiente.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Changements globaux et écosystèmes forestiers

Les activités humaines modifient le système terrestre depuis des millénaires (Goudie, 2006). L'anthropisation des biomes terrestres s'est aussi intensifiée au cours des derniers siècles avec la révolution industrielle et l'explosion démographique des populations humaines (Ellis et al., 2010), basculant le système terrestre dans une nouvelle ère géologique : l'Anthropocène (Lewis & Maslin, 2015). À l'aire de l'Anthropocène, les changements globaux modifient les écosystèmes à la fois de manière directe par l'usage des sols et l'exploitation des ressources naturelles (Foley, 2005), et de manière indirecte au travers des changements climatiques liés au relargage massif de gaz à effet de serre dans l'atmosphère (Grimm et al., 2013).

D'une part, les usages des sols et l'exploitation des ressources forestières modifient l'étendue et la distribution du couvert forestier à l'échelle globale (Foley, 2005; Meyfroidt & Lambin, 2011; Hansen et al., 2013). À une échelle régionale, ces activités peuvent aboutir à des modifications profondes dans la structure, la composition et la dynamique des paysages forestiers (ex. : Axelsson et al., 2002; Urbieta et al., 2008). Dans l'est de l'Amérique du Nord, les populations autochtones ont modifié la naturalité des forêts depuis plusieurs milliers d'années (Delcourt & Delcourt, 2004; Abrams & Nowacki, 2008; Munoz & Gajewski, 2010; Munoz et al., 2014). Par la suite, les changements d'usage des sols liés à la colonisation européenne et à l'industrialisation ont engendré un bouleversement des écosystèmes, avec généralement une fragmentation, un rajeunissement, une homogénéisation et une augmentation des espèces de début de succession à l'échelle du paysage (Lorimer & White, 2003; Friedman & Reich, 2005; Rhemtulla et al., 2009; Riitters et al., 2012; Thompson et al., 2013).

D'autre part, les changements climatiques modifient les écosystèmes forestiers à travers différents processus. Premièrement, les changements de température et de régime de précipitation peuvent entraîner des déplacements de distribution des espèces, des communautés et des biomes (ex. : Williams et al., 2004; Chen et al., 2011; Grimm et al., 2013). À l'interface des forêts tempérée et boréale dans l'est de l'Amérique du Nord, on s'attend à un remplacement des taxons boréaux par des taxons plus tempérés au cours des prochaines décennies (McKenney et al., 2007; Iverson et al., 2008; Fisichelli et al., 2014; Reich et al., 2015). Deuxièmement, les changements climatiques entraînent des changements majeurs dans les régimes de perturbations naturels comme les feux (Westerling, 2006; Flannigan et al., 2009) et les épidémies d'insectes défoliateurs (Haynes et al., 2014).

La compréhension de l'histoire des paysages forestiers, qui a abouti à la formation des paysages actuels sous l'influence des activités humaines et dans des conditions climatiques en mutation, est donc essentielle (Rhemtulla & Mladenoff, 2007). Ces connaissances sont non seulement cruciales pour la conservation des écosystèmes et de la biodiversité (Foster et al., 2003; Willis et al., 2007) mais permettent aussi de mieux anticiper les évolutions futures des écosystèmes dans le contexte des changements globaux (Petit et al., 2008; Robertson et al., 2012).

1.2 Aménagement écosystémique et états de références historiques

Une importante volonté de gestion durable des forêts s'est développée dans les dernières décennies à l'échelle globale, entraînant le déplacement des modèles de gestion centrés sur la production vers des nouveaux modèles d'aménagement qui intègrent en plus des critères écologiques et sociaux (Davis, 2005). En Amérique du Nord, cette transition s'est faite en faveur d'un aménagement écosystémique (Kohm & Franklin, 1997; Gauthier, 2009; Larocque, 2015). Dans le but d'assurer le maintien de la biodiversité, l'aménagement écosystémique vise à maintenir les écosystèmes dans leurs gammes de variabilité naturelle (Gauthier, 2009; Larocque, 2015). Les pratiques sylvicoles doivent maintenant s'inspirer des dynamiques spatio-temporelles générées par les perturbations naturelles, qui servent d'états de référence (Seymour et al., 2002; Perera et al., 2008; Kneeshaw & Bergeron, 2015). Cependant, dans certaines régions, il n'existe aujourd'hui plus ou pas assez de paysages non impactés par les activités humaines pour dresser des états de références reflétant la dynamique naturelle des forêts. Dans ce cas de figure, il est possible de se baser sur des états de références historiques (Egan & Howell, 2001), comme les forêts en place avant la colonisation européenne et l'exploitation industrielle : les forêts précoloniales ou préindustrielles.

D'un autre côté, l'utilisation d'états de références historiques pour l'aménagement écosystémique comporte des limites. Dans le contexte de changements climatiques, une utilisation « stricte » des caractéristiques d'écosystèmes du passé comme états de référence pourrait aboutir à des écosystèmes forestiers non viables dans le futur (Choi et al., 2008). Les états de références historiques ne doivent donc pas être pris comme des cibles ultimes, mais devraient plutôt constituer une base de réflexion et d'inspiration pour développer un aménagement adaptatif aux changements climatiques (Millar et al., 2007; Choi et al., 2008; Gagné et al., 2015).

1.3 Le Témiscamingue : contexte biogéographique et historique

Les travaux présentés dans cette thèse sont centrés sur la région du Témiscamingue à l'extrémité sud-ouest de la province canadienne du Québec (Figure 1.1), et dont nous dressons ici un bref portrait biogéographique et historique. Le climat régional varie entre continental humide et boréal, avec des températures moyennes et des précipitations totales (normales annuelles 1981-2010) variant respectivement de 5,2 °C et 918 mm à l’extrémité sud de la région (Rapide des Joachims) à 2,3 °C et 885 mm au nord (Montbéliard). En conséquence, les forêts mixtes de cette région représentent la zone de transition entre les forêts tempérées et boréales (Rowe, 1972), correspondant aux domaines bioclimatiques de l’érablière à bouleau jaune et de la sapinière à bouleau jaune selon la classification provinciale (Robitaille & Saucier, 1998).

La région a été libérée des glaces il y a environ 9 000 à 10 000 ans pour laisser place, dans un premier temps, aux vastes lacs pro-glaciaires Barlow et Ojibway (Veillette, 1983; Dyke, 2004). Ces lacs pro-glaciaires sont à l'origine d'une importante quantité de dépôts argileux dans les basses altitudes de la région (Vincent & Hardy, 1977), alors que les plus hautes altitudes du Bouclier canadien, restées émergées après la déglaciation, sont dominées par des dépôts de tills glaciaires. Une végétation boréale s'est installée immédiatement après la déglaciation dans la région, et a été colonisée par les forêts mixtes des Grands Lacs et du St Laurent il y a environ 7 000 à 8000 ans (Liu, 1990).

Dans cette région, les perturbations représentent le principal moteur de la dynamique des forêts. Durant les derniers siècles, le cycle de feux était relativement court dans le domaine de la sapinière à bouleau jaune (188-314 ans ; Grenier et al., 2005), et augmentait vers le sud dans le domaine de l'érablière à bouleau jaune (373-694 ans ; Drever et al., 2006). La fréquence des feux a aussi significativement diminué dans toute la région depuis la fin du Petit Âge glaciaire vers 1850 (Bergeron & Archambault, 1993; Bergeron et al., 2006). Plusieurs épidémies de tordeuse des bourgeons de l'épinette ont également contribué à la dynamique des forêts au cours des derniers siècles (Bouchard et al., 2005, 2006a, 2006b).

Les perturbations humaines se sont aussi progressivement intensifiées au cours des deux derniers siècles. Des populations autochtones sont présentes dans la région depuis au moins 8 000 ans, et les populations algonquines présentes avant l'arrivée des Européens peuvent être grossièrement estimées à plusieurs milliers d'individus (Couture, 1983; Riopel, 2002). Cependant, leurs modes de gestion du territoire et leurs impacts écologiques n'ont pas été documentés précédemment. Au XIX^{e} siècle, les marchands de bois ont progressivement remonté la vallée de la rivière des Outaouais et entrepris les premiers chantiers sur les bords des lacs Témiscamingue et Kipawa entre 1830 et 1850 (Riopel, 2002). Depuis cette époque jusqu’au début du XX^{e} siècle, la très grande majorité des chantiers au Témiscamingue sont des coupes sélectives des grands pins, dont le bois équarri est flotté le long de la rivière des Outaouais vers les grands centres économiques du Sud. La construction du « *Kipawa Mill* » en 1917 à Témiscaming a marqué le début d’une nouvelle ère forestière dans la région. À partir de cette date, pour alimenter le nouveau moulin à papier en bois de pulpe, les coupes à diamètres limites d'arbres de plus petite taille sont devenues majoritaires et de plus en plus importantes (Lienert, 1966). La colonisation du territoire et la mise en culture des terres argileuses du nord-ouest de la région du territoire ont progressé en parallèle à l'expansion du secteur forestier, et la population d'origine européenne du Témiscamingue a évolué de quelques centaines en 1890 à presque 30 000 en 1950 (Riopel, 2002).

1.4 Les archives de l'arpentage primitif

L'ensemble de cette thèse se base sur les informations contenues dans les archives de l'arpentage primitif du Témiscamingue. L'arpentage primitif avait pour but de délimiter les nouvelles limites administratives permettant d'attribuer des territoires pour la colonisation ou l'exploitation forestière. Ces archives représentent donc les plus anciennes sources écrites décrivant les caractéristiques des forêts au Québec, et plusieurs études récentes ont montré le fort potentiel de ces archives pour reconstituer la composition des forêts préindustrielles (Dupuis et al., 2011; Terrail et al., 2014). Trois types d'observations concernant les forêts peuvent être trouvés dans ces archives : des listes de taxons (ex : *pins, épinettes, merisier et quelques érables*), des types de couverts forestiers (ex. : *bois mixtes, taillis*, etc.), ainsi que des observations de perturbation (ex. : *brûlé, chablis*, etc.). Les archives disponibles au Témiscamingue correspondent à des arpentages de cantons et de concessions forestières. Les cantons ont généralement été arpentés le long de leurs limites extérieures (16 km x 16 km), et le long des rangs (subdivisions espacées de 1,6 km). Les concessions forestières étaient de tailles variables, et seulement leurs limites ont été arpentées. En tout, 95 carnets rapportant des travaux d'arpentage réalisés sur le terrain entre 1854 à 1935 ont été passés en revue et transposés sous forme de base de données géoréférencée (Figure 1.1). Cette base de données contient 11 349 observations, dont 9725 font mention de taxons. La zone divisée en cantons lors de la colonisation, située dans le nord-ouest du Témiscamingue, présente aussi une plus grande densité d'observations d'arpentage (Figure 1.1).

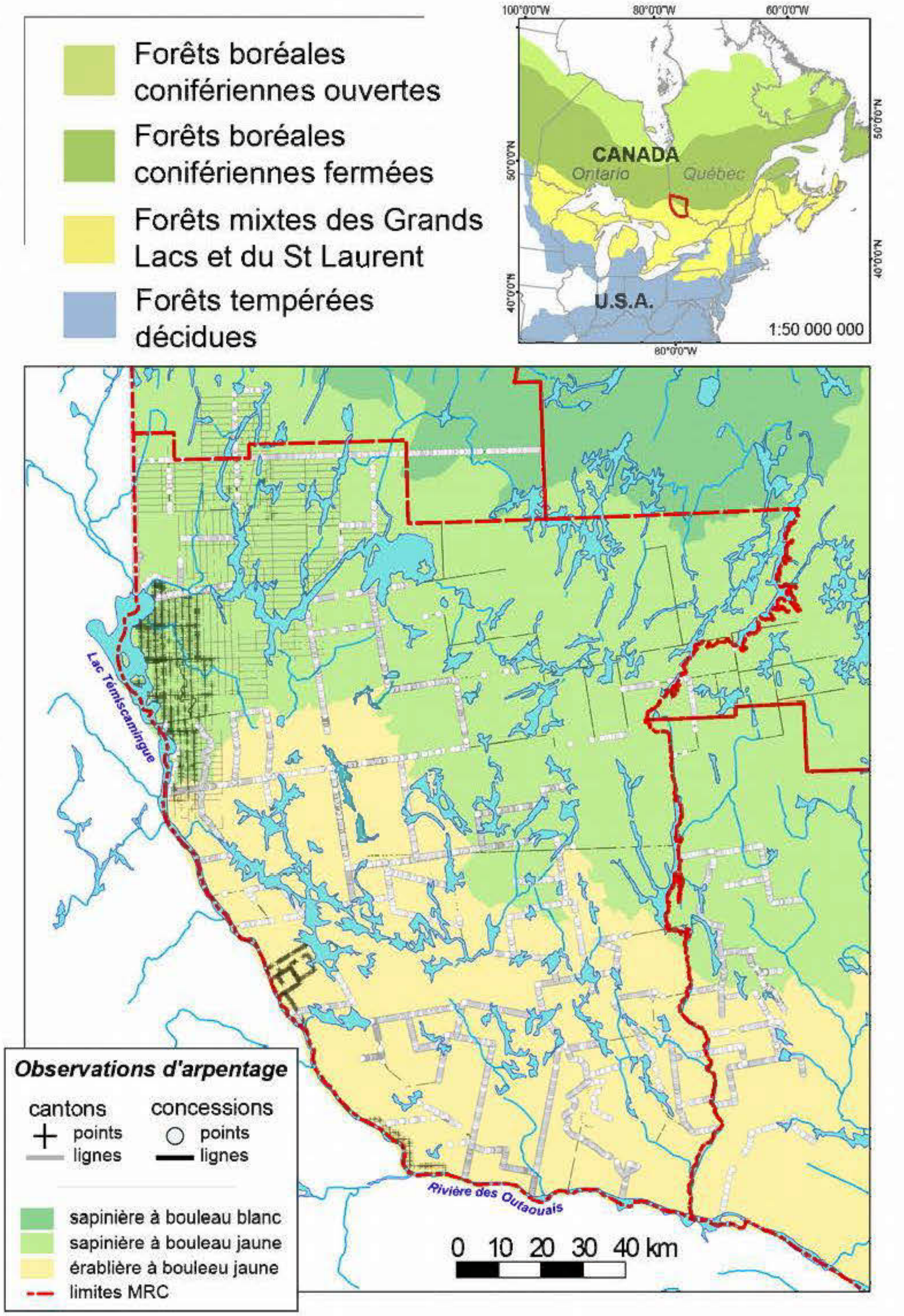

Figure 1.1 Localisation du Témiscamingue et base de données historique.

1.5 Objectifs

À partir de la base de données décrite plus haut, l'objectif général de cette thèse est d'explorer les caractéristiques de la composition des forêts préindustrielles et des changements de composition survenus depuis cette époque au Témiscamingue. Ce thème principal se décline en quatre objectifs plus précis, qui correspondent aux chapitres qui structurent cette thèse.

L'objectif du premier chapitre est de caractériser la composition des forêts préindustrielles et les changements de composition à l'échelle du paysage. Ce premier chapitre s'est concentré sur la portion nord-ouest de notre région d'étude, où la forte densité d'observation historique permettait une approche cartographique avec une bonne résolution spatiale. Des regroupements statistiques sous contrainte spatiale ont été utilisés pour identifier des structures spatiales dans les paysages préindustriels et les changements de composition survenus depuis.

Pour le deuxième chapitre, l'objectif est d'identifier les changements de composition spécifiques aux peuplements qui n'ont subi que des perturbations de faible intensité (épidémies de tordeuse des bourgeons de l'épinette et coupes partielles anciennes) depuis l'époque préindustrielle. Une approche méthodologique originale basée sur le réarpentage d'observations historiques a été développée pour répondre à cet objectif.

L'objectif du troisième chapitre est d'analyser l'évolution des communautés le long des gradients environnementaux depuis l'époque préindustrielle. Les communautés préindustrielles ont été reconstituées à partir d'un sous-ensemble de la base de données historique couvrant l'ensemble de la région d'étude, et les communautés modernes ont été documentées à partir des cartes écoforestières. Des analyses multivariées ont permis de comparer la diversité-β et l'influence des gradients environnementaux sur la composition des forêts préindustrielles et modernes.

Le quatrième chapitre, qui fait office de conclusion générale à cette thèse, a pour but de répondre aux questions plus appliquées liées à l'aménagement écosystémique des forêts Témiscamingue. À partir des résultats présentés dans les précédents chapitres, nous dressons un portrait global des forêts préindustrielles au Témiscamingue, pour finalement discuter des cibles de composition à atteindre et des pratiques sylvicoles qui permettraient d'y parvenir.

CHAPITRE II

PRE-INDUSTRIAL LANDSCAPE COMPOSITION PATTERNS AND POST-INDUSTRIAL CHANGES AT THE TEMPERATE-BOREAL FOREST INTERFACE IN WESTERN QUEBEC, CANADA.

Victor Danneyrolles, Dominique Arseneault & Yves Bergeron

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2.1 Abstract

Questions: What were the pre-industrial forest landscape composition patterns? Which factors had structured the pre-industrial landscape patterns? How have pre-industrial landscape patterns and post-industrial disturbances controlled composition changes?

Location: Study area comprises 4175 km^2 at the temperate-boreal forest interface of southwestern Quebec (Canada).

Methods: Reconstruction of the pre-industrial composition is based on an original early land survey dataset (1874-1935). Composition changes were computed by comparing historical data with modern forest inventories. Landscape scale patterns and composition changes were assessed through spatially constrained clustering analysis.

Results: Pre-industrial forest composition was structured across the landscape by the combination of environmental gradients (topography, deposits, drainage, etc.) and recurrence of fire. Frequency and intensity of fires were most likely the main drivers of forest dynamics and composition across the landscape. Black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) dominated hilly areas affected by former fires; aspen (*Populus tremoloides*) dominated lowlands following recent fire. White cedar (*Thuja occidentatlis*) and pines (*Pinus* spp.) dominated areas probably affected by small surface fires. New disturbance regimes that were subsequently incurred by human activities have shifted the pre-industrial landscape mosaic and have led to the current landscapes. Composition changes included a replacement of conifers by early-successional species within settled or burned areas, and the maintenance of conifers and an increase in cedar dominance in areas affected by partial disturbance.

Conclusions: Post-industrial composition changes must be perceived as complex interactions between pre-industrial landscape patterns and natural and human disturbances. Such land-use legacies could be important drivers of future landscape change and should be investigated and considered when predicting future climate-induced ecological changes.

