UNIVERSITÉ DU QUÉBEC À RIMOUSKI

IMPACT DES PERTURBATIONS ANTHROPIQUES ET DU CLIMAT SUR LA COMPOSITION DES FORÊTS DE L'EST DU QUÉBEC AU XX^{e} SIÈCLE

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RÉSUMÉ

Depuis la révolution industrielle, les pressions anthropiques sur les écosystèmes terrestres se sont accrues et ont causé des transformations importantes des biomes à l'échelle globale. La documentation et la compréhension des causes de ces changements et leurs conséquences sont importantes pour le maintien et la gestion durable des écosystèmes naturels. Dans le cas des écosystèmes forestiers, l'écologie historique et la modélisation sont des approches qui permettent d'optimiser cette compréhension. L'objectif général de cette thèse est de décrire le changement de la composition forestière pendant le 20ème siècle et comprendre ses causes dans une forêt tempérée nordique du sud-est du Canada.

La forêt mixte de la région administrative de Bas Saint Laurent dans l'Est du Québec constitue un exemple intéressant. Cette zone est située à la transition entre la forêt boréale au nord et la forêt tempérée au sud et est sensible aux changements climatiques. Elle a été intensivement exploitée par l'industrie forestière et impactée par les feux de colonisation depuis l'arrivée des européens. La compagnie forestière Price & Brothers, qui a opéré dans la région pendant les 19ème et 20ème siècles, a laissé des archives qui représentent une source de données historiques exceptionnelle constituée d'un réseau d'environ 16000 placettes d'inventaire réparti sur 3200 km^2, ainsi que des cartes d'opérations permettant une reconstitution spatialement explicite du régime des perturbations.

Connaitre les patrons spatio-temporels du régime des perturbations anthropiques constitue une étape importante dans la compréhension des changements de la composition forestière. Dans le premier chapitre de cette thèse, nous avons utilisé des cartes des perturbations historiques et modernes afin de reconstituer le régime des perturbations anthropiques du 20ème siècle. Nous avons décrit la répartition et l'intensification des coupes et des feux à travers des caractéristiques comme la période de rotation et la superficie. Ce travail nous a permis de décrire la progression géographique des perturbations anthropiques dans le paysage, suivant le contexte socio-économique. Les coupes forestières se sont déplacées depuis la proximité des cours d'eaux principaux vers l'intérieur des terres, ce qui reflète la transition du transport du bois par les rivières initialement, vers les routes forestières. La plupart des feux ont été localisés en basses altitudes, proche des terres privées, ce qui suggère des feux d'origine anthropique.

Comprendre la contribution relative des perturbations anthropiques, du climat et de l'environnement physique sur la composition actuelle des peuplements forestiers est l'objectif du deuxième chapitre. Dans les étés de 2012 et 2013 nous avons re-échantillonné 743 placettes d'inventaire de la compagne Price & Brothers. Nous avons ensuite utilisé les données spatialement explicites des perturbations issues du premier chapitre, celles du climat extrapolées spatialement par BioSIM 11, et des caractéristiques stationnelles pour identifier les variables explicatives responsables de la composition forestière. Nos résultats montrent qu'il existe une augmentation des érables et des peupliers, et une densification du bouleau blanc. La surface terrière du bouleau jaune et celles des conifères (sapin baumier, épinettes, et thuya) ont légèrement augmenté. La surface terrière actuelle des taxons étudiés a été expliquée, dans un ordre décroissant, par la surface terrière spécifique en 1930, les caractéristiques stationnelles, le climat, et les perturbations anthropiques du 20ème siècle. La combinaison des effets des perturbations anthropiques et du climat s'est principalement traduite par l'augmentation des érables, tandis que l'effet des perturbations anthropiques du 20ème s'est traduit par l'augmentation de peupliers associés aux feux et par l'augmentation du bouleau jaune associé aux coupes partielles.

L'amélioration et la validation des modèles de succession par trouées se heurtent au manque des données historiques indépendantes. Dans le troisième chapitre, nous avons évalué le degré auquel le modèle ZELIG-CFS prédit le développement à long terme des forêts mixtes de notre aire d'étude, en considérant l'histoire des perturbations. Quand les perturbations ont été considérées, les prédictions de l'épinette blanche et du bouleau blanc ont été améliorées. En même temps, la surface terrière des espèces à feuillage décidu (érable rouge, érable à sucre, et peuplier faux-tremble) a été systématiquement sous-estimée par le modèle. Une meilleure intégration d'une probabilité de reproduction végétative et le couplage du modèle à des fonctions qui simulent les probabilités des perturbations sont toutes des avenues d'améliorations suggérées à la suite de cette étude.