Keywords: *Abies balsamea,* Historical forest ecology, Land use legacies, Naturalness, *Picea mariana, Pinus strobus, Populus tremuloides,* Spatially constrained clustering, *Thuja occidentalis.*

Nomenclature : Farrar (1995)

2.2 Résumé

Questions : Quels étaient les patrons des paysages forestiers préindustriels? Quels facteurs étaient à l'origine de cette structuration spatiale? Comment la structure du paysage préindustriel et les perturbations survenues depuis ont-elles contrôlé les changements de composition?

Localisation : La zone d'étude représente un paysage de 4175 km^2 à l'interface des forêts tempérées et boréales du sud-ouest du Québec (Canada).

Méthodes : La reconstitution de la composition préindustrielle est basée sur des données d'arpentage primitif (1874-1935). Les changements de composition ont été évalués par comparaison des données historiques avec des inventaires forestiers modernes. Des structures à l'échelle du paysage ont été déterminées par des regroupements statistiques sous contrainte spatiale.

Résultats : La composition des forêts préindustrielles était structurée à l'échelle du paysage par la combinaison de gradients environnementaux (topographie, dépôts de surface, etc.) et par la récurrence des feux. La fréquence et l'intensité de feux étaient vraisemblablement les principaux moteurs de la dynamique forestière et de la composition à l'échelle du paysage. Les épinettes noires (*Picea mariana*) et le sapin baumier dominaient les coteaux anciennement brûlés; le peuplier faux-tremble (*Populus tremuloides*) dominait les basses plaines affectées par des feux récents. Le cèdre (*Thuja occidentalis*) et les pins (*Pinus* spp.) dominaient des zones probablement affectées par des feux de surface de petite superficie. Les nouveaux régimes de perturbations engendrés par les activités humaines ont ensuite transformé la mosaïque forestière préindustrielle. On observe un remplacement des conifères par les feuillus de début de succession dans les zones récemment brûlées ou colonisées, et un maintient des conifères ainsi qu'une augmentation en dominance du cèdre dans les zones affectées par des perturbations partielles.

Conclusions : Les changements post-industriels de composition doivent être perçus comme le résultat d'interactions entre la structure du paysage préindustriel et les perturbations naturelles et humaines. Ce type de legs des usages des sols pourraient aussi influencer la dynamique future des paysages forestiers, et devraient donc être considérés dans les prévisions de changements écologiques liés au climat.

Mots-clefs : *Abies balsamea,* Écologie forestière historique, Legs des usages des sols, Naturalité, *Picea mariana, Pinus strobus, Populus tremuloides,* Regroupement statistique sous contrainte spatiale, *Thuja occidentalis*.

Nomenclature : Farrar (1995)

2.3 Introduction

Since thousands of years before the industrial era, human populations have altered the forest naturalness through their use of lands and resources from northern boreal forest (Johnson & Miyanishi 2012) to rainforest (Willis et al. 2004). During the last few centuries, industrialisation and land-use intensification has dramatically transformed the global forest cover (Houghton 1994; Foley 2005; Ellis et al. 2010). In northeastern America, native populations have modified the pre-settlement forest landscape through use of fire, forest clearing, wild plants and animal population management (Day 1953; Denevan 1992; Delcourt & Delcourt 2004; Abrams & Nowacki 2008; Denevan 2011). Thereafter, European colonial settlement contributed to major transformation of forest landscape characteristics, which are generally considered as younger and more fragmented than pre-industrial landscape (Mladenoff et al. 1993; Whitney 1994; Foster et al. 1998; Lorimer 2001).

Composition changes that have been observed since pre-industrial times in eastern North America are mainly the result of human activities (Thompson et al. 2013; Nowacki & Abrams 2015). Yet, significant climate change has also occurred between the pre-industrial period and the present time in North America (Mann & Jones 2003; Moberg et al. 2005; Gennaretti et al. 2014) and the relative importance of land-use and climate effects on vegetation changes over the last several centuries remains a lively debate (Pederson et al. 2014; Abrams & Nowacki 2015; Nowacki & Abrams 2015). Biogeographic transition zones also appear to be especially sensitive to climate change (Parmesan et al. 2005; Beckage et al. 2008), such as the temperate-boreal forest interface (Fisichelli et al. 2014; Reich et al. 2015).

Understanding the development of current forest landscapes under disturbance regimes that have been modified by human activities is fundamental to anticipating how present-day forests will evolve in a global change context (Foster et al. 2003; Schrott et al. 2005; Rhemtulla & Mladenoff 2007; Gillson 2009; Ewers et al. 2013). Many studies have used historical land survey records to reconstruct pre-industrial forest composition (Whitney 1994), and some have developed methodological tools to map and interpret these data at the landscape scale (Manies & Mladenoff 2000; Schulte et al. 2002; He et al. 2006; Rhemtulla et al. 2007; Dupuis et al. 2011). At the landscape scale, pre-industrial forest composition was commonly structured by the combination of environmental gradients and disturbance history (Lewis & Ferguson 1988; White & Mladenoff 1994; Lorimer 2001; Schulte et al. 2002; Schulte et al. 2007; Abrams & Nowacki 2008; Boucher et al. 2009; Josefsson et al. 2010). Different land-use conditions subsequently may have led to different dynamic trajectories across the landscape (Wallin et al. 1994; Bellemare et al. 2002; Turner et al. 2003; Hermy & Verheyen 2007; Boucher & Grondin 2012; Boucher et al. 2014; Grondin et al. 2014). Accordingly, to understand current landscapes, ecologists should consider interactions between (1) pre-industrial landscapes patterns, (2) environmental gradients, and (3) natural and human disturbances.

In this study we reconstruct pre-industrial forest composition at the temperate-boreal forest interface, based on an original dataset of early land survey records. Our aims were to highlight both regional changes and the existence of distinct pre-industrial landscapes. We discuss three questions: (1) which factors had structured the pre-industrial landscape patterns? (2) How was the pre-industrial landscape modified by native populations? (3) How have interactions between pre-industrial patterns and 20th century disturbances controlled composition changes to produce present-day forest landscape patterns?

2.4 Study area

The study area covers 4175 km^2 in the Témiscamingue region, which is located in southwestern Quebec (47°30'N, 79°00'W; Figure 2.1a). Mixed forests in the region represent the transition zone between northern temperate hardwood and southern boreal conifer-dominated forests (Rowe 1972), and which corresponds to the balsam fir-yellow birch bioclimatic domain according to the provincial classification system (Robitaille & Saucier 1998). Surface deposits are mainly divided between clays deposited by the pro-glacial Barlow Lake in lowland areas (Vincent & Hardy 1977) and glacial till along with rocky outcrops in upland areas. According to data averaged from four weather stations in the study area, mean annual temperature is 2.7 °C and mean annual precipitation is 888 mm (1981-2010 time period).

In this region, the topographic gradient is linked to factors that influence the establishment and growth of different tree species, such as drainage, nutrient availability, soil depth, microclimate (Fraser 1954; MacHattie & McCormack 1961; Brown 1981) and disturbances. The natural fire rotation period has been estimated to be about 200 years long in the region (Grenier et al. 2005), and spruce budworm (*Choristoneura fumiferana*) outbreaks have also been identified as an important disturbance of natural forest dynamics over the last several centuries (Bouchard et al. 2005; 2006a; 2006b).

Native populations have occupied the study area for at least 5000 years (Riopel 2002). The Algonquin/Anishinaabe tribes were nomadic hunter-gatherers, and totalled from about 800 to few thousand individuals (Couture 1983; Riopel 2002), but their impact on the forest remains unknown. From the 18th century, the region was frequented by Euro-Americans, who were engaged in the fur trade. Logging did not begin until 1840, and was mainly focused on selective cutting of tall pine trees until 1917 (Riopel 2002). From 1917 until the end of the 20th century, partial cutting of spruces (*Picea* spp.) and balsam fir (*Abies balsamea*) for wood pulp became the main logging activity following the construction of a paper mill in the city of Témiscaming (Lienert 1966). Clear-cutting practices emerged with the mechanization of forestry in the 1970s. European settlement evolved in parallel with the forest industry, and the Euro-American population grew from a few hundred people in 1890 to nearly 30,000 in 1950 (Riopel 2002).

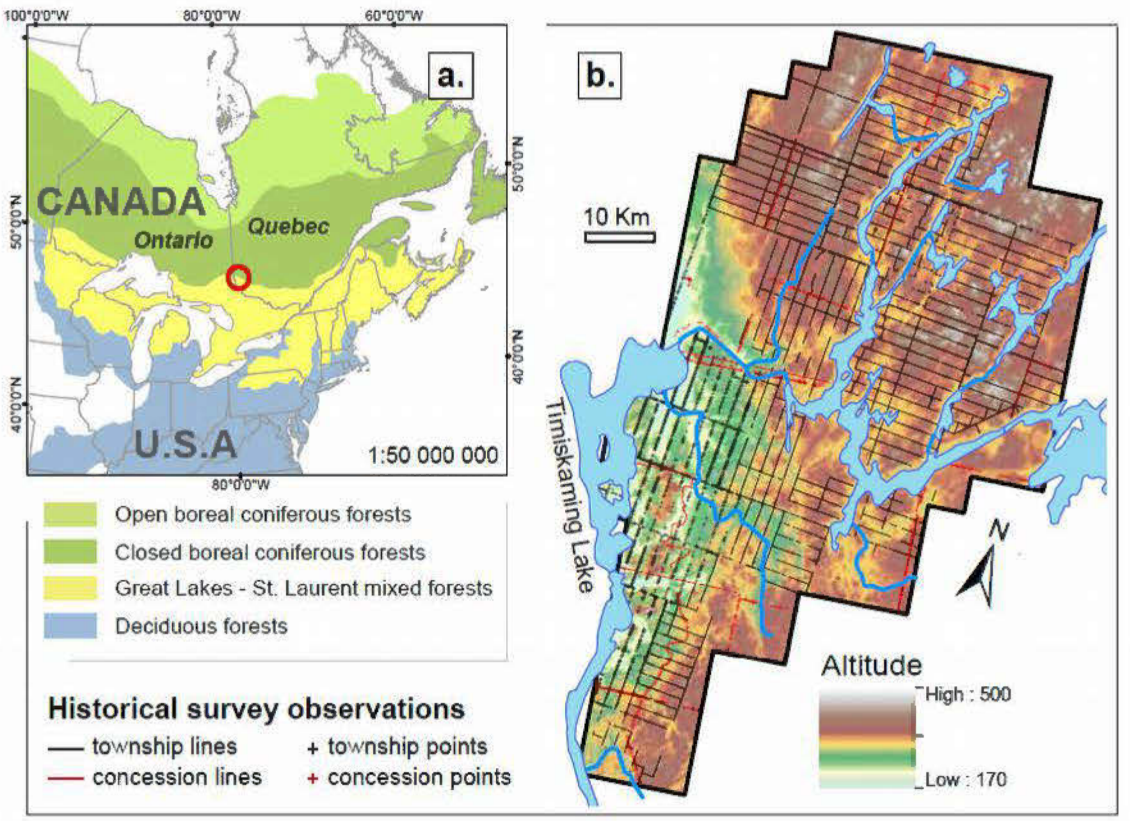

Figure 2.1 Location of the study area (a) and distribution of historical survey data (b).

2.5 Methods

2.5.1 Database construction

This study is based on 36 logbooks from the surveys of 16 townships and 10 forest concessions by 16 different surveyors between 1874 and 1935. In the province of Quebec, public lands were divided into townships of about 16 km x 16 km (10 miles x 10 miles) and further subdivided into parallel ranges that were 1.6 km wide. Surveys were conducted along the boundaries of the township and range lines. Forest concessions varied in sizes, but only their boundaries were surveyed. Three observation types concerning forests are found in these archives: taxa lists (*e.g.*, pine, spruce, white birch and a few maples), forest cover types (*e.g.*, hardwood, softwood, etc.) and disturbance observations (*e.g.*, burnt, windthrow, etc.). In this study, only observations that mentioned taxa were selected.

The historical database comprises 5207 observations that are unevenly spread across the study area (Figure 2.1b), and which mention at least one tree taxon. Observations are divided into two geometric types: (1) line descriptions that clearly indicate a beginning and an end, and (2) regularly or irregularly distributed point observations along the surveyed lines. In order to incorporate these two observation types into a same database, point observations were weighted, based on their mean spacing (the mean of the distances to the previous and next observations), while the weight of each line description corresponded to its lengths (Dupuis et al. 2011). For all observations, a rank was assigned to each taxon listed according to its position in the taxa list, assuming that this position reflects their relative basal area (Terrail et al. 2014). These data were then precisely geo-referenced as lines or point with modern cadastral maps built from these early land surveys.

To assess changes between pre-industrial and modern composition, data from the historical survey records were compared with the Quebec government's forest inventories from the last three decades (1980, 1990, and 2000). These inventories are based on 0.04 ha plots that are distributed proportionally according to the surface area of different types of productive forest stands (capable of producing at least 30 $m^3.ha^{-1}$ timber in less than 120 years). Within the plots, all stems >2 cm DBH (Diameter at Breast Height; 1.3 m) of each species are measured and inventoried, and used here to calculate basal area ($m^2.ha^{-1}$) by species. Finally, a rank was assigned to each taxon according to its relative basal area within modern plots. Some species (spruces, maples, pines, poplars) within the modern database were grouped at the genus level to match the taxa mentioned by surveyors. Taxa mentioned in less than 5% of taxa lists of both historical and modern databases were grouped as “others”.

2.5.2 Data analysis

Three different composition indices were computed for both historical and modern databases. First, an overall prevalence index was computed as the percentage occurrence of each taxon in all taxa lists, regardless of its rank in those lists. Second, an frequency index (F_{ir}) was computed for each taxon occurring in the first four ranks of enumeration in the taxa lists (*i.e.* r = 1, 2, 3, 4 ; Scull & Richardson 2007) using the formula :

$$F_{ir} = (N_{ir} / M_r) \text{ x } 100$$

where N_{ir} is the number of times taxon i is ranked at position r, and M_r is the total number of observations that include at least r taxa. Third, the dominance index represents the frequency of occurrence of each taxon i at the first ranking position (*i.e.* $r = 1$).

To compare pre-industrial and modern compositions at the landscape scale, the study area was divided into 25 km^2 cells (5 km x 5 km). Prevalence and dominance indices were computed for each epoch and each cell with at least 5 observations. This resulted in two grids, respectively containing 129 and 155 cells for the pre-industrial and modern periods (modern inventories were more uniformly spread, allowing a larger number of cells to be retained).

Spatially constrained clustering (Legendre & Fortin 1989; Legendre & Legendre

2012) was then used to determine geographically homogeneous areas of pre-industrial and modern composition. The test determines agglomerative clusters, with a spatial contiguity constraint, for a distance matrix that is calculated from multivariate data (Legendre 2011; Legendre & Legendre 2012). Prevalence and dominance index values of each taxon and each cell were converted to an Euclidean distance matrix. Clustering was then computed on the basis of this matrix, constrained by a geographical distance matrix between cells. Optimal numbers of groups were chosen by cross-validation to minimize residual error. Within each group, prevalence and dominance indices were re-computed and expressed as diagrams attached to the results maps (Figures 2.2a and 2.2c).

Spatially constrained clustering was used with 11 environmental and historical variables. The 11 variables represent three types of surface deposits (lacustrine clay, glacial till and rocky deposits), three types of drainage, four variables related to settlement (agricultural land, urban land, paved roads and secondary roads), and one variable representing burned areas during the 20th century (geo-referenced data from aerial photographs and remote sensing data dated from 1924 to 2011; SOPFEU database). The vast majority of burned areas dated from the period 1930-1950, and mainly from the 1930s. Apart from paved and secondary roads, which were expressed in kilometers, all other variables were expressed as percentages of land area per cell. This data matrix was standardized and then converted to a Euclidean distance matrix prior to spatially constrained clustering. All clustering analysis were performed with the “const.clust” package (version 1.2; http://numericalecology.com/rcode) included in the R freeware (version 3.1.2; R Foudantion for Statistical Computing; Vienna; Austria; http://www.r-project.org/.).

2.6 Results

In the pre-industrial era (Table 2.1), spruces (*Picea* spp.), balsam fir (*Abies balsamea*) and paper birch (*Betula papyrifera*) were the most frequently mentioned taxa (78.1 % to 65.7 % of all taxa lists). Pines (*Pinus* spp.), poplars (*Populus* spp.), white cedar

(*Thuja occidentalis*) and yellow birch (*Betula alleghaniensis*) were also common (31.5 to 14.2 %). The most dominant taxa (listed as rank 1) were spruces and fir (46.5 % and 20.8 %, respectively). Spruces were more frequently mentioned at rank of 1 than ranks 2-4, indicating that they tended to dominate the canopy when present.

Comparison of pre-industrial and modern forest composition highlights significant changes at the regional scale (Table 2.1). Maples (*Acer* spp.) and poplars have experienced the greatest prevalence increases (+47.0 % and +38.5 %, respectively). With regards to dominance, poplars and paper birch increased by +19.9 % and +8.1 %, while spruce and fir decreased by -27.6 % and -7.8 %.

At the landscape scale, spatially constrained clustering highlights a strong pattern within the composition of the pre-industrial forests (Figure 2.2a). In group 1a the most frequent and dominant taxa were spruces, fir and paper birch. Group 2a differed from the first group by its stronger balsam fir dominance. Dominated by white cedar, pines and poplars, Group 3a clearly stood out from the rest of the study area. Group 4a covered the southern portion of the study area and was dominated by poplars, spruce and paper birch. In contrast, the modern era (Figure 2.2c) comprises five groups dominated by conifers, mainly spruces and fir, but also including two groups where white cedar is among the three dominant taxa (groups 4c and 5c). The remaining four modern groups cover the rest of the study area, and are dominated by poplars, spruces, paper birch and fir. Spatially constrained clustering based on environmental and historical variables retained six groups (Figure 2.2b). Group 1b correspond to mixed drainage-deposit hills not settled or burned during the 20th century. Groups 2b and 3b represent areas of mixed drainage-deposit hills which have largely burned over the period 1930-1950. Finally, groups 4b, 5b and 6b were mostly settled during the 20th century (cropland and urbanization) in lowlands dominated by lacustrine clay deposits.

These environmental-historical groups highlight strong patterns of compositional changes across the landscape. Groups 2b and 3b, which were burnt between 1930 and

1950, experienced a sharp decrease in prevalence and dominance of spruces and fir, and concomitant strong increases of poplars. Conifers dominance generally decreased slightly in settlement groups (4b, 5b and 6b) while the prevalence and dominance of poplars and paper birch increased. Group 1b, which was not burned or settled during the 20th century, exhibited a slight decrease in spruces and fir and also experienced an increase in dominance of white cedar. Finally, maples experienced a sharp increase in prevalence over time in all groups.

Table 2.1 Total prevalence index and ranked frequency index (*Fir*) of major taxa throughout the study area for pre-industrial (1874–1935) and modern (1980–2009) periods. The dominance index corresponds to $F_{ir} = 1$.

Taxa	**1874-1935** (n=5207)					**1980-2009** (n=4749)				
	prev.	F_{ir} (%)				prev.	F_{ir} (%)			
	(%)	1	2	3	4	(%)	1	2	3	4
Spruces	78.1	46.5	22.9	11.0	8.6	71.7	18.9	16.2	17.1	17.1
Fir	70.4	20.8	44.9	11.6	9.4	70.7	13.0	16.9	20.3	17.4
Pines	31.5	5.2	4.0	5.2	15.3	24.2	8.0	5.2	4.6	4.8
Cedar	19.8	3.1	2.3	5.1	16.3	15.2	5.2	2.7	2.3	3.1
Larch	8.0	1.9	3.3	2.4	2.2	4.7	0.7	1.3	1.2	1.5
Poplars	24.8	8.7	4.0	5.0	17.3	63.4	28.6	15.3	10.5	7.3
Paper birch	65.7	7.3	15.0	55.4	17.3	78.8	15.4	23.0	20.9	17.7
Yellow birch	14.2	1.7	3.5	4.2	13.5	6.9	1.6	1.5	1.2	1.5
Maples	1.1	0.1	0.1	0.1	0.1	48.1	3.1	8.3	12.3	16.4
Others	4.6	4.7	0.0	0.0	0.0	46.2	5.5	9.5	9.6	13.2
Total		100.0	100.0	100.0	100.0		100.0	100.0	100.0	100.0

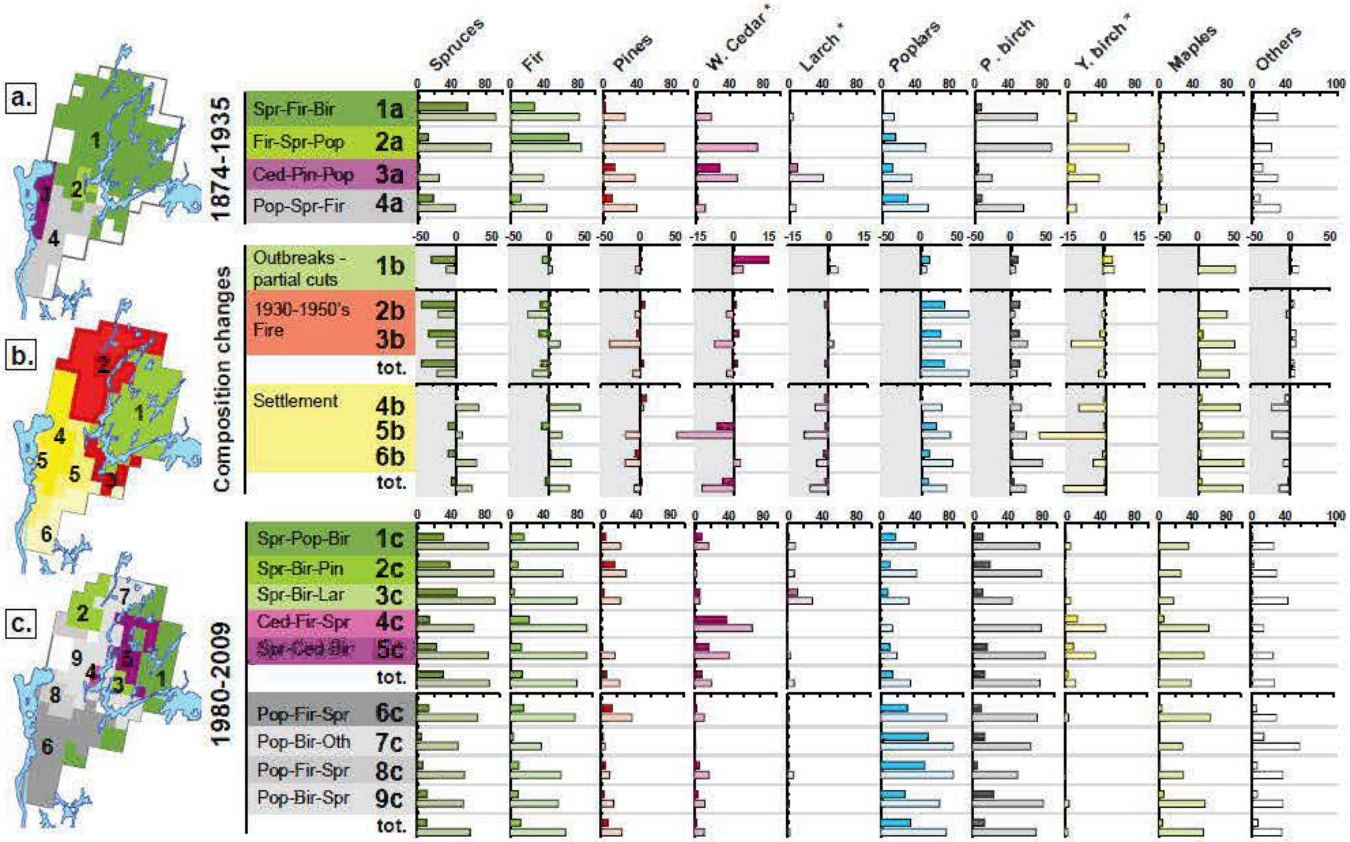

Figure 2.2 Spatially constrained clustering groups with pre-industrial (a) and modern (c) compositions. Spatially constrained clustering groups with environmental and historical variables (b). For each taxon, histograms represent dominance index (header in full colour bar) and frequency index (bottom light colour bar) in percentage for composition groups (a and c) and differences between modern and pre-industrial composition for environment– historical groups (b). Composition groups are captioned by their first three dominant taxa (Spr: spruce, Fir: balsamfir, Bir: paper birch, Pop: poplars, Ced: white cedar, Pin: pines, Lar: larch, Oth: other). Note that histograms (b) of the taxa captioned by a * are represented on a smaller scale (15%, +15%).

2.7 Discussion

2.7.1 Pre-industrial composition and vegetation changes at the regional scale

Our results show a regional strong increase in early-successional (poplars, paper birch) and mid-successional (maples) deciduous taxa at the expense of pre-industrial dominant conifers (mainly spruces and fir). Regional pre-industrial forest composition and post-industrial changes similar to our study area have been widely documented across eastern temperate and boreal North America (Siccama 1971; Lorimer 1977; Abrams 1998; Bürgi et al. 2000; Jackson et al. 2000; Dyer 2001; Cogbill et al. 2002; Friedman & Reich 2005; Pinto et al. 2008; Dupuis et al. 2011; Thompson et al. 2013). Studies in northern Europe have reported a post-industrial rejuvenation of forest landscapes, although modern forest management and intentional suppression of deciduous trees have shifted composition from mixed to coniferous forest (Östlund et al. 1997; Axelsson et al. 2002; Lilja & Kuuluvainen 2005).

The land survey records used in this study were conducted at the end of the Little Ice Age (Mann & Jones 2003; Moberg et al. 2005; Gennaretti et al. 2014). Regional annual mean temperatures have since increased by approximately 1°C (http://berkeleyearth.lbl.gov/locations/47.42N-79.34W, accessed july 23, 2015). Eastern Canadian climate has also become moister (Tardif & Bergeron 1997; Zhang et al. 2000; Girardin et al. 2004) and, combined with fire suppression policies, has led to a sharp decrease in fire frequency (Bergeron & Archambault 1993; Bergeron et al. 2006). Such changes could have shifted regional composition from cold-adapted to warm-adapted taxa and from fire-adapted to fire-sensitive taxa (Nowacki & Abrams 2008; Hanberry et al. 2012). However, these climate-related changes do not seem to have significantly influenced our results since the taxa having experienced the greatest increase (poplars and paper birch) are boreal fire-adapted species (Perala 1991; Safford et al. 1991). Increase in prevalence of Maples (mostly red maple, *Acer rubrum*; according to modern inventories) could be due to rising temperatures

(Tremblay et al. 2002; Fisichelli et al. 2014; Zhang et al. 2015) and have also been associated with the decrease in fire activity (Nowacki & Abrams 2008). On the other hand, red maple is a "super generalist" species that is largely favoured by disturbance (Walter & Yawney 1991; Abrams 1998, Fei & Steiner 2009), even including fire at its northern range limit in the study area (Zhang et al. 2014).

2.7.2 Pre-industrial composition at the landscape scale

Spatially constrained clustering analysis highlights spatial structure in pre-industrial composition at the landscape scale (Figure 2.2a). Most of the study area was dominated by spruces (group 1a). Currently, black spruce (*Picea mariana*) is the main species in the study area, so it is very likely that it also dominated the pre-industrial landscape. Abundant glacial and rocky deposits in this hilly region and frequent fires in the pre-industrial period (Grenier et al. 2005) promoted black spruce, due to its semi-serotinous cones that allow it to establish after fires (Viereck 1983; Viereck & Johnston 1990) and to maintain strong dominance in the landscape (De Grandpré et al. 2000; Pham et al. 2004; Bouchard et al. 2008; Cyr et al. 2012).

The area that was dominated by trembling aspen (currently the main species present in the area, group 4a) in the preindustrial landscape corresponded to an early successional stage and, in fact, was described as an area of "*old burnt*" by surveyors in the 1880s (data not shown), which probably corresponded to a 1870s fire. Trembling aspen is a fire-adapted species and is favored by lacustrine clay deposits (Bergeron & Charron 1994; Bergeron 2000) that are abundant in these lowland area.

Finally, the area co-dominated by white cedar and pines in the pre-industrial period represents a contradictory association (group 3a). White cedar is a fire-sensitive and shade-tolerant late-successional species (Johnston 1990; Hofmeyer et al. 2009), while white pine (*Pinus strobus*) and red pine (*Pinus resinosa*), which are currently the main pine species in this area, are fire-adapted species (Wendel & Smith 1990; Flannigan 1993; Abrams 2001). Small-scale surface fires could maintain uneven-aged stands of white pine (Quinby 1991; Abrams 2001), and could also allow the maintenance of white cedar in the landscape. Landscapes surrounding large lakes such as Lake Témiscamingue may show strong spatial variation in terms of fire frequency and intensity compared to adjacent mainland landscapes (Bergeron 1991; Drobyshev et al. 2010) and could therefore explain the occurrence of small surface fires in this area.

2.7.3 Native Americans and naturalness of the pre-industrial landscape

Land use practices of Algonquin-Anishinaabe population inhabiting the study area during pre-industrial times are not documented. However, use of fire has been reported as a common practice for Algonquin tribes (Clark & Royall 1996; Williams 2003; Munoz & Gajewski, 2010). Hunter-gatherers population usually burned small patches for habitation, to improve travelling and to manage wild animal or plant populations (Lewis & Ferguson 1988; Gottesfeld 1994). Although large crown fires which have widely favoured black spruce or poplars seem mainly linked to fire-favorable climatic conditions at the end of the Little Ice Age (Bergeron et al. 2006; Clifford & Booth 2015), the Lake Témiscamingue area was an important transit path and summer occupation spot during pre-industrial times (Riopel 2002), and white cedar and pines which co-dominated the area were important keystone species for Algonquin communities (Danielsen 2002; Uprety et al. 2013). Consequently, it seems likely that Algonquin population used to manage this area and that they promoted dominance of white cedar and pines through small scale surface burning or other management practices. Localized modification by native community within the forest landscape have been widely documented across northeastern America (Delcourt & Delcourt 2004; Black et al. 2006; Munoz et al. 2014) and northern Europe (Josefsson et al. 2009; Josefsson et al. 2010; Rautio et al. 2015).

2.7.4 Post-industrial changes at landscape scales

Areas that were widely burned during the period 1930-1950 (mostly in the 1930s) recorded a shift from dominance of fire-adapted black spruce to early successional deciduous trembling aspen. The likely explanation for this shift is the high logging activity that prevailed during the 1920s and 1930s in the study area (Lienert 1966). These cuts may have removed much of the black spruce aerial seed bank, which allowed trembling aspen to become dominant after the 1930s large fires. Settled territories also showed a shift from dominance of main pre-industrial conifers to trembling aspen and paper birch (groups 4b, 5b and 6b) which could clearly be explained by disturbances related to settlement (land clearing, logging, settlement fires, etc.).

The northeastern part of the study area, which neither burned nor was settled during the 20th century, shows a smaller decrease in black spruce pre-industrial dominance compared to burned areas, and an increased dominance of white cedar. Increased dominance of white cedar can be attributed to spruce budworm outbreaks (Frelich & Reich 1995; Bergeron 2000; Bouchard et al. 2006b), whose main hosts are balsam fir and spruces, as well as former partial cuts of large pines and spruces trees (Heitzman et al. 1997; Larouche et al. 2011).

2.7.5 Implication for forest restoration and management

In this regional context, composition restoration through forest management should aim to promote conifer dominance. This could be achieved through partial cutting in mixed stands dominated by trembling aspen to accelerate succession towards coniferous stands (Man et al. 2008; Bose et al. 2014). However, considering the potential impacts of climate change, it would be important to develop an adaptive restoration plan (Harris et al. 2006; Millar et al. 2007; Choi et al. 2008). The pre-industrial dominance of some conifers (black spruce, pine) was largely the result of a higher fire frequency compared to those anticipated for the future (Bergeron et al. 2006). Moreover, the increase of deciduous species abundance throughout the 20th century probably accentuated this phenomenon by decreasing forest fire susceptibility (Nowacki & Abrams 2008; Terrier et al. 2013). Restoration measures could seek to promote dominance of late-successional conifers and deciduous species, which are not dependent on fire (balsam fir, white spruce, white cedar, yellow birch).

2.8 Conclusion

Combinations of environmental gradients, recurrence of natural disturbance and maybe Native Americans land-use have structured distinct pre-industrial landscapes. Frequency and intensity of fires were the main drivers of forest dynamics and composition across the landscape. Fire remained an important driver of post-industrial compositional changes, but the appearance of Euro-American disturbances, including logging and settlement fires, disrupted historical forest dynamics. Consequently, Euro-American settlement has led to a major shift of the forest composition at the regional scale, promoting a strong dominance of early successional deciduous species. Climate change did not seem to have an important influence on the compositional changes that are documented in this study.

These results document the forest naturalness within the region, and then bring tools for forest management and restoration. These also help to create a baseline for future climate-driven changes, which are predicted to be quite dramatic in biogeographic transition zones (Parmesan et al. 2005). Many forest landscapes such as our study area are recovering from major land-use changes (Rudel et al. 2005; Foley 2005), which can control forest dynamics much more than climate changes (Bodin et al. 2013; Abrams & Nowacki 2015; Nowacki & Abrams 2015). Thus, land-use legacies could be considerable drivers of future landscape changes and should be seriously considered when modelling and predicting future climate-driven ecological changes.

2.9 Acknowledgements

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CHAPITRE III

LONG-TERM COMPOSITIONAL CHANGES FOLLOWING PARTIAL DISTURBANCE REVEALED BY THE RE-SURVEY OF LOGGING CONCESSION LIMITS IN THE NORTHERN TEMPERATE FOREST OF EASTERN CANADA.

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3.1 Abstract

Land use changes that are linked to European settlement of North America have transformed north-eastern temperate forest landscapes. Many studies report a regional increase of young early-successional forests due to high disturbance rates since the preindustrial era (fire, land-clearing, clear-cuts). In this study, we document specific compositional changes to present day mature forest landscapes, which have only been managed with partial cutting (high-grading and diameter-limit cuts) since the preindustrial era in south-western Quebec. We re-surveyed 108 forest observations that were extracted from logbooks of former logging concession limits (surveyed between 1870 and 1890). Results highlight an increase in mid- to late-successional shade-tolerant taxa (*Betula alleghaniensis*, *Thuja occidentalis*, *Acer saccharum*) at the expense of preindustrial dominant conifers (*Abies balsamea, Pinus strobus*). Former logging activities and spruce budworm outbreaks appear to be the main drivers of these changes, which were also strongly structured across the topographic gradient. To some extent, these results highlight the relevance of partial cutting management since it has allowed long-term maintenance of a mid- to late-successional forest composition, while also pointing the need for *Pinus strobus* restoration. We conclude that by allowing site-specific comparisons, the re-survey of historical observations greatly improve the analytical strengths of historical reconstruction.

Keywords: Forest succession, historical ecology, ecosystem-based management, preindustrial forests, presettlement forests.

3.2 Résumé

La colonisation européenne de l'est de l'Amérique du Nord a engendré une profonde transformation des paysages forestiers. De nombreuses études ont décrit une augmentation des jeunes forêts de début de succession comme conséquence des forts taux de perturbation liés à la colonisation (feux, défrichement, coupes à blanc). Dans cette étude, nous documentons les changements de composition spécifiques à des paysages forestiers aujourd'hui matures, qui n'ont été exploités que par des coupes partielles (coupes d'écrémage et coupes à diamètre limite) depuis l'époque préindustrielle. Nous avons réarpenté 108 observations de composition issues de rapports d'arpentage d'anciennes limites de concessions forestières (arpentées entre 1870 et 1890). Les résultats indiquent une augmentation de taxons de milieux à fin de succession (*Betula alleghaniensis*, *Thuja occidentalis*, *Acer saccharum)* au détriment des conifères dominant à l'époque préindustrielle (*Abies balsamea, Pinus strobus*). Ces changements de composition sont principalement la conséquence des coupes et des épidémies de tordeuse des bourgeons de l'épinette, et se sont aussi largement structurés le long du gradient topographique. Ceci témoigne de la pertinence de l'aménagement par coupes partielles, puisqu'il a permis le maintien d'une composition de milieux à fin de succession. Cependant, la restauration des populations de *Pinus strobus* parait aussi nécessaire. Nous concluons qu'en permettant la comparaison de sites appariés, le réarpentage d'observations historiques améliore remarquablement la compréhension des changements de composition survenus depuis l'époque préindustrielle.

Mots clefs : Succession forestière, écologie historique, aménagement écosystémique, forêts préindustrielles, forêts précoloniales.

3.3 Introduction

Global change is responsible for major shifts in forest ecosystems characteristics. In north-eastern North America, land use changes that are linked to European settlement have transformed forest landscapes (Whitney 1994). Modern landscapes are generally considered to be younger, and composed of an increased proportion of early-successional species compared to preindustrial landscapes (Mladenoff et al. 1993; Foster et al. 1998; Dupuis et al. 2011; Thompson et al. 2013). Knowledge of forest composition prior to Euro-American settlement is therefore used as a reference for restoration and forest management (Egan & Howell 2001; Foster et al. 2003).