Mots clés : écologie forestière; écologie historique; perturbations anthropiques; archives; forêt préindustrielle; forêt tempérée nordique; changement de composition; climat; modèle de dynamique par trouée.

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Abb	*Abies balsamea*.
Ace	*Acer* spp.
Acr	*Acer rubrum*.
Acs	*Acer saccharum*.
alt	Altitude.
Bea	*Betula alleghaniensis*.
Bep	*Betula papyrifera*.
CO35	Cut over (1895 – 1935).
CO65	Cut over (1935 – 1965).
CP05	Partial cut (1965 – 2005).
CT05	Total cut (1965 – 2005).
DBH	Diameter at breast height.
Drain	Drainage classes.
FIRE	Fires (1895 – 2005).
Fluv	Fluvial deposit.

Frx *Fraxinus nigra*.

GDD Growing degree-days.

Glac Glacier deposit.

Lar *Larix laricina*.

LSL Lower Saint Lawrence.

Orga Organic deposit.

Pia *Picea abies*.

Pic *Picea* spp.

Pic *Picea* spp.

Pig *Picea glauca*.

Pim *Picea mariana*.

Pin *Pinus* spp.

Pin *Pinus* spp.

Pinr *Pinus resinosa*.

Pins *Pinus strobus*.

Pir *Picea rubens*.

PL Plantations (1955 – 2005).

Pob *Populus balsamifera*.

Pop *Populus* spp.

Pot	*Populus tremuloides*.
PR	Private land.
Prcp	Precipitation.
RDA	Redundancy analysis.
SBW	Spruce Budworm outbreaks (1975 – 2005).
Tho	*Thuja occidentalis*.
Tmax	maximum temprature.
Tmean	Mean temprature.
Tmin	Minimum temprature.
Ulm	*Ulmus americana*.
water	distance from closest water course.
Wthr	Weathering deposit.

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INTRODUCTION GÉNÉRALE

0.1. Anthropocène et changements globaux

Les activités humaines ont influencé les écosystèmes de la biosphère terrestre depuis des millénaires (Dearing et al. 2006). Cependant, depuis la révolution industrielle, la pression anthropique sur les écosystèmes s'est accrue. La croissance exponentielle de la population humaine mondiale ainsi que les progrès technologiques ont permis une exploitation massive des ressources naturelles (Houghton 1994, Vitousek 1994, Clark et al. 2001, Ellis et al. 2010, Steffen et al. 2011). Entre les années 1700 et 2000, la majorité de la biosphère terrestre est passée d'un état quasi naturel à un état où les zones agricoles et les installations humaines sont devenues omniprésentes (Ellis et al. 2010). Les impacts humains profonds à l'échelle globale ont amené certains auteurs à proposer l'époque de l'«Anthropocène » pour désigner une nouvelle ère géologique dominée par l'activité humaine (Crutzen et Ramanathan 2000, Crutzen et Steffen 2003). Documenter et comprendre les changements globaux est nécessaire non seulement pour la conservation des écosystèmes naturels, mais également pour maintenir un environnement viable pour les générations d'êtres humains à venir.

Le changement climatique d'origine anthropique est l'un des plus importants agents des changements globaux. Le suivi du climat au cours du dernier siècle montre que les températures du globe sont en augmentation (Mann et al. 1999, IPCC 2013). Au cours du 20ème siècle, et avec l'influence humaine sur le climat, la température du globe a déjà augmenté de 0.6°C (Houghton et al. 2001). Les trois dernières décennies enregistrent successivement des températures de surface terrestre de plus en plus chaude comparée aux décennies antérieures depuis 1850 (IPCC 2013). Les températures et les précipitaions devraient continuer d'augmenter au 21ème siècle avec des augmentations plus rapides vers les latitudes nordiques.