In northern temperate forests, several studies have reported that preindustrial landscapes were dominated by old uneven-aged forests (Lorimer & White 2003; Boucher et al. 2009), the dynamics of which were mainly controlled by natural partial disturbances (gaps, insect outbreaks). In order to maintain forest landscapes within their range of natural variability, ecosystem-based management of these forests should be based mainly upon different types of partial cutting (Seymour et al. 2002; Raymond et al. 2009). In south-western Quebec, a substantial proportion of the landscape has only been managed through partial cutting (high-grading and diameter-limit cuts) since the preindustrial era. These present day mature forest landscapes appear to have followed distinct post-industrial compositional trajectories, compared with those of highly disturbed landscapes, which were converted into younger early-successional forests (Danneyrolles et al. 2016). The knowledge of long-term compositional changes after these types of partial cutting management could help in assessing the relevance of such practices, and in developing management tools adapted to these mature forest landscapes.

Reconstructions of post-industrial compositional changes that are methodologically based on regional-scale comparisons between historical data-sets (i.e. historical land survey data) and modern forest inventories commonly reveal general trends (eg. Friedman & Reich 2005; Thompson et al. 2013). However, these reconstructions are not sufficiently reliable to properly characterize more precise compositional changes that concern only specific landscapes. Since the main objective of this study was to document specific compositional changes that occurred in landscapes having only been managed by partial cutting, our reconstruction is based on the re-survey of historical observations (i.e. historical and modern observations that were paired at the same location). Yet, few studies have used this original methodological approach (Siccama 1971; Fahey & Lorimer 2014), even though it may allow a deeper understanding of long-term compositional changes. More particularly, we addressed two main questions: (1) what were the main drivers of these compositional changes? (2) How have environmental gradients, particularly the topographic gradient, structured these compositional changes?

3.4 Study area

The study covers an area of about 4000 km^2 along the south-west boundary of the Canadian province of Quebec (Fig. 3.1). The forests in the study area form the northern end of the Great Lakes St. Lawrence mixed forest region (Rowe 1972), which also corresponds to the limits between the maple-yellow birch and balsam fir-yellow birch bioclimatic domains of the provincial classification (Robitaille & Saucier 1998). The principal surface deposits are either undifferentiated or rocky glacial till. The closest weather station (Barrage Témiscamingue, 46°42'N, 76°06'W; 181 m asl.) has recorded a mean annual temperature of 4.9°C and annual total precipitation of 937 mm for the period 1981-2010.

Elevation varies from 290m to 415m (asl.). Several factors that are related to topography influence forest composition (drainage, nutrient availability, soil depth and micro-climate ; MacHattie & McCormack 1961). Natural stand-replacing fire rotation has been estimated to be about 200 years in duration within the balsam fir-yellow birch domain (Grenier et al. 2005), and 500 years within the maple-yellow birch domain (Drever et al. 2006). Outbreaks of spruce budworm (*Choristoneura fumiferana*) also have been identified as a major source of disturbance of forest dynamics over the last century (Bouchard et al. 2006a,b).

First Nations have inhabited the study area for at least 5000 years (Riopel 2002). However, patterns of land use and management by Algonquin tribes during preindustrial times remain unknown. Logging did not begin until 1840, and was mainly focused on high-grading cutting of tall pines trees (*Pinus* spp.) until 1917 (Riopel 2002). Following the construction of a paper mill in the city of Témiscaming in 1917, diameter-limit cuts of smaller diameter spruces (*Picea* spp.) and balsam fir (*Abies balsamea* [L.] Mill.) for wood pulp became the main logging activity until the end of the 20th century (Lienert 1966), although high-grading cutting of tall trees for lumber remained frequent.

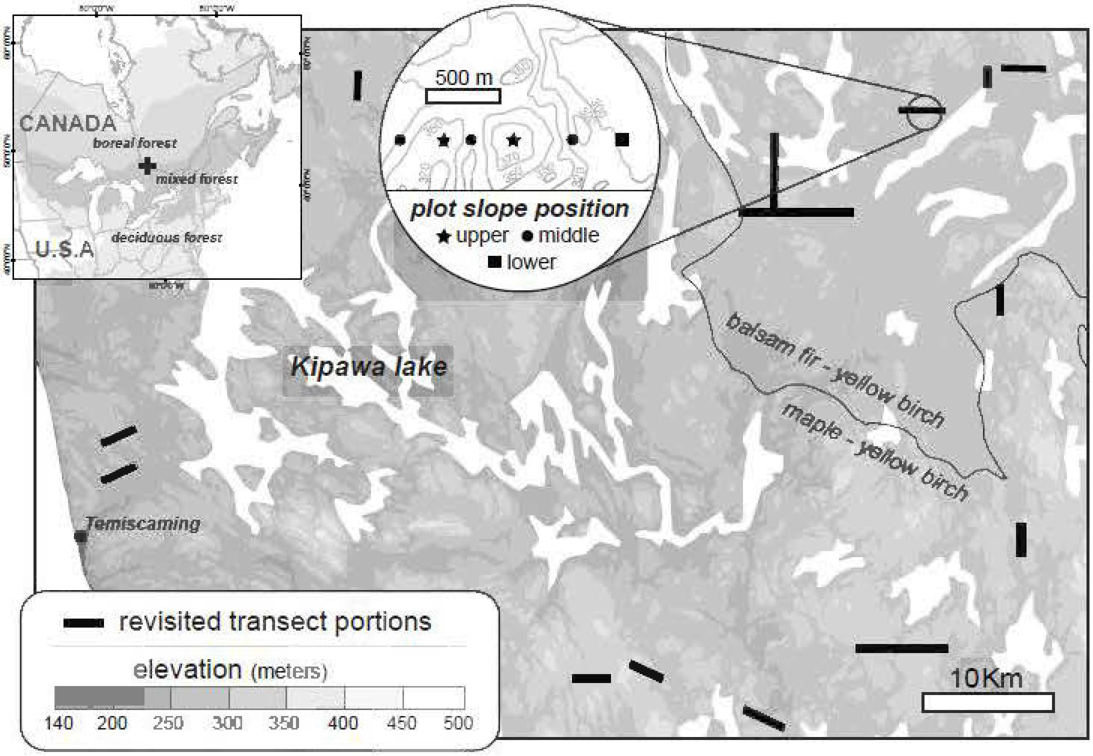

Figure 3.1 Study area, localization of re-surveyed transect portions, and illustration of the three topographic positions.

3.5 Material and methods

3.5.1 Site selection and field measurements

This study is based on the re-survey of 108 historical observations of forest composition that were extracted from 10 logbooks reporting the first survey of logging concession boundaries, which were realized by four different surveyors between 1870 and 1890. These logbooks contain point observations mentioning taxa lists (e.g., *"Pine, spruce, birch, cedar and a few maples"*), which were usually 10 chains (about 200 m) apart along the survey lines. Point observations have been geo-referenced using historical maps with a resolution of about 20 meters. These 10 logbooks were selected for their consistent methodology.

A total of 108 observations that were to be re-surveyed had been selected according to four criteria. (1) Observations had to be spaced at least 200 m apart to minimize spatial auto-correlation. (2) To restrict sampling to the most ecologically accurate observations, only taxa lists mentioning at least two taxa were retained (90 % of selected observations mentioned three to five taxa). (3) To document dynamic trajectories of forests that had not experienced stand-replacing disturbance since preindustrial times, observations that were retained had to be located in present-day mature forests. These forests corresponded to a dominant age class of 90 year, 120 year, or as uneven-aged in the modern forest maps (Berger 2008). Their old ages had to be confirmed in the field through the presence of old trees and irregular structure. (4) Only observations that were located within 4 km of the road network were finally retained.

In the field, each observation point was registered using a GPS with a 10 m precision. These locations determined the centres of 11.28 m diameter circular plots of (400 m^2). Within each plot, all stems greater than 10 cm in diameter at breast height (DBH, 1.3 m) were inventoried at the species level, and their DBH measured. Evidence of former cuts (stumps) or spruce budworm outbreaks (standing or lying dead stems) were recorded if they were recognizable either inside of or in proximity to the plots.

3.5.2 Data-base construction and analysis

For all historical and modern observations, taxa were classified according to 5 abundance ranks (r). Despite the possible existence of bias in these types of ranked list, for example giving more prominence to highly visible or commercially valuable taxa, a recent study demonstrated that taxa positions within lists are well correlated with their relative basal area (Terrail et al. 2014). Thus, for historical observations, taxa were ranked according to their position in the taxa list. The dominant taxon (first position in the list) was ranked as 4; the following two taxa in the list were ranked as 3 and 2, and rank 1 was assigned to the remaining taxa in the list. For example, the observation "*Pine, spruce, yellow birch, cedar and a few maples*" would have been transcribed as pines ($r = 4$), spruces ($r = 3$), yellow birch ($r = 2$), cedar ($r = 1$), maples ($r = 1$) and ($r = 0$) for non-cited taxa. The same process was used to assign ranks to taxa that were inventoried in the re-surveyed plots, according to their relative basal area. Some species from the modern plots were grouped at the genus level to match the taxa that were mentioned by surveyors, while rarely mentioned taxa (<5%) within historical and modern observations were grouped in as "others". Taxa that represented less than 5% of the total basal area of a plot were removed from the list, to obtain an equivalent number of taxa for historical and modern observations.

Several simple metrics were used to document changes in forest composition. First, frequency and dominance indices were computed (Scull & Richardson 2007; Dupuis et al. 2011). The frequency index represents the proportion of taxon occurrences regardless of rank (i.e., $r \neq 0$), while the dominance index represents the proportion of taxon dominance (i.e., $r = 4$). These indices were computed for each taxon and for each period, within the whole data-set and for three topographic positions (lower slopes, middle slopes and upper slopes; Fig. 3.1). Second, a simple relative rank difference (D_i) was computed according to the formula:

$$D_i = R1880_{ip} - R2014_{ip}$$

where $R1880_{ip}$ corresponds to the rank of taxon i within plot p during the period 1870-1890, and $R2014_{ip}$ is the rank of taxon i within plot p in 2014. Paired sample tests (Wilcoxon signed-rank tests) were used to assess the significance of rank differences ($R1880_{ip}$ vs. $R2014_{ip}$) for the entire data-set and by topographic position.

Table 3.1 Dominance and frequency indices of each taxon in the 1870-1890 preindustrial period and in 2014 for the whole data-set ($n = 108$).

	1870-1890		2014	
TAXA	Dom.	Freq.	Dom.	Freq.
Balsam fir	45.9	87.2	7.3	51.4
Pines	16.5	56.9	2.8	7.3
Spruces	7.3	37.6	2.8	32.1
W. cedar	8.3	41.3	27.5	59.6
Y. birch	17.4	62.4	36.7	82.6
Maples	1.8	7.3	19.3	51.4
P. birch	2.8	25.5	1.8	29.4
Other	0.0	6.4	1.8	12.8

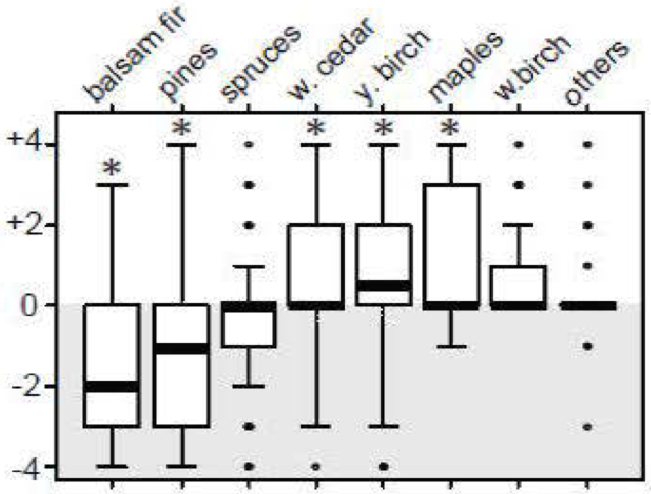

Figure 3.2 Relative rank difference (D_i) of each taxon for the whole data-set (n = 108). The asterisks indicate significant (P < 0.001) rank differences (Wilcoxon signed-rank test).

3.6 Results

During the preindustrial period (1870-1890), the 108 stands were dominated by balsam fir (*A. balsamea*), pines (*Pinus* spp.) and yellow birch (*Betula alleghaniensis* Britten) with dominance indices of 46 %, 17 % and 17 %, respectively (Table 3.1). Although less dominant, eastern white cedar (*Thuja occidentalis* L.), spruces (*Picea* spp.) and paper birch (*Betula papyrifera* Marshall) were frequent (41 %; 37 % and 28 %, respectively; Table 3.1). Evidence of former partial cuts (stumps) and spruce budworm outbreaks (numerous standing and lying dead stems) were found in all stands. Unfortunately, an obvious distinction between these two kinds of disturbance was not always possible, and most stands had likely been subjected to both kinds of disturbance during the 20th century.

These stands have experienced major composition changes since the end of the 19th century. Overall balsam fir dominance decreased from 46 % to 7 % (Table 3.1), while its ranking within plots significantly decreased by an average of 1.6 ranks (Fig. 3.2). Balsam fir preindustrial dominance was high at the three topographic positions (Fig. 3.3) but its ranks mostly decreased at mid- and upper slope positions (Fig. 3.4). Consequently, balsam fir has maintained a greater dominance on lower slopes (Fig. 3.3), with a high density of small stems (Fig. 3.5). Despite these changes, balsam fir is still one of the most frequent taxa in the study region, with an overall frequency of occurrence greater than 50% (Table 3.1).

The taxon “pines” corresponds mainly to white pine (*Pinus strobus* L.; Table 3.2). This taxon experienced a sharp decrease in dominance (from 17 % to 3 %) and frequency (57 % to 7 %; Table 3.1) since preindustrial times. Pine rankings within plots significantly decreased for the entire data-set (Fig. 3.2) at all topographic positions (Fig. 3.4), especially on lower slopes where pine was very dominant during preindustrial times.

Overall yellow birch dominance increased from 17% to 37%, while its frequency also increased from 62 % to 83 % (Table 3.1). Its rank within plots significantly increased for the whole data set (Fig. 3.2), particularly on lower and mid-slopes where it was less abundant during preindustrial times (Fig. 3.3 and 3.4). Yellow birch is currently characterized by low densities of large stems (Fig. 3.5). Its dominance and frequency are constant along the topographic gradient (Fig. 3.3).

Dominance and frequency of white cedar have increased from 8 % to 28 % and from 41 % to 60 % respectively (Table 3.1). White cedar ranking within plots has significantly increased for the entire data-set (Fig. 3.3), especially on lower and middle slopes positions (Fig. 3.4), where cedar is currently the most abundant taxon.

The taxon “maples” corresponds mainly to sugar maple (*Acer saccharum* Marshall; Table 3.2). This taxon experienced the strongest increase in dominance (from 2 % to 19 %) and frequency (7 % to 76 %; Table 3.1). Maple ranking within plots significantly increased for the whole data-set (Fig. 3.2), especially on middle and upper slopes (Fig. 3.4) where maples currently are remarkably abundant.

Spruces and paper birch have not experienced significant changes in their abundance in the whole data-set (Fig. 3.2) and at all topographic positions, except for spruces, which decreased significantly on lower slopes (Fig. 3.3).

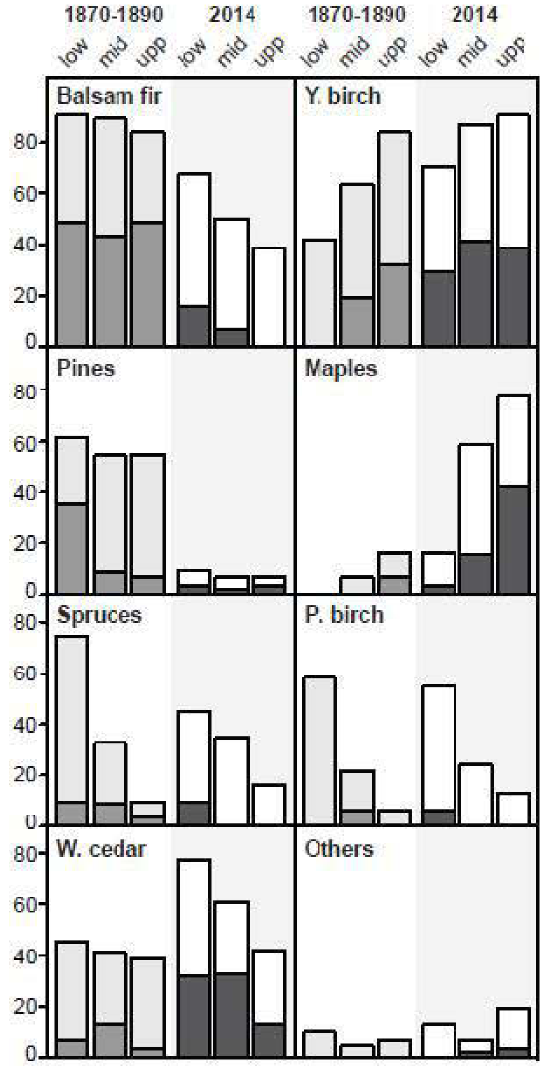

Figure 3.3.

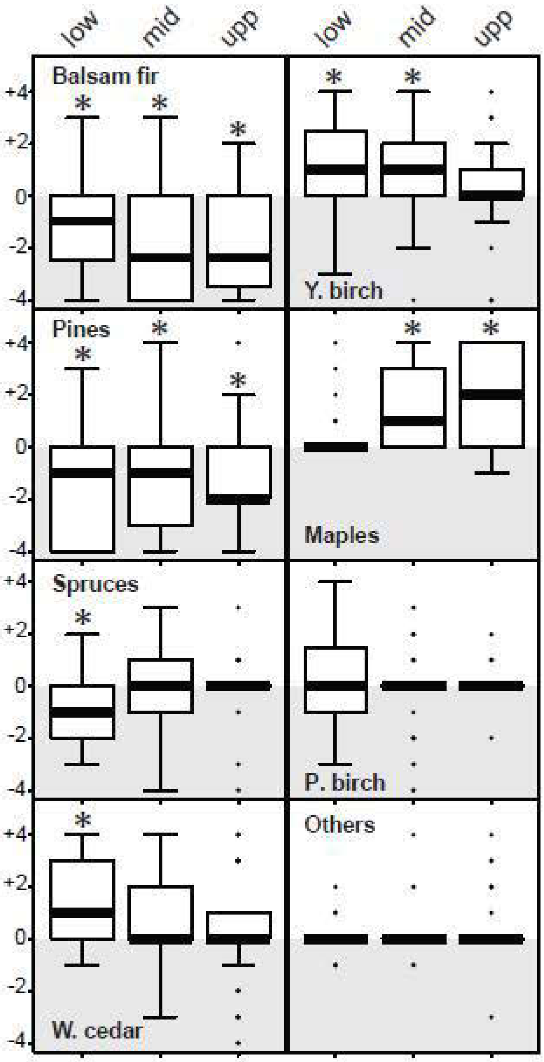

Figure 3.4

Figure 3.3 Dominance (dark grey) and frequency (light grey) of each taxon during the 1870-1890 period and in 2014, for lower slope (low; $n = 31$), mid-slope (mid; $n = 46$) and upper slope (upp; $n = 31$) positions.

Figure 3.4 (a) Relative rank difference (D_i) of each taxa for lower slope (low; $n = 31$), mid-slope (mid; $n = 46$) and upper slope (upp; $n = 31$) positions. The asterisks indicate significant ($P < 0.01$) rank differences (Wilcoxon signed-rank tests).

Table 3.2 Details of species of pines, spruces and maples that were cited by surveyors (1870-1890) and identified on the field (2014). In many cases, surveyors cited these taxa at the genus level, so the data have been regrouped by genus level for the remaining analyses.

	1870-1890		2014	
TAXA	Dom.	freq.	Dom.	freq.
white pine	16.5	27.5	2.8	7.3
red pine	x	x	x	0.9
pines	x	29.4	x	x
ALL pines	16.5	56.9	2.8	7.3
sugar maple	x	x	19.3	40.7
red maple	x	x	x	30.6
maples	1.8	7.3	x	x
ALL maples	1.8	7.3	19.3	51.3
white spruce	x	x	0.9	28.7
black spruce	x	x	1.9	8.3
spruces	7.3	37.6	x	x
ALL spruces	7.3	37.6	2.8	32.1

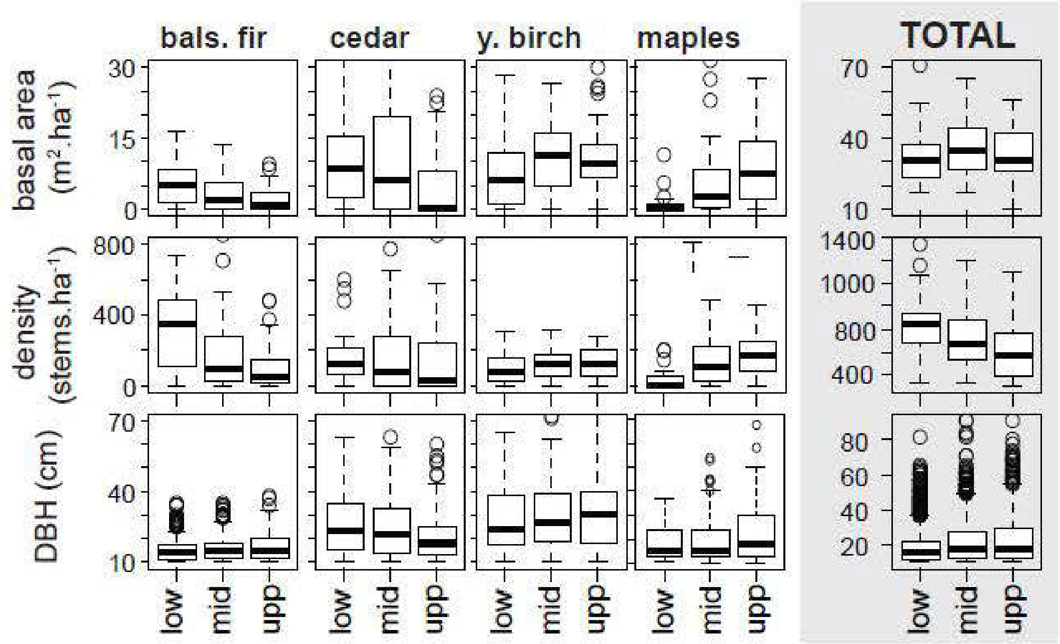

Figure 3.5 Overall structural characteristics of present-day forests (total), and of the four currently most abundant taxa by topographic position.

3.7 Discussion

Our results attest to major compositional shifts in mature stands over the last 130 years. Industrial logging started towards the end of the 19th century with high-grading cutting of tall pines, then intensified from 1917 (Témiscaming paper mill construction) onward with diameter-limit cutting of smaller spruces and balsam fir (Lienert 1966; Riopel 2002). These former management practices were mainly focused on harvest, and did not aim to favour particular stand characteristics. Intensive exploitation of pines was undoubtedly the main factor explaining their disappearance from these stands. Diameter-limit cuts at the beginning of the 20th century may also explain, in part, the decline in balsam fir abundances. The widespread mortality in balsam fir populations caused by the two major spruce budworm outbreaks of the 20th century (1910-1930 and 1970-1990; Bouchard et al. 2006a,b) has been superimposed on the impacts of logging activities. Surprisingly, the abundance of spruces has not significantly decreased in these stands (except on lower slopes), while they represented the main target species for the paper industry. This likely reflect the fact that spruces were not particularly dominant in these stands in preindustrial times, and thus their diminution is not as marked as for balsam fir or pines.

Parallel with the decrease in abundance of balsam fir and pines, our results highlight a strong increase in mid- to late-successional shade-tolerant taxa (yellow birch, white cedar, sugar maple). As such, our results contrast with the increase in early-successional intolerant taxa (eg. poplars, paper birch) that has been documented in highly disturbed area within the region (Pinto et al. 2008; Danneyrolles et al. 2016) and more generally in north-eastern North America (eg. Friedman & Reich 2005; Boucher et al. 2006; Bouchard et al. 2006a; Dupuis et al. 2011; Thompson et al. 2013). Canopy openings created by partial cuts and spruce budworm outbreaks are clearly the main driver that favoured the recruitment of shade-tolerant taxa (Heitzman et al. 1997; Gasser et al. 2010; Duchesne & Prévost 2013; Larouche & Ruel 2015).

Moreover, the large amount of stumps and rotten wood generated by these disturbances may have favoured the regeneration of yellow birch (Lambert et al. 2016) and sugar maple (Caspersen & Saprunoff 2005).

The compositional changes were also significantly structured across the topographic gradient. Lower slopes remained dominated by conifers (white cedar, balsam fir, spruces), while upper slopes became dominated by hardwood species (sugar maple and yellow birch). These divergent trajectories could be explained by distinct site characteristics. First, the colder and moister micro-climate of poorly drained lower slopes may have favoured the increase in white cedar, where it can multiply by layering (Hofmeyer et al. 2009), while also allowing balsam fir and spruces to maintain an important abundance. Conversely, well-drained upper slopes, which lie outside of cold air drainage areas, were particularly favourable to the development of sugar maple (Barras & Kellman 1998). A second possible explanation for these divergent trajectories is that lower slopes were dominated by conifers in preindustrial times, while yellow birch dominated a large proportion of upper slopes. Thus, the greater abundance of deciduous litter could have promoted the establishment of sugar maples at mid- and upper slope positions (Barras et Kellman 1998; Caspersen et Saprunoff 2005), while conifer-dominated lower slopes have been more resistant to the development of hardwoods.

3.8 Conclusions

Our study documents the long-term cumulative effects of partial cutting management and spruce budworm outbreak on north-eastern temperate forest composition. Although these former management practices (high-grading and diameter-limit cuts) focused on harvest and did not aim to favour particular stand characteristics, they allowed mid- to late-successional forest composition to persist. Thus, to some extent, our results highlight the relevance of partial cutting management in north-eastern temperate forests.

Nevertheless, these former management practices have led to significant compositional changes, which bring out an important avenue for restoration and management of these mature forest landscapes. Particularly, white pine populations that had been present in the area for thousands of years (Liu 1990), and which were largely removed by the early 20th century logging activities, should be restored. Stands and seed-trees preservation could ensure the establishment of white pine trees in adjacent cuts areas (Uprety et al. 2013). However, the strong expansion of sugar maple have led to stable deciduous stands, given that maple litter tends to inhibit regeneration of conifers (Barras & Kellman 1998). Thus, these stands should be carefully managed in order to maintain or reintroduce white pine. Irregular shelterwood systems can allow the maintenance of mid-tolerant species, such as white pine or yellow birch, in uneven-aged stands dominated by shade-tolerant species (Raymond et al. 2009; Suffice et al. 2015). Moreover, enrichment planting within patch cuts (Fahey & Lorimer 2013; Hébert et al. 2013) could be used to reintroduce white pine in stand from which it was completely removed.

More broadly, our study also demonstrate the analytical strength of site-specific comparisons through the resurvey of historical observations (Fahey & Lorimer 2014). This methodological approach was highly relevant to characterize compositional changes with precise spatial resolution and allowed us to distinguish different dynamics trajectories across the topographic gradient. Such an approach can be used to complement regional-scale comparisons between historical land survey data and modern forest inventories (eg. Friedman & Reich 2005; Thompson et al. 2013) in order to refine our knowledge of post-industrial dynamics trajectories across disturbance or environmental gradients.

3.9 Acknowledgements

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CHAPITRE IV

ANTHROPOGENIC DISTURBANCES STRENGTHENED TREE COMMUNITY-ENVIRONMENT RELATIONSHIPS AT THE TEMPERATE-BOREAL INTERFACE OF EASTERN CANADA

Victor Danneyrolles, Yves Bergeron & Dominique Arseneault

Article à soumettre

4.1 Abstract

1. Disturbance may have various effects on community composition (β-diversity) and its relationships with environmental gradients. On the one hand, disturbance may lead to a spatial homogenization (decreasing β-diversity) and a decoupling of community-environment relationships by favoring a small pool of disturbance-adapted taxa across the whole environmental gradients. On the other hand, disturbance may increase β-diversity as well as the strength of community-environment relationships by increasing habitat filtering of communities.

2. We analyzed the response of tree communities to the increased disturbance rates linked to European settlement at the temperate-boreal interface of eastern Canada. We used a reconstruction of preindustrial tree communities based on historical land survey records (1854-1935), along with modern data, to assess changes in tree β-diversity patterns and community-environment relationships.

3. In preindustrial times, environmental variables explained only a small proportion of β-diversity since dominant taxa were present on the whole range of environmental gradients, whereas habitat specialists were very rare. However, preindustrial tree communities were spatially structured over large landscapes units, which we speculate was the results of preindustrial fire history.

4. Between preindustrial and modern times, our analysis highlights an increase in β-diversity as well as in the proportion of β-diversity explained by environmental variables. Increased disturbance rates have favored early-successional habitat specialists taxa and reduced the habitat breath of preindustrial generalists, thus increasing strength of community-environment relationships.

5. *Synthesis.* Our study shows that antrhopogenic disturbances may significantly interact with other abiotic filters that structure β-diversity patterns such as habitat filtering. This also suggests that the effects of disturbance on community-environment relationships are strongly dependent upon functional traits of species within the regional pool, particularly whether early- and late-successional species are

habitat generalists or specialists. Thus, it may be very difficult to generalize relationships between disturbance and β-diversity across ecosystems if analyses are limited to the taxonomic diversity.

4.2 Résumé

1. Les perturbations peuvent avoir différents effets sur la composition des communautés (diversité-β). D'un côté, les perturbations peuvent engendrer une homogénéisation spatiale (diminution de la diversité-β) et un découplage des relations communauté-environnent en favorisant un petit nombre des taxons généralistes sur l'ensemble des gradients environnementaux. D'un autre côté, les perturbations peuvent augmenter la diversité-β et la force des relations communauté-environnent en augmentant l'effet des filtres d'habitat.

2. Nous avons analysé la réponse des communautés d'arbre à l'augmentation des taux de perturbations associés à la colonisation européenne à l'interface tempéré-boréal de l'est du Canada. Nous avons utilisé une reconstitution des communautés préindustrielles basé sur des archives historiques d'arpentage (1854-1935), comparées avec des données modernes, pour évaluer les changements dans les patrons de diversité-β ainsi que dans les relations communautés-environnement.

3. À l'époque préindustrielle, les variables environnementales n'expliquait seulement qu'une faible proportion de la diversité-β dans la mesure ou les taxons dominant étaient présent sur toute la gamme des gradients environnementaux, alors que les spécialistes étaient rares. Cependant, les communautés préindustrielles étaient spatialement structurées sur des grandes unités de paysages, ce que nous spéculons être le résultat de l'histoire des feux préindustriels.

4. Entre l'époque préindustrielle et moderne, nos résultats montrent une augmentation de la diversité-β ainsi que le la proportion de diversité-β expliquée par les variables environnementales. L'augmentation des taux de perturbations a favorisé des taxons de début de succession spécialistes du point de vue des habitats, et a réduit la gamme d'habitats occupé par les généralistes dominants à l'époque préindustrielle.

5. *Synthèse.* Notre étude montre que les perturbations anthropiques peuvent significativement interagir avec d'autres filtres abiotiques qui structurent la diversité-β, comme les filtres d'habitats. Ceci suggère aussi que les effets des perturbations sut

les relations communauté-environnent dépendent fortement des traits fonctionnel des espèces du bassin régional, particulièrement si les espèces de début et de fin de succession sont généralistes ou spécialistes du point de vue des habitats. Les relations entre perturbation et diversité-β pourraient donc être très difficile à généraliser si les analyses se limitent à la diversité taxonomique.

4.3 Introduction

Within a regional species pool (γ-diversity), variation in community composition (β-diversity) is thought to reflect niche processes such as environmental filtering and biotic interactions, as well as neutral processes such as ecological drift and stochastic dispersion (Vellend, 2010; Chase & Myers, 2011; Götzenberger et al., 2012). The relative importance of environmental filtering is generally dominant when the regional species pool is small, as in northern temperate and boreal tree communities where the γ-diversity includes only a few common tree species (Myers et al., 2013). The knowledge of how environmental gradients generate diversity across forest landscapes represents a critical issue in the era of global changes, which exert their most powerful impacts by shifting disturbance regimes. For example, climate change alters fire regimes (Westerling et al., 2006; Flannigan et al., 2009) and insect outbreaks (Haynes et al., 2014). Land-use alters natural disturbance regimes (Bowman et al., 2011) and add new purely anthropogenic disturbances (eg. agriculture, forestry; Foley, 2005).

Disturbances represent key drivers of ecological diversity (Fraterrigo & Rusak, 2008) and may have various effects on β-diversity patterns. On the one hand, gradients of disturbance frequency and intensity influence spatial heterogeneity in community structure and composition (eg. Carreño-Rocabado et al., 2012; Cyr et al., 2012; Gennaretti et al., 2014a). Moreover, disturbances can also lead to diverging community structure and composition across environmental gradients (Cooper et al., 2003; Pausas & Verdú, 2008; Harvey & Holzman, 2014) and even increase the strength of community-environment relationships (Hogan et al., 2016). On the other hand, disturbances may lead to spatial homogenization and decoupling of community-environment relationships by promoting a small pool of disturbance-tolerant generalists species across the whole environmental gradients (eg. Chase, 2007; Vellend et al., 2007). This latest phenomenon has been widely reported in European and northeastern American forests that were submitted to long-term intensive land-use (eg. Schulte et al., 2007; Vellend et al., 2007; Hanberry et al., 2012a, 2012b; Thompson et al., 2013). A better knowledge of how disturbances alter β-diversity patterns and their relationships with environmental gradients would represent an advance in community assembly theory, and also improve our ability to conserve and restore biodiversity in human-modified forest landscapes (Socolar et al., 2016).

In this study, we explore the long-term response of tree communities to the increased disturbance rates linked to European settlement and industrialization at the temperate-boreal interface of eastern Canada. We used a reconstruction of preindustrial communities based on historical land survey records (1854-1935), along with modern data, to assess changes in tree β-diversity patterns and community-environment relationships. One common way to asses the relative importance of community-environment relationships is to partition the β-diversity into fractions explained by environmental variables (eg. Cottenie, 2005; Legendre et al., 2009; Myers et al., 2013). We used this methodological framework to test two diametrically opposed hypotheses:

1. *The homogenization-decoupling hypothesis*. Preindustrial tree communities were strongly structured by habitat and natural disturbance filters, which generated diversified landscapes. Increased disturbance rates following European settlement subsequently favored a small pool of more disturbance-tolerant generalist taxa across the whole environmental gradients. In this case, we expect a spatial homogenization (i.e. decrease in β-diversity) and a decoupling of community-environment relationships (i.e. decrease in the proportion of β-diversity explained by environmental variables).

2. *The heterogenization-strengthening hypothesis*. Preindustrial dominant taxa were generalist regarding environmental gradients and thus generated relatively homogeneous landscapes. Increased rates of disturbances following European settlement subsequently increased spatial heterogeneity and habitat filtering by favoring more specialist taxa and reducing the habitat breadth of preindustrial

generalists. This alternative hypothesis predicts increase in β-diversity as well as in the strength of community-environment relationships.

4.4 Material and methods

4.4.1 Study area and historical background

The study area covers 22 000 km^2 in eastern Canada (Fig. 4.1). The region is located at the transition between temperate mixedwood and boreal conifer-dominated forests (Rowe, 1972), and corresponds to the maple-yellow birch and balsam-fir yellow birch bioclimatic domains according to the provincial classification (Robitaille & Saucier, 1998; Fig. 4.1). Mean annual temperature and total precipitations (1981-2010) range from 5.2 °C and 918 mm at the southern extremity of the study area (Rapide des Joachims), to 2.3 °C and 885 mm to the north (Montbéliard). Surface deposits correspond to clays deposited by the pro-glacial Barlow Lake in lowland areas (Vincent & Hardy, 1977), and glacial tills along with rocky outcrops in upland areas. In this region, several factors that influence the establishment and growth of tree species are linked to the topographic gradient (drainage, nutrient availability, soil depth, micro-climate; Fraser, 1954; MacHattie & McCormack, 1961; Brown, 1981).