Le changement climatique est susceptible d'avoir un effet majeur sur la dynamique des écosystèmes et les aires de répartition des espèces (Walther et al. 2002, Root et al. 2003, Kullman et KjÄLlgren 2006). Le climat peut modifier les processus écologiques comme la compétition (Connell 1961, Woodward 1987, Davis et al. 1998, Clark et al. 2011) et la fréquence d'occurrence des perturbations en forêt (Bergeron et al. 2004, Frelich et Reich 2009b, Fisichelli et al. 2012, Seidl et al. 2017). Ces phénomènes peuvent en retour modifier la composition et la productivité des forêts. Le climat est aussi un facteur important qui influence l'aire de répartition géographique des espèces. Une méta-analyse effectuée par Parmesan and Yohe (2003) a montré une migration des espèces vers les pôles de l'ordre de 6,1 km par décennie. Ces auteurs ont estimé que sur 460 espèces qui ont subi une altération de leur répartition géographique, 81% ont agi dans la direction prédite par le changement climatique actuel. Les aires de répartition des espèces changent d'une manière «individualiste» avec des vitesses et dans des directions différentes d'un taxon à l'autre. Cependant, il est possible que plusieurs espèces changent leurs aires de répartition simultanément si le changement dans les conditions environnementales affecte chacune de ces espèces (Frey 1992). La majorité des analyses de l'effet des changements climatiques sur les forêts ont été effectuées à de grandes échelles spatiales (globale, nationale ou régionale). Cependant, le changement climatique interagit avec les conditions locales qui affectent la composition et la structure forestière (Iverson et Prasad 1998, Fisichelli et al. 2014). Il est donc, aussi important de considérer les effets des changements climatiques à l'échelle des sites et des paysages forestiers.

Un autre agent des changements globaux est l'utilisation des terres. Autour du globe, les besoins grandissants d'une population mondiale en croissance ont causé de profonds changements à la structure et aux processus de la dynamique des écosystèmes (Foley et al. 2005). Dans les écosystèmes forestiers, on observe des changements majeurs comme la déforestation, la fragmentation des habitats, la dégradation des sols, la perte de biomasse et des stocks de carbone associés, la transformation de la structure d'âge et la composition des espèces, et la perte ou l'introduction des espèces (Uhl et Kauffman 1990, Gerwing 2002, Steffen et al. 2004). Ces changements couplés aux observations des impacts du climat créent un doute quant à la capacité des forêts à maintenir leur biodiversité et un apport durable des services dans le futur (Kellomäki et al. 2008, Malhi et al. 2008, Phillips et al. 2009).

0.2. Les forêts tempérées nordiques de l'Est de l'Amérique du Nord

À l'est de l'Amérique du Nord, les forêts tempérées nordiques couvrent la région des Grands Lacs, du Minnesota, du Wisconsin, le nord du Michigan, le nord du Maine, ainsi que l'est et le centre de l'Ontario et le sud du Québec (Little 1971, Pastor et Mladenoff 1992, Breckle 2002). Des zones de végétation similaires existent également dans les montagnes des Appalaches (Beckage et al. 2008). Ces forêts sont composées de peuplements mixtes de conifères et de feuillus ou d'une mosaïque des peuplements purs de feuillus ou de conifères (Breckle 2002). La répartition des différents peuplements est régie par les facteurs physiques comme l'altitude, la pente et l'exposition (Siccama 1971, Lorimer 1977, White et Mladenoff 1994), de même que par l'histoire des perturbations (Frelich 2002).

Les forêts tempérées nordiques représentent la zone de transition entre la forêt boréale au nord et la forêt tempérée au sud. Les espèces d'arbres tempérées et boréales y atteignent respectivement leurs limites nord et sud de répartition. Elles peuvent pousser ensemble sur un gradient de température relativement étroit (Goldblum et Rigg 2010), et sont plus sensibles au changement climatique lorsqu' elles sont à leur limites de répartition (Iverson et Prasad 1998, Scheller et Mladenoff 2005, Frelich et Reich 2009a). De ce fait, les zones de transition comme la forêt tempérée nordique sont des endroits propices pour détecter les signes précoces des changements de composition forestière en conséquence des changements des températures et des précipitations (di Castri et al. 1988, Parmesan et al. 2005).

Les forêts tempérées nordiques de l'est de l'Amérique du Nord continuent à être influencées par le changement climatique. Le $20^{ème}$ siècle a été très probablement plus chaud que le $19^{ème}$ siècle (Anchukaitis et al. 2017, Gennaretti et al. 2017). De plus, les projections futures suggèrent que le changement climatique continuera à influencer la composition et la structure des forêts tempérées nordiques (Iverson et Prasad 1998, Scheller et Mladenoff 2005, Duveneck et al. 2014, Boulanger et al. 2019). On anticipe que les espèces tempérées proches de leur limite de répartition nordique vont répondre fortement en croissance à l'augmentation des températures, tandis que la réponse en croissance des espèces boréales proches de leur limite de répartition sud est moins évidente avec des réponses stables ou négatives selon les espèces et leur localisation (Reich et Oleksyn 2008). L'érable à sucre et l'érable rouge sont des espèces tempérées qui devraient migrer vers le nord à partir de leurs aires de répartition actuelles avec une augmentation de leur abondance (Goldblum et Rigg 2005, Fisichelli et al. 2014, Boisvert-Marsh et al. 2019). Comme pour la température, le changement du régime de précipitation peut avoir un effet important sur la composition des forêts. La variabilité des précipitations en interaction avec les facteurs environnementaux (microtopographie, type de sol, couvert végétal) est susceptible d'affecter l'humidité du sol, qui a son tour peut affecter la régénération et la survie des différentes espèces (Chesson et Huntly 1997). Dans la zone de transition des forêts tempérées nordiques, la régénération des arbres est sensible aux gradients de précipitation (Fisichelli et al. 2013).