The time period covered by the historical data (1854-1935) corresponds to the end of the Little Ice Age (LIA; approx. 1250 AD – 1850 AD; Gennaretti et al., 2014b). The drier climate of the LIA was particularly favorable to fires in certain parts of eastern North America (Bergeron & Archambault, 1993; Bergeron et al., 2006; Clifford & Booth, 2015) and, in our study area, large crown fires were frequent in the north (Grenier et al., 2005) and their frequency decreased to the south (Drever et al., 2006). First Nations population in the region at that time can be roughly estimated at several thousand individuals (Couture, 1983; Riopel, 2002), and had rather localized ecological impacts across the landscape (Danneyrolles et al., 2016a). Industrial logging began at the end of the 19th century, and mainly focused on selective cutting of tall pine trees (*Pinus* spp.; Riopel, 2002). At the beginning of the 20th century, Euro-American settlement and temporary favorable climatic conditions engendered an important peak of burned area (approx. 1910-1930; Lefort et al., 2003; Grenier et al., 2005). Logging activities intensified following the construction of a paper mill in Témiscaming in 1917, which led to the rapid development of partial cutting of small diameter spruces (*Picea* spp.) and fir (*Abies balsamea*; *Lienert, 1966)*. Clear-cutting practices emerged with the mechanization of forestry in the 1970s. During the last two centuries, the study area has also experienced three major spruce budworm outbreaks (Choristoneura fumiferana; 1840-1865; 1910-1930; 1970-1990; Bouchard et al., 2006a, 2006b).

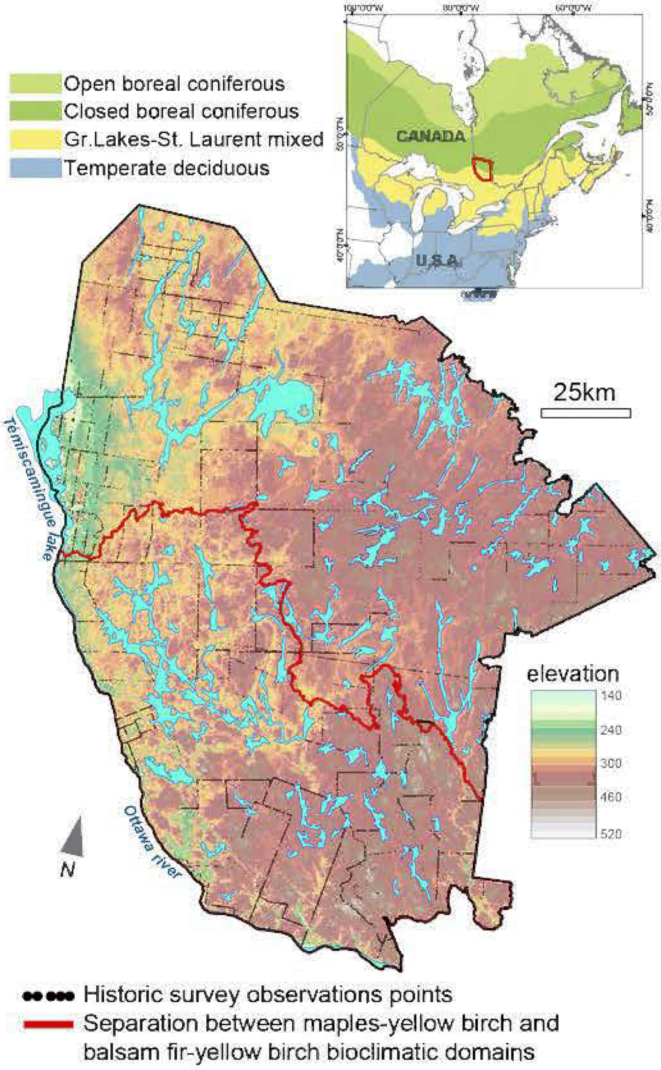

Figure 4.1 Study area and location of historical observations

4.4.2 Community and environmental data

In total, 5910 observations on preindustrial forest communities were extracted from 79 logbooks reporting land surveys of township and forest concession limits conducted from 1854 to 1935. These observations were precisely geo-referenced using historical and modern digital cadastral maps, and are usually spaced apart from 200 to 300 m along transects scattered over the study area (Fig. 4.1). For this study, only taxa list observations were retained (eg.: "*Pine, spruce, yellow birch, cedar and a few maples*"). Assuming that the rank of taxa in these lists reflects their relative abundance (Terrail et al., 2014), for each observations, taxa were classified by 5 ranks (r) : from rank 4 (dominant) to rank 0 (absent). These observations are also divided into two geometric types: line description (only those with length < 300 m were retained; 29% of observations) and point observations (71% of observations).

Modern forest communities were documented with modern forest maps (photo-interpretation 2001-2011; 1/20000; Berger, 2008) in order to assign a modern equivalent of composition to each historical observation (see detailed method in Appendix A). These maps delimit stands by identifying the main taxa present in the canopy, and thus allowed the construction of dominance and presence maps for each taxon. A relative rank of abundance (r) was then assigned to taxa based on their relative cover in the intersection between (1) a 100 m buffer zone around each point or line center of historical observations, and (2) Thiessen polygons generated by these observations. Some species from this modern data-set were grouped at the genus level to match the taxa mentioned by surveyors, while rarely mentioned taxa (< 5%) within historical and modern observations were grouped as "others". This method constrained a very similar number of taxa per observation (α-diversity) in the historical and modern data (Fig. 4.2).

Several environmental variables (Table 4.1) were used to analyze community-environment relationships. Latitude was retained to represent the regional climatic gradient. Eight other variables linked to the topographic gradient were derived from modern forest maps (Berger, 2008) : elevation (Fig. 4.1) as well as slope, drainage and five class of surface deposits (Table 4.1 and Appendix B). In order to analyze the effects of disturbance types on change in community composition, a map of the four main postindustrial disturbances (Appendix B) was constructed from (1) modern forest maps (partial cuts, clear-cuts and spruce budworm outbreaks after 1960; Berger, 2008), and (2) the areas burned during the twentieth century reconstructed in previous studies (Grenier et al., 2005; Drever et al., 2006; Lesieur et al. unpublished data).

Table 4.1 Description of environmental variables (see maps in Appendix B).

Variables	Description
Latitude	Latitude at the center of observations
Elevation	Elevation from an 1 : 50 000 elevation model at the center of observations.
Slope	Five class from low slopes (1) to high slopes (5) derived from modern forest maps (Berger 2008) at the center of observations
Drainage	Seven class from poorly drained (1) to very well drained (7) derived from modern forest maps (Berger 2008) at the center of observations.
Surface deposits (5 variables)	Five variables representing relative cover area [within 100 m buffer-Thiessen intersections polygons] of till, clay, sand, rocky and organic deposits derived from modern forest maps (Berger 2008)

4.4.3 Data analysis

First, we calculated the overall β-diversity represented by the multivariate dispersion (Anderson et al., 2006) of all sites for each time period. Only taxa presence-absence were retained for the β-diversity analysis because this metric is considered to be a robust measure of community composition (Anderson et al., 2011; Bastow Wilson, 2012) and avoids potential bias in abundances of preindustrial and modern data. Taxa presence-absence was used to compute dissimilarity matrices (Sørensen dissimilarity; Legendre & De Cáceres, 2013) and then multivariate dispersion (i.e. β-diversity) was defined as the dissimilarity from individual sites to the centroid of all sites. We finally tested for difference in β-diversity between the two times period with permutation-based test of multivariate homogeneity of group dispersion using the "betadisper" function of the R vegan package (Oksanen et al., 2014).

Second, we partitioned the β-diversity (Legendre et al., 2005, 2009; Peres-Neto et al., 2006) into components explained by environmental and spatial variables through redundancy analysis (RDA; Legendre & Legendre, 2012) for each time period. Taxa presence-absence was again chosen to represent community composition. The nine environmental variables (Table 4.1) were used to construct third-degree polynomial equations (27 monomials). Monomials with exponents allow the modeling of non-linear relationships between environmental and responses variables (Legendre et al., 2009). Community spatial structure was analyzed with distance-based Moran's eigenvector maps (dbMEM ; Dray et al., 2012). In brief, dbMEM analysis produce a set of orthogonal spatial variables based on the XY coordinates of sites (a total of 1217 dbMEM for our 5910 sites), which are then used as explanatory variables. First, β-diversity was partitioned between (1) environmental variables and (2) spatial variables (dbMEM). Second, the same process was used to partition the β-diversity explained by different environmental variables, represented by 4 sets of monomials: (1) latitude; (2) elevation, (3) slope and drainage and (4) surface deposit. A forward selection with permutation test on the increase in R^2 at each step (999 permutations, 5% significance level) was then used to select the environmental and dbMEM variables that significantly best explained the variations of communities (Blanchet et al., 2008), which were retained in the final model. Analyses of dbMEM were performed with the “PCNM” function of the PCNM package (Legendre et al., 2013), variation partitioning and forward selection were performed with the “varpart” and “ordistep” functions, respectively, both included in the R vegan package (Oksanen et al., 2014).

In order to visually represent the compositional changes across environmental gradients, a principal component analysis (PCA) was performed with environmental variables (Table 4.1) of all sites. Among surface deposits, only tills and clays were retained since they cover more than 80 % of the study area (Appendix B). All variables were standardized before analysis. Taxa centroids within sites scores of the PCA were then calculated, for each time period, and were then positioned on the first two principal components. Dispersion ellipses of the four types of 20th century disturbances were also calculated using the standard error and a confidence interval of 95%.

Finally, to describe the compositional changes, indices of dominance and prevalence (Scull & Richardson, 2007; Terrail et al., 2014) were calculated for both periods. A weight was first assigned to each observations based on their mean spacing (Dupuis et al., 2011), and dominance and prevalence indices were then calculated according to the formula:

$$F_{ir} = N_{ir} / M_r$$

where N_{ir} is the total weight of taxon i at rank r in taxa lists, and M_r is the total weight of observations. The dominance index represents the F_{ir} of taxa at the dominant rank (i.e. r=4), and prevalence index represent the F_{ir} of taxa whatever their ranks in lists (i.e. r>0). Monte-Carlo paired test (modern rank of taxa i vs. preindustrial rank of taxa i, 10 000 permutations) were used to determine the significance of these changes. To map preindustrial and modern communities, the prevalence index was calculated for 73 ecological districts (homogeneous physiographic zones, approximately ranging from 50 to 500 km^2 ; Robitaille & Saucier, 1998) comprising more than fifteen observations for each period.

4.5 Results

4.5.1 Patterns of β-diversity and variation partitioning

Observed β-diversity was slightly but significantly ($p<0.001$) higher in modern than preindustrial communities (Fig. 4.2), despite the fact that our data constrained a similar distribution of α-diversity within sites. During preindustrial times, one fifth of the β-diversity was spatially structured (20%; Fig. 4.3). Less than half of this spatial structure can be related to environmental variables (8%) and environmental variables alone explained only a very small proportion of the β-diversity (3%; Fig. 4.3), mostly accounted for by latitude (Table 4.2). The proportion of β-diversity explained by environmental variables has almost doubled between preindustrial and present times (from 11% to 21%), and more than two thirds of this variation is now spatially structured (15%). This environmentally-explained β-diversity is essentially linked to the combination of gradients in elevation, latitude and surface deposits (Table 4.2).

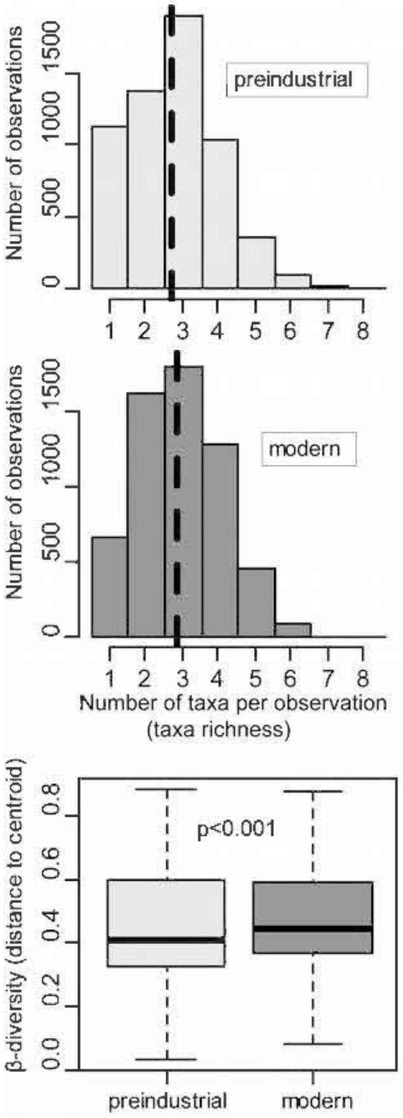

Figure 4.2 Histograms of taxa richness (dashed lines represent mean number of taxa per observation) and β-diversity (i.e. multivariate dispersion) for each time period.

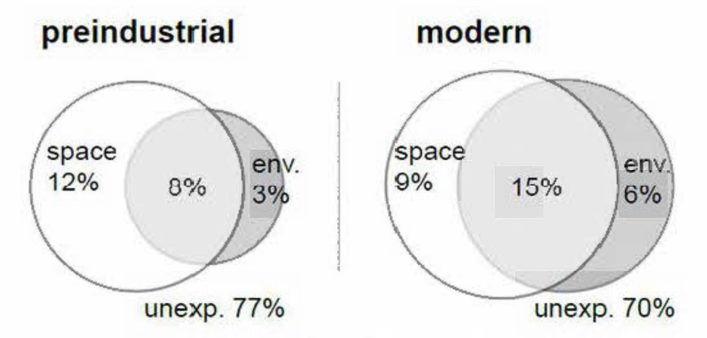

Figure 4.3 Venn diagrams of variation partitioning for environmental and spatial (dbMEM) data-sets. Values indicate adjusted R^2 (percent of variance explained) by individual and intersection fractions, and unexplained variation is showed under diagrams.

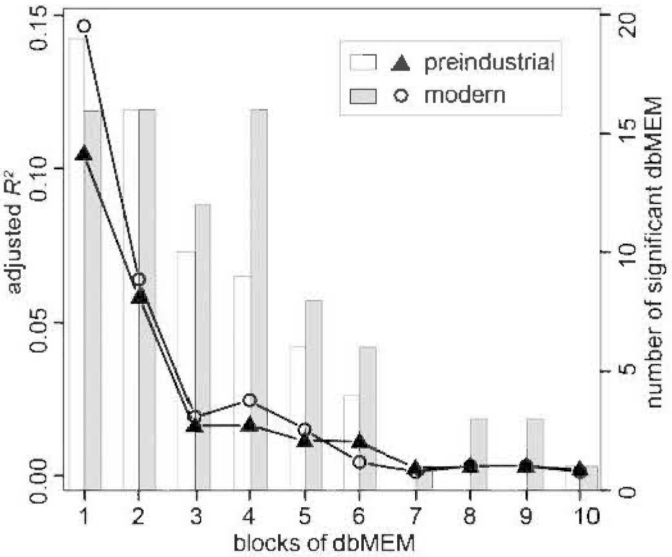

Figure 4.4 Spatial structure of composition assessed by number of significant dbMEM after forward selection (histogram) and adjusted R^2 (curves) for successive blocks of 20 dbMEM, representing the gradation from the broadest (block 1) to the finest scales (block 10).

Table 4.2 Comparison of Variation partitioning results between preindustrial and modern time periods for environmental data-sets. Values indicate adjusted R^2 for [all.]: variation explained by each environmental data-set and including intersections with other datasets; [ind.]: variation explained by each environmental data-set and not explained by other data-sets.

	preindustrial		**modern**	
	[all.]	[ind.]	[all.]	[ind.]
latitude	0.07	0.04	0.11	0.04
elevation	0.04	0.01	0.12	0.04
slope – drainage	0.03	0.01	0.05	0.01
surface deposit	0.03	0.01	0.10	0.02

Figure 4.4 shows a decomposition of spatially structured β-diversity for successive blocks of 20 dbMEM, representing the gradation from regional broad-scaled (block 1) to finer-scaled spatial structure (block 10). Both preindustrial and modern communities show the same trend of large landscape units of homogeneous composition at the regional scale rather than finer-scaled patches at the local scale. The total proportion of spatially structured variation increased slightly from preindustrial to modern times (from 20% to 24%; Fig. 4.3), mostly reflecting an increase in regional broad-scaled spatial structures (Fig. 4.4).

4.5.2 Compositional changes across environmental gradients

PCA analysis (Fig. 4.5) illustrates the evolution of taxa along environmental gradients between preindustrial and modern times. The two first principal components explain 65% of the total environmental variance. The first principal component (42% of variance explained) separates the northern and lower elevations sites dominated by clay deposits, from southern and higher elevation sites dominated by glacial till deposits. The second principal component (23% of variance explained) separates sites according to slope and drainage characteristics.

Table 4.3 Preindustrial and modern dominance and prevalence indices (% of all observations) for the entire study area. Δ indicates the results of Monte-Carlo paired tests (+/-:alternative hypothesis; *p<0.01; **p<0.001; NS. Non-significant).

	preindustrial		**modern**		
TAXA	dom.	prev.	dom.	prev.	Δ
Spruces	27.9	57.2	16.3	36.7	-**
Balsam fir	18.2	59.4	7.4	41.9	-**
Pines	18.6	45.9	9.3	26.5	-**
White cedar	4.7	17.2	3.9	18.1	NS.
Larch	2.9	10.9	0.7	2.6	-**
Poplars	5.5	13.9	19.6	37.7	+**
Paper birch	11.0	35.0	20.6	59.4	+**
Yellow birch	9.1	29.4	11.1	32.0	NS.
Maples	1.2	4.7	10.1	34.8	+**
Others	0.8	3.5	1.0	4.1	+**

At preindustrial times, balsam fir (*Abies balsamea*) was the most prevalent taxon (59,4%; Table 4.3) and was located at the center of environmental gradients (Fig. 4.5), thus tending to be ubiquitous within the study area (Fig. 4.6). The presence of the two other most dominant preindustrial taxa showed contrasted patterns across the latitudinal gradient, with spruces (*Picea* spp.) being more prevalent in the north, and pines (*Pinus* spp.) in the south. Birches (*Betula* spp.) were the most prevalent deciduous taxa (Table 4.3), with paper birch (*Betula papyrifera*) being more prevalent in the north, and yellow birch (*Betula alleghaniensis*) in southern higher elevations (Fig. 4.5).

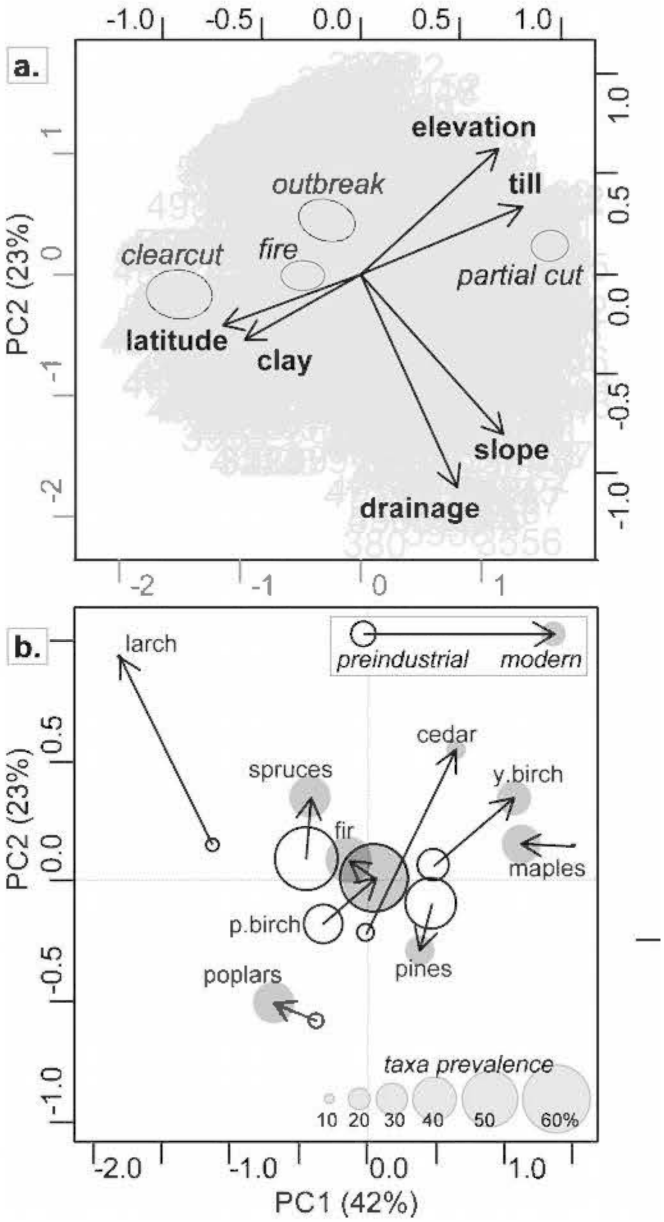

Figure 4.5 Principal component analysis (PCA), axis 1 explains 42% and axis 2 explains 23% of environmental variability. Biplot (a) shows position of sites and correlations of environmental variables with axes 1 and 2. Ellipses depict the 0.95 confidence limit standard errors of main 20th-century disturbances within the sites scores. Plot (b) shows the centroids of taxa presence within the sites scores, during both preindustrial (black circle) and modern (gray circle) period, circles surface are proportional to taxa prevalence.

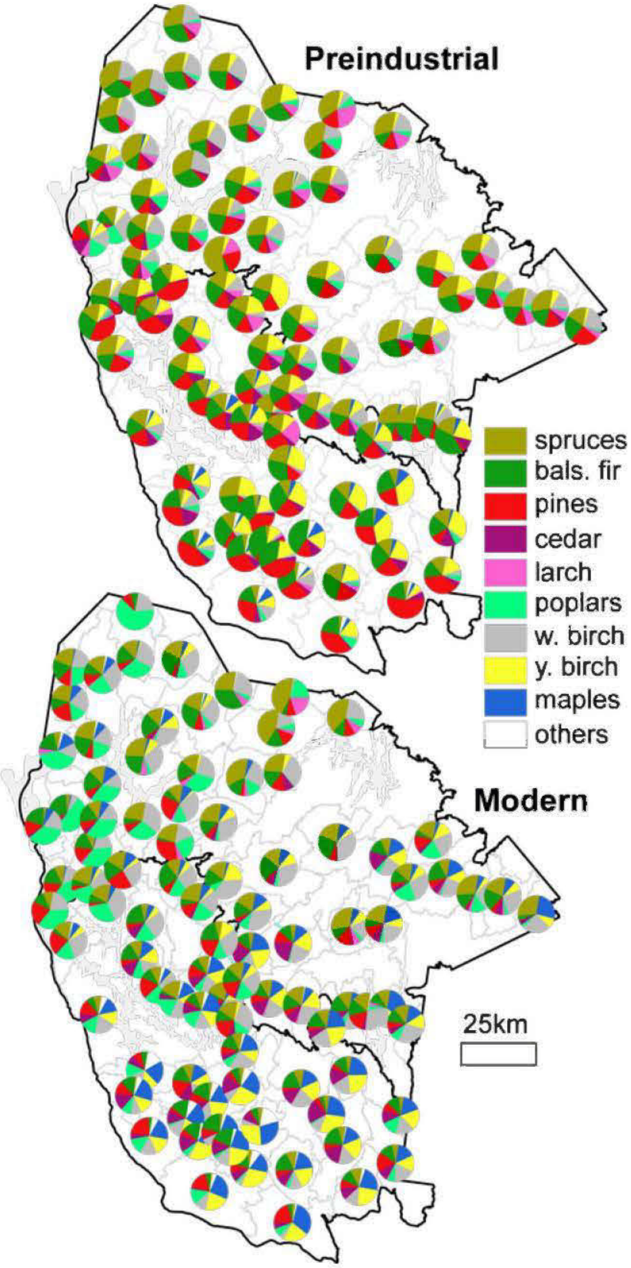

Figure 4.6 Relative prevalence of each taxa in each ecological district with more than 15 observations.

Significant composition changes occurred between preindustrial and modern times (Table 4.3), which were structured across environmental gradients (Fig. 4.5). Poplars (*Populus* spp.) experienced an important increase in dominance and prevalence (+14.1% and +23.8%, respectively; Table 4.3), mainly on northern and lower elevation sites dominated by clay deposits (Fig. 4.5). The dominance and prevalence of paper birch have also significantly increased (+9,6 % et +24,4 %, respectively; Table 4.3), which set this taxon at the center of present-day environmental gradients (Fig. 4.5). Maples (*Acer* spp.) dominance and prevalence significantly increased (+8,9 % and +30,1 %; respectively; Table 4.3) on the southern and higher elevation sites of the region dominated by till deposits (Fig. 4.5).

The remaining taxa have tended to move toward extremities of environmental gradients. Spruces experienced a sharp decrease in dominance and prevalence (-11.5% et -20.5%, respectively; Table 4.4) mostly away from poorly drained lower slopes (Fig. 4.5). Larch also maintained better on poorly drained lower slopes (Fig. 4.5). Conversely, pines experienced a sharp decrease in dominance and prevalence (-9.3% et -19.5%, respectively; Table 4.3) away from well-drained steep slopes (Fig. 4.5). Balsam fir remained close at the center of environmental gradients (Fig. 4.5), despite a significant decrease in dominance and prevalence (-10.8% et -17.5%, respectively; Table 4.3). Eastern white cedar (*Thuja occidentalis*) and yellow birch did not experience significant changes in abundance (Table 4.3), but tended to move and specialize toward southern and higher elevations dominated by glacial till deposits (Fig. 4.5).

4.6 Discussion

Our results largely reject the homogenization-decoupling hypothesis and tend to confirm the heterogenization-strengthening hypothesis. Modern overall β-diversity was significantly but only slightly higher than preindustrial β-diversity (Fig. 4.2), thus our data did not record a strong spatial heterogenization. However, our results clearly show an increase in the strength of tree community-environment relationships (Fig.

4.3). This contrasts with several previous studies that demonstrated the homogenization-decoupling trend as a consequence of European settlement in northeastern North America (eg. Schulte et al., 2007; Hanberry et al., 2012a, 2012b; Thompson et al., 2013).

4.6.1 Environmental ubiquity of preindustrial dominant taxa

An important aspect of our findings is that environmental variables only explained a small proportion of preindustrial β-diversity. This may reflects unmeasured environmental factors (eg. micro-site conditions, biotic interactions), but above all the strong environmental ubiquity of the most abundant preindustrial taxa. Spruces, pines and mostly balsam fir tended to be present on the whole range of environmental gradients, whereas environmental specialists (eg. poplars, maples) were very rare. Nevertheless, preindustrial β-diversity was only slightly lower than modern β-diversity, and was spatially structured over large landscape units. We speculate that legacies of LIA fire history likely explain this regional broad-scaled spatial structure of preindustrial communities. Fire-sensitive taxa (balsam fir, yellow birch, white cedar) tended to be more frequent in areas that had not been subjected to high fire frequency during the LIA (Cyr et al., 2012), whereas fire-prone taxa (spruces, pines, paper birch) dominated the rest of the study area. Spatial patterns of natural disturbance had likely been the key mechanism that structured preindustrial β-diversity at the landscape scale, while habitat filtering was less important.

4.6.2 Increased β-diversity and strengthening of community-environment relationships

Increased disturbance rates following European settlement have favored more specialized taxa across environmental gradients. Poplars have mostly increased on northern lowland dominated by clay deposit, which allow its vigorous multiplication by roots suckers after disturbances (Bergeron & Charron, 1994; Bergeron, 2000). Conversely, maples have become dominant on well-drained and warmer upper slopes of southern higher elevations where they were more competitive (Barras & Kellman, 1998; Danneyrolles et al., 2016b). Paper birch was the most generalist taxa to have increased after European settlement (Safford et al., 1991), and is currently present on the whole range of environmental gradients. While environmental specialists have benefited from increased disturbance rates, preindustrial generalists have tended to specialize to narrowed habitats at the extremities of the topographic gradient. Boreal conifers (spruces, balsam fir) were restricted to poorly drained lower slopes, where colder and wetter conditions allowed them to maintain an important competitive advantage (Barras & Kellman, 1998; Danneyrolles et al., 2016b). Conversely, pines were restricted to low productive xeric steep slopes, where they kept a strong competitive advantage (Abrams, 2001).

Disturbance diversity have also increased following European settlement, with the addition of logging to fire and insect outbreaks, which have been frequent since the early 20th century (Grenier et al., 2005; Bouchard et al., 2006a; Drever et al., 2006). This likely explains a part of the increase in overall β-diversity between preindustrial and modern times. More particularly, the opposition between landscapes that have been subjected to stand-replacing disturbance (fire, clear-cuts) and partial disturbance (spruces budworm outbreaks, partial cuts) has generated divergent dynamics trajectories (Danneyrolles et al., 2016a, 2016b).

4.6.3 Broader theoretical and practical significance

There is yet no consensus about effects of disturbance upon β-diversity and community-environment relationships. For example, a meta-analysis has shown that past agricultural land-use tended to decrease β-diversity as well as the importance of habitat filtering of forest plant communities (Vellend et al., 2007). Using an experimental approach, Myers et al. (2015) found that prescribed burning increased β-diversity but did not change the relative importance of habitat filtering. Hogan et al. (2016) showed that past land-use increased habitat filtering of tropical forest communities. Similarly, our study shows that increased disturbance rates have resulted in an increase in the strength of community-environment relationships by favoring early-successional habitat specialists (poplars and maples) and reducing the habitat breath of taxa that had been more generalists (spruces and pines). This suggests that effects of disturbance on community-environment relationships are strongly dependent upon functional traits of species within the regional pool, particularly whether early- and late-successional species are habitat generalists or specialists. Thus, it may be very difficult to generalize relationships between disturbance and β-diversity across ecosystems if analyses are limited to the taxonomic diversity.

Human activities cause β-diversity to increase, decrease or remain unchanged depending on the processes involved and the scale of observation (Socolar et al., 2016). Our study highlights that human-induced changes in the disturbance regime may significantly alter the various mechanisms that generate β-diversity at the landscape scale. Such changes may persist for decades to century, or even be irreversible (Dupouey et al., 2002), and represent critical issues for the understanding of ecosystem dynamics in the era of global changes.

4.6 Acknowledgments

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CHAPITRE V

CONCLUSION GÉNÉRALE

5.1 Portrait général des forêts préindustrielles du Témiscamingue

À l'époque préindustrielle, l'ensemble de la région était dominé par les épinettes (*Picea* spp.), le sapin baumier (*Abies balsamea*) et les pins (*Pinus* spp. ; Tableau 5.1). Au sud, les pins, le sapin baumier et le bouleau jaune (*Betula alleghaniensis*) dominaient à eux trois plus de 66 % du domaine de l'érablière à bouleau jaune. Le domaine de la sapinière à bouleau jaune au nord était largement dominé par les épinettes (36 %) accompagnées par le sapin et le bouleau à papier (*Betula papyrifera*) qui étaient également très présents. Le gradient climatique régional (latitude et altitude) avait donc une influence sur la composition des forêts, avec un remplacement progressif de la dominance des pins au sud par les épinettes au nord. Le sapin, très abondant, tendait à être omniprésent sur l'ensemble de la région d'étude (Figure 5.1).

La fréquence et l'intensité des feux représentaient d'importantes variables explicatives de la composition et de la structure spatiale des forêts (chapitres II et VI). En comparaison avec aujourd'hui, le climat plus sec du Petit Âge glaciaire (PAG; approx. 1300-1850; Gennaretti et al., 2014) était à l'origine d'une plus grande fréquence des feux dans la région (Bergeron et al., 2006). Les portions du territoire qui n'avaient pas connu de forte fréquence des feux pendant le PAG étaient dominées par des espèces sensibles aux feux (sapin, bouleau jaune, cèdre ; *Thuya occidentalis*), alors que les autres portions étaient dominées par les taxons adaptés aux feux (épinettes noires ; *Picea mariana*, pins, bouleaux blanc). Les grands feux de couronne au nord (Grenier et al., 2005) favorisaient plutôt des paysages dominés par les épinettes noires (*Picea mariana*; chapitre II). Au sud, des feux moins fréquents (Drever et al., 2006), et possiblement de plus faible intensité, favorisaient le maintien des pins (principalement le pin blanc; *Pinus strobus,* et dans une moindre mesure le pin rouge; *Pinus resinosa*).

Tableau 5.1 Pourcentages de dominance et de prévalence (voir méthodes en Chapitre IV) pour les domaines bioclimatiques de l'érablière à bouleau jaune et de la sapinière à bouleau jaune.

	Érablière à bouleau jaune					**Sapinière à bouleau jaune**				
	preindus.		moderne			preindus.		moderne		
TAXON	dom.	prev.	dom.	prev.	Δ	dom.	freq.	domi.	prev.	Δ
Épinettes	16,8	37,7	10,6	26,7	-**	36,4	72,9	21,0	44,7	-**
Sapin	20,5	60,5	4,5	35,8	-**	16,5	58,5	9,8	46,8	-**
Pins	31,5	63,7	11,4	34,7	-**	8,8	31,7	7,6	19,8	-**
Cèdre	4,4	18,4	6,5	26,3	+**	5,0	16,2	1,8	11,5	-**
Mélèze	2,0	7,1	0,0	0,4	-**	3,6	14,0	1,2	4,4	-**
Peupliers	2,7	7,7	12,7	31,5	+**	7,7	18,8	25,1	42,7	+**
Boul. Blanc	4,3	16,5	17,1	54,3	+**	16,1	49,8	23,4	63,5	+**
Boul. Jaune	14,4	41,9	16,3	50,9	+**	5,0	19,3	6,8	16,9	-**
Érables	2,3	9,0	18,8	54,0	+**	0,3	1,2	3,1	19,4	+**
Autres	0,9	4,4	2,1	8,1	+**	0,7	2,8	0,1	0,8	-**

5.2 Les changements de composition : deux grandes trajectoires dynamiques

Les changements de composition survenus depuis l'époque préindustrielle se résument à un remplacement des taxons résineux par des taxons feuillus (Tableau 5.1). Ce changement de composition peut être schématisé par deux principales trajectoires dynamiques (Figure 5.1) : (1) les forêts qui ont brûlées ou ont subi des coupes totales durant le XXe siècle, et qui sont aujourd'hui jeunes. (2) Les forêts qui n'ont subi que des perturbations partielles durant le XXe siècle, et qui sont aujourd'hui plus âgées.

Les forêts qui ont brûlé ou subi des coupes totales sont principalement localisées au nord et à basse altitude (Figure 5.1). Ces forêts ont été rajeunies et ont subi une forte augmentation de dominance et de présence des feuillus de début de succession (peupliers ; *Populus* spp., bouleau blanc, érable rouge ; *Acer rubrum*). Bien que les feux fréquents à l'époque préindustrielle contribuaient à favoriser la dominance des épinettes noires, la combinaison des premières coupes industrielles pour l'industrie papetière avec les grands feux du début du XX^e siècle a abouti au remplacement des épinettes noires par des feuillus de début de succession (chapitre II). Le peuplier faux-tremble (*Populus tremuloides*) est devenu dominant sur les dépôts argileux des basses altitudes où il est particulièrement compétitif, alors que le bouleau blanc domine sur les dépôts de tills des moyennes altitudes (chapitre II et VI). Parallèlement, les peuplements d'épinette noire qui abondaient dans cette zone de la région à l'époque préindustrielle ont été restreints vers les bas de pentes moins bien drainés (chapitre IV).

Les forêts qui n'ont connu que des perturbations de plus faible intensité (coupes partielles et épidémies de tordeuse des bourgeons de l'épinette) sont aujourd'hui plus âgées, et se situent plutôt au sud et sur les plus hautes altitudes (Figure 5.1). Dans ces forêts, le pin blanc et le sapin ont subi une importante diminution, qui a particulièrement profité à l'érable à sucre (*Acer saccharum*), et dans une moindre mesure au bouleau jaune et au cèdre (chapitre III et VI). L'érable à sucre est devenu dominant sur les hauts de pente, alors que le cèdre et les peuplements rémanents de sapin occupent plutôt les bas de pentes (chapitre III). Les feuillus de début de succession (bouleau blanc et peupliers) ont aussi augmenté, mais plus faiblement que dans les forêts jeunes du nord de la région. Les pins blancs et rouge qui étaient abondants dans cette partie la région d'étude à l'époque préindustrielle ont été confinés vers les fortes pentes bien drainées (chapitre VI).