Les forêts tempérées nordiques doivent également s'ajuster à une augmentation de la fréquence, de l'intensité, et de la superficie des perturbations anthropiques, avec la progression du front de colonisation (Foster et al. 1998, Steffen et al. 2004, Foley et al. 2005, Ellis et al. 2010). Dans la partie sud des forêts tempérées nordiques, le régime de perturbations naturelles a été modifié par l'ajout des nouvelles perturbations anthropiques ainsi que par la suppression des feux (Frelich 2002). Avant la colonisation européenne, les forêts tempérées nordiques de l'est de l'Amérique du Nord étaient soumises à un régime de perturbations secondaires incluant les chablis et les épidémies d'insectes ainsi que des rares feux naturels et des feux anthropiques des populations authochtones (Lorimer 1977, Fahey et Reiners 1981, Payette et al. 1990, Frelich et Lorimer 1991, Lorimer et White 2003, Fraver et al. 2009, Blarquez et al. 2018). Dans le paysage post-industriel, les coupes forestières et les feux anthropiques sont devenus une importante cause de mortalité et de dynamique forestière (Bergeron et al. 1998, Foster et al. 1998, Lorimer 2001, Blanchet 2003, Friedman et Reich 2005, Canham et al. 2013).

Les coupes forestières sont actuellement la source de mortalité la plus importante en comparaison aux autres perturbations naturelles et anthropiques combinées (Boucher et Grondin 2012, Canham et al. 2013). Les sites jamais coupés sont rares et souvent associés à des contraintes physiques (e.g. pentes), et économiques (e.g. intérêts des propriétaires terriens, distance des routes) (Butler et al. 2016). Dans la forêt tempérée nordique du sud est du Québec, dans la première moitié du 20ème siècle, il a été estimé que si les coupes continuent à se faire au même taux chaque année, la forêt sera épuisée en bois de sciage au bout de 20 ans (Guay 1942). Les incendies volontaires pour le défrichement des terres et les pratiques agroforestières représentent une autre pression importante (Cwynar 1977, Wein et Moore 1977, 1979, Blanchet 2003, Steffen et al. 2011, Boucher et al. 2017, Danneyrolles et al. 2019, Terrail et al. 2019). En Amérique du Nord, beaucoup de feux de colonisation, pendant le 19ème et le début du 20ème siècle, ont brûlé hors de contrôle sur de grandes superficies forestières (Blanchet 2003, Terrail et al. 2019).

Comparé à l’époque préindustrielle, la composition et la structure des forêts tempérées nordiques postindustrielles ont été profondément modifiées à l'échelle des sites et des paysages (Orwig et Abrams 1994, Whitney 1994, Foster et al. 1998, Fuller et al. 1998, Orwig et Abrams 1999, Abrams 2003). Cela s’est traduit par une augmentation des espèces comme l’érable à sucre (*Acer saccharum* Marsh.) (Brisson et Bouchard 2003, Dupuis et al. 2011), l’érable rouge (*Acer rubrum* L.) (Whitney 1994, Abrams 1998, Whitney et DeCant 2003), les peupliers (*Populus spp.*) (White et Mladenoff 1994, Foster et al. 1998, Fuller et al. 1998, Leahy et Pregitzer 2003) et le bouleau blanc (*Betula papyrifera* Marsh.) (Siccama 1971, Whitney 1994, Abrams 1998, Bürgi et al. 2000, Hall et al. 2002, Leahy et Pregitzer 2003, Dupuis et al. 2011). À l'inverse, on a observé une diminution des espèces tolérantes à l’ombre comme l’épinette blanche (*Picea glauca*), et le thuya (*Thuja occidentalis* L.) (Jackson et al. 2000b, Friedman et Reich 2005, Boucher et al. 2006b, Dupuis et al. 2011). On a également assisté à un rajeunissement de la forêt et une fragmentation importante de la matrice forestière (Mladenoff et al. 1993, Foster et al. 1998, Boucher et al. 2009b, Terrail 2013).