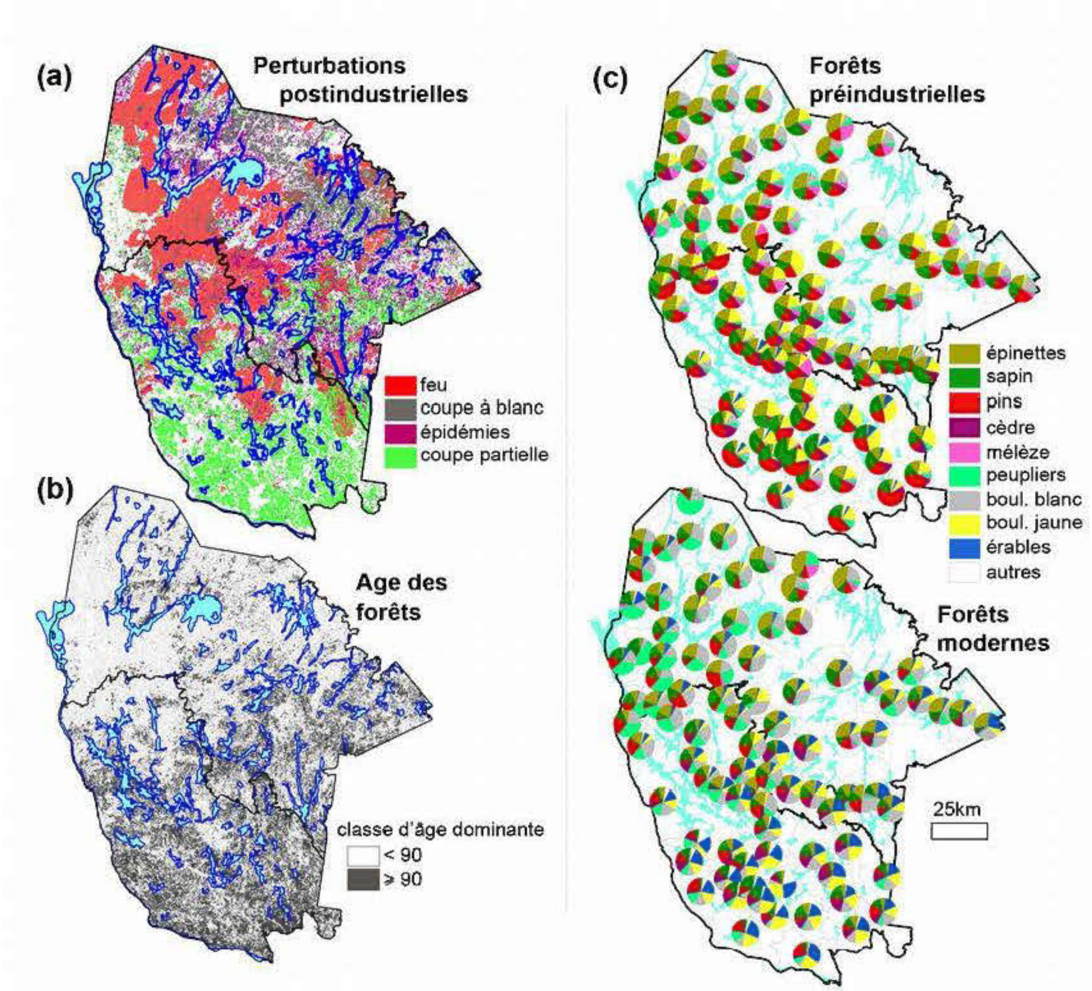

Figure 5.1 Cartes des principales perturbations post-industrielles (a) et de l'âge actuel des forêts (b) reconstituées à partir des cartes écoforestières du 4e décennal. Les cartes (c) montrent les changements la fréquence d'occurrence de chaque taxon par district écologique pour les époques préindustrielle et actuelle (voir méthodes chapitre IV). Notez que dans la carte (a), la cartographie écoforestière ne prend pas en compte les perturbations partielles anciennes (coupes et épidémies de la première moitié du XX^{e} siècle.).

5.3 Quelles espèces cibles dans un contexte de restauration adaptative ?

En termes de composition, face au phénomène général d'enfeuillement de la région, l'aménagement écosystémique doit avoir pour principal objectif de favoriser la dominance des conifères. Cependant, dans le cadre des changements climatiques et de leurs conséquences indirectes (ex. : changements de régime de perturbations naturelles), les états de références historiques doivent être analysés prudemment pour établir les objectifs d'un aménagement écosystémique adaptatif (Choi et al., 2008; Gagné et al., 2015).

L'abondance préindustrielle des épinettes noires était largement favorisée par une plus importante fréquence des feux à cette époque, et leur abondance a fortement diminué suite à l'addition des coupes et des feux du début du XX^{e} siècle. Les épinettes représentent encore aujourd'hui les espèces les plus prisées par les acteurs industriels régionaux, et leurs populations devraient donc être restaurées. Cependant, dans le contexte d'une diminution générale de la fréquence des feux dans la région (Bergeron et al., 2006), il semble plus approprié de favoriser des peuplements diversifiés, avec une importante proportion de conifères moins dépendants des feux que l'épinette noire (ex. : épinettes blanches, sapins, pins blancs, pins rouges, cèdres).

Les pins blancs étaient très abondants dans le paysage préindustriel et, bien qu'ils aient aussi été favorisés par les feux, cette espèce peut se maintenir en absence de feux (Quinby, 1991; Abrams, 2001; Uprety et al., 2013b). Le pin blanc représente une espèce clef pour la biodiversité (Rogers & Lindquist, 1992; Naylor, 1994), et dans la culture des communautés autochtones de la région (Uprety et al., 2013a). Les populations de pin rouge (*Pinus resinosa*) ont également subi un important déclin depuis l'époque préindustrielle. Malgré qu'elles soient plus strictement dépendantes des feux (Rudolf, 1990; Flannigan, 1993), ces populations représentent aussi un important enjeu de conservation (Anand et al., 2013). Ces populations de pins blancs et pins rouges, présentes dans la région depuis plusieurs milliers d'années (Liu, 1990), et décimées par les coupes du début du XX^{e} siècle, doivent donc être restaurées, au moins en partie.

Le sapin a connu un important déclin, particulièrement dans la partie sud de la région d'étude en conséquence de deux importantes épidémies de tordeuse des bourgeons de l'épinette du XX^{e} siècle (Bouchard et al., 2006b), et dans une moindre mesure des coupes partielles du début du siècle (chapitre II). Malgré cette importante diminution, le sapin est resté très présent dans les forêts actuelles avec dans certains peuplements une forte densité de petites tiges en régénération, et pourrait donc connaître un regain de dominance dans les prochaines décennies. D'un autre côté, les populations de sapin pourraient aussi subir des déclins cycliques dans la mesure où le Témiscamingue représente un important foyer de l'épidémie de tordeuse des bourgeons de l'épinette actuellement en développement (Ministère des Forêts, de la Faune et des Parcs, 2015). Étant donné ce statut incertain du sapin, qui par ailleurs apparaît être particulièrement vulnérables aux changements climatiques (Duveneck et al., 2014; Gagné et al., 2015), il ne semble pas pertinent de chercher à favoriser les populations de sapin.

Les abondances du cèdre et du bouleau jaune ont diminué dans le domaine de la sapinière à bouleau jaune, principalement comme conséquence des coupes et des feux du début du siècle. Ces espèces à longue durée de vie sont considérées comme de bonnes candidates à un aménagement adaptatif aux changements climatiques (Gagné et al., 2015), et devraient donc faire partie des espèces cibles pour l'aménagement écosystémique au Témiscamingue.

5.4 Quelles pratiques sylvicoles pour répondre aux enjeux de composition ?

5.4.1 Filtre brut : des coupes pour éviter l'enfeuillement

Les coupes partielles permettent de limiter l'envahissement par les feuillus de début de succession, tout en laissant la régénération résineuse préétablie se développer dans la canopée (Man et al., 2008; Prévost et al., 2010a; Bose et al., 2014). Ce type d'aménagement représente donc un bon moyen de rétablir une composition à dominance résineuse par un aménagement écosystémique des forêts. Les forêts matures du Témiscamingue, qui n’ont subi que des coupes partielles et des épidémies de tordeuses depuis l'époque préindustrielle, offrent d'ailleurs une rétrospective intéressante sur la validité de ce type d'aménagement (chapitre II). Dans une certaine mesure, ces forêts témoignent de la pertinence de l'usage des coupes partielles, car ces dernières ont permis le maintien d'espèces de milieu à fin de succession (érables à sucre, bouleau jaune, cèdre). Malgré tout, les anciens modes de coupes partielles (écrémage des pins et coupes à diamètres limites des conifères) ont largement contribué à la raréfaction des conifères et au développement de l'érable à sucre. Aussi, les coupes partielles contemporaines (ex. : coupes de jardinage, coupes par trouées, coupes progressives) sont plus appropriées que ces coupes partielles anciennes pour éviter l'enfeuillement (Raymond et al., 2009; Prévost et al., 2010b), et doivent être associées aux approches de filtres fins développées plus bas.

D'un autre côté, les forêts préindustrielles ayant été perturbées par les feux, une proportion modérée du territoire devrait être aménagée sous forme de forêts équiennes par des coupes de régénération (avec rétention variable), sans pousser les forêts en dehors de leur plage de variations naturelles (Grenier et al., 2005; Drever et al., 2006). Néanmoins, ces coupes de régénération devraient être suivies pour éviter la progression des feuillus de début de succession (peupliers, bouleau blanc) et assurer la régénération d'espèces résineuses (naturelle ou par replantation).

5.4.2 Filtres fins : rétention, plantation et exigences écologiques de régénération

La présence de semenciers dans le paysage permet d'assurer un meilleur approvisionnement en graines, et donc de favoriser la régénération des taxons rares (Caspersen & Saprunoff, 2005). L'effet positif de la distance aux semenciers sur la régénération des espèces cibles citées plus haut a aussi été clairement démontré (épinette blanche, cèdre ; Asselin et al., 2001, pin blanc ; Uprety et al., 2013b, bouleau jaune ; Drobyshev et al., 2014). Il serait donc pertinent d'établir des seuils d'abondance et de répartition des semenciers dans le paysage pour chacune de ces espèces cibles, pour assurer une régénération naturelle efficace.

Si la présence de peuplements rémanents dans le paysage est déjà trop faible pour assurer une régénération naturelle suffisante, des plantations de réintroduction doivent être envisagées. Les plantations sont généralement faites après des coupes à blanc, et pourraient donc être planifiées dans les peuplements soumis à ce type d'aménagement. Les plantations d'enrichissement dans des coupes partielles par trouées représentent aussi un bon moyen de réintroduire des espèces rares dans le paysage (Fahey & Lorimer, 2013; Hébert et al., 2013). Ce procédé permettrait par exemple de réintroduire des conifères longévifs (épinettes blanches, pins blancs et pins rouges) dans les peuplements purs d'érable à sucre qui tendent naturellement à inhiber le recrutement de ces taxons (Barras & Kellman, 1998). Cette pratique pourrait aussi permettre de réintroduire des espèces à faible capacité de recolonisation (ex. : cèdre, épinette blanche) dans les forêts jeunes dominées par des feuillus de début de succession.

Les exigences écologiques propres à chacune des espèces cibles, comme les substrats et conditions de germination, doivent aussi être pris en compte lors des chantiers de coupes. La présence de troncs en décomposition représente un facteur important dans l'établissement du cèdre et des épinettes blanches (Simard et al., 1998, 2003). Le recrutement du bouleau jaune nécessite soit une mise à nu du sol minéral (sentiers de débardage, scarification), soit la présence de troncs de bouleau ou de conifères en décomposition (Lambert et al., 2016). L'utilisation de feux de surface contrôlés pourrait finalement permettre de restaurer des peuplements denses de pins blancs et de pins rouges (McRae et al., 1994; Thompson et al., 2006).

5.5 Conclusions

Les forêts préindustrielles du Témiscamingue étaient largement dominées par les conifères (épinettes, sapin, pins) et ont par la suite connu un important enfeuillement au cours du XX^{e} siècle. L'aménagement écosystémique au Témiscamingue devrait donc viser à favoriser la dominance des conifères. Dans un contexte d'aménagement adaptatif, ces objectifs devraient aussi particulièrement viser à favoriser des conifères capables de se maintenir en absence de feux (pin blanc, épinette blanche, cèdre). Ces objectifs peuvent être atteints par des pratiques sylvicoles adaptées. Premièrement, l'utilisation de différents types de coupes partielles (coupes par trouées, coupes progressives, coupes de jardinage) permettrait de limiter l'envahissement par les feuillus de début de succession, tout en laissant la régénération résineuse préétablie se développer dans la canopée (filtre brut). Deuxièmement, des approches de filtre fin devraient assurer le maintien et le rétablissement de certaines espèces cibles. Parmi ces approches, la définition de seuils d'abondance de peuplements rémanents dans le paysage pour chacune des espèces cibles assurerait la possibilité d'une régénération naturelle efficace. Dans le cas où ces seuils seraient déjà dépassés, des plantations de réintroduction après coupes sont à envisager. Enfin, les exigences écologiques des espèces doivent être considérées lors des chantiers de coupes.

5.6 Remerciements

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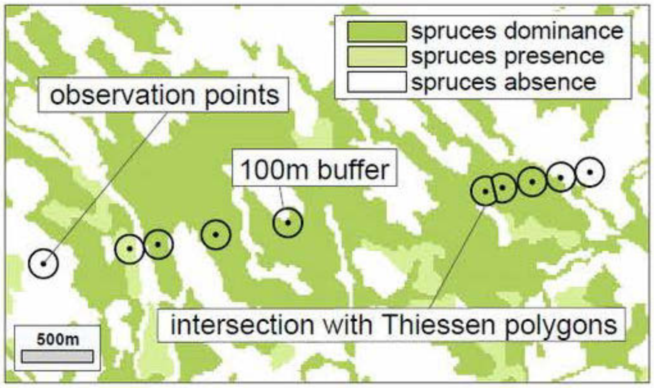
APPENDIX A

Method used to assign a modern equivalent of composition to each historical observation.



Method used to assign a modern equivalent of composition to each historical observation. The 1/20 000 maps delimit photo-interpreted stand polygons and give the main taxa present in the canopy (Berger, 2008). These stand polygons were used to construct both dominance and presence maps of the nine taxa (presence maps represent areas where a taxon is present; regardless of dominance). The following map also illustrates polygons *j* as intersections between 100 meters buffers and Thiessen polygons (Brassel & Reif, 1979) generated by the historical observations points or line centers.

- Rank 4 is assigned to the taxon with the maximum relative covering of dominance in *j*.
- Rank 3 is assigned to the second taxon with the maximum relative covering of dominance, only if this taxa dominance covers ≥ 30% of the forested area, otherwise rank 3 is assigned to the taxon with the maximum relative covering of presence in *j*.
- Rank 2 is assigned to the taxon with the maximum relative covering of presence in *j* if it is not already ranked as 3, otherwise rank 2 is assigned to the second taxon with the maximum relative covering of presence in *j*.
- Rank 1 is then assigned to all taxa covering ≥ 10% in dominance or ≥ 25% in presence of the forested area in *j*.
- Rank 0 is finally assigned to all taxa covering < 10% in dominance or < 25% in presence of the forested area in *j*.

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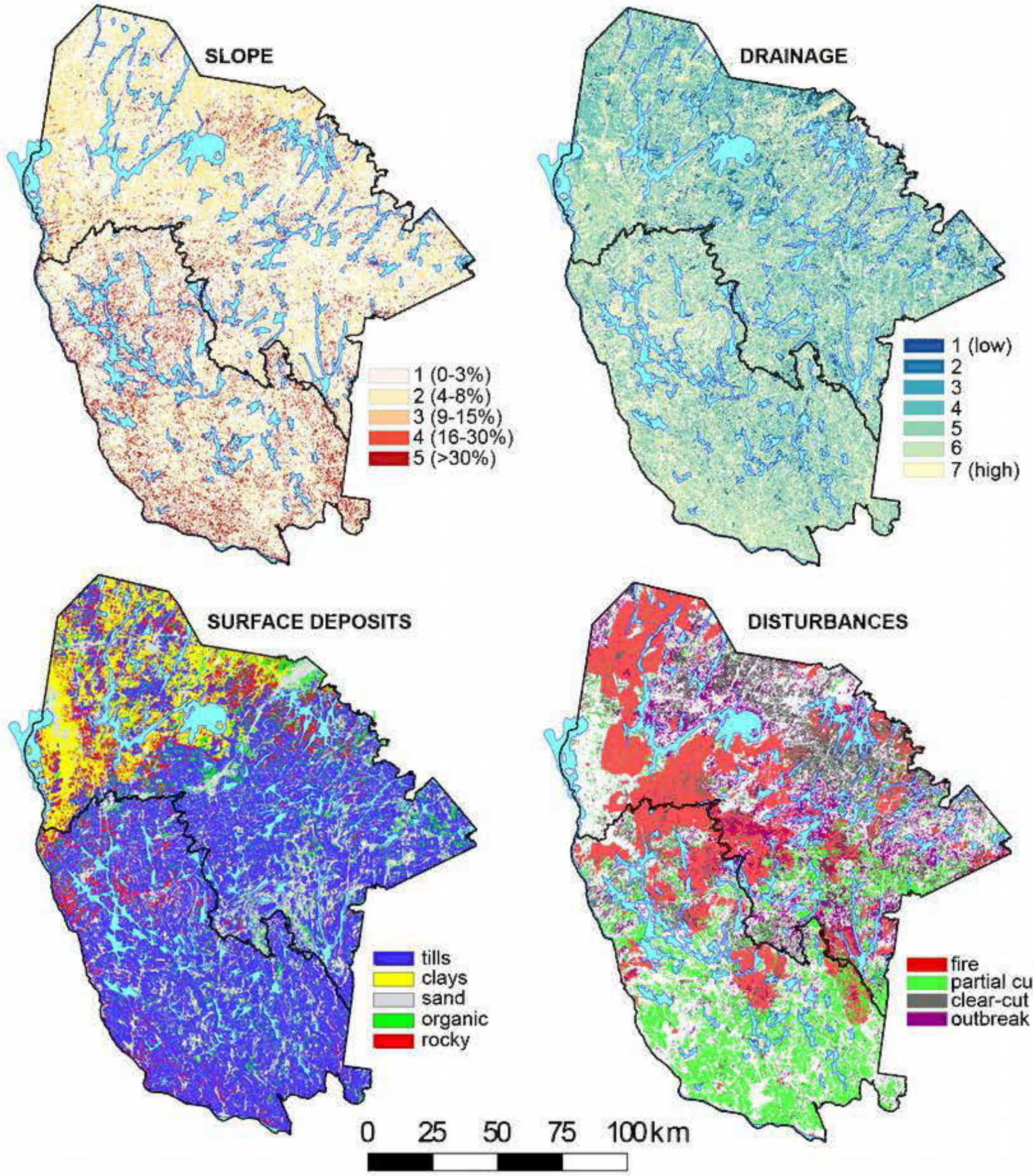
APPENDIX B

Maps of environmental variables and disturbances.

Maps of environmental variables derived from modern forest maps (Berger, 2008) and map of the four main 20th century disturbances constructed from modern forest maps (partial cuts, clear-cuts and spruce budworm outbreaks after 1960; Berger, 2008), and areas burned during the 20th century reconstructed in previous studies (Grenier et al., 2005; Drever et al., 2006; Lesieur et al. unpublished data).



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