Aujourd’hui, les écosystèmes forestiers sont plus fragmentés et subissent davantage d’effets de bordure (Houghton 1994) tandis que les forêts jamais exploitées sont de plus en plus rares (Brisson et al. 1988, Nowacki and Trianosky 1993, Whitney 1994, Bouchard et al. 2005, Boucher et al. 2017). Comprendre les causes de changement de la composition forestière est nécessaire pour la compréhension de la dynamique forestière, la prise de décisions pour gérer les écosystèemes et prévoir leur réponse aux changements climatiques. L’investigation des causes de changements implique de mesurer les écarts de composition entre les forêts préindustrielles et les forêts actuelles et clarifier la part respective de chaque facteur de changement. Relativement, peu d’études ont pris en compte les différents agents de changement des forêts en même temps pour comparer leur importance relative (Krankina et al. 2005, Gimmi et al. 2010, Landhäusser et al. 2010, Fisichelli et al. 2014, Nowacki et

Abrams 2015, Plieninger et al. 2016, Vayreda et al. 2016, Danneyrolles et al. 2019) à cause de la rareté des données historiques exhaustives.

0.3. Aménagement écosystémique

L'aménagement écosystémique est un concept qui vise à maintenir les forêts aménagées dans leur limite de variabilité naturelle tout en assurant la soutenabilité à long-terme de la gestion des ressources. Les caractéristiques des forêts préindustrielles ont été suggérées comme état de référence (Landres et al. 1999, Harvey et al. 2002, Lindenmayer et Franklin 2002) pour établir des cibles d'aménagement. Dans les forêts tempérées nordiques de l'est de l'Amérique du Nord, cela implique de concevoir des méthodes d'aménagement afin d'imiter les effets du régime de perturbation naturelle principalement composé de perturbations secondaires (Lorimer 1977, Frelich 2002). Au Québec, le concept d'aménagement écosystémique a été recommandé par le gouvernement dans sa réforme du régime forestier (MRNFQ 2008) et est en vigueur depuis 2013.

Une des principales exigences pour mettre en œuvre l'aménagement écosystémique est d'identifier les caractéristiques des forêts préindustrielles. Notamment dans les régions où les sites forestiers non perturbés par l'exploitation sont rares ou peu représentatifs comme dans la zone tempérée (Nowacki et Trianosky 1993). Les forêts non-perturbées sont souvent de petites tailles, difficiles d'accès, situées dans des milieux humides ou sur des pentes abruptes. De plus, toutes ces forêts d'aujourd'hui sont impactées par les changements globaux, à travers les changements climatiques, et la modification du cycle de l'azote et une fragmentation généralisée de la matrice forestière environnantes (Vitousek 1994, Clark et al. 2001, Steffen et al. 2004).

0.4. Les outils d'investigation

Dans le contexte des changements globaux et des pressions qu'ils exercent sur les écosystèmes naturels, le lien entre les efforts pour comprendre le passé des écosystèmes forestiers (écologie historique) et pour projeter leur évolution dans le futur (modélisation) est de plus en plus pertinent (Gimmi et Bugmann 2013). Cette combinaison permet d'optimiser la compréhension du changement écologique pour fournir une base théorique plus robuste pour un aménagement écosystémique. Cependant, la combinaison entre la modélisation et l'écologie historique demeure généralement limitée par la faible portée spatiale et temporelle des données historiques (Anderson et al. 2006).

0.4.1. L'écologie historique

En l'absence de témoins naturels, l'écologie historique est un des meilleurs outils pour décrire et comprendre la dynamique et le fonctionnement des forêts préindustrielles (Swetnam et al. 1999, Egan et Howell 2001). À des résolutions et échelles spatiotemporelles différentes, plusieurs approches sont utilisées. À l'échelle des régions et des millénaires, les forêts du passé et leur dynamique peuvent être reconstitué à partir de l'analyse pollinique et l'analyse des macro-restes dans les carottes sédimentaires. La palynologie permet de préciser les taxons, parfois les espèces, mais il est souvent difficile de préciser la région source de pollen à cause de la dispersion sur des grandes distance par le vent (Fuller et al. 1998, Foster et al. 2002). Pour l'échelle séculaire et une échelle spatiale des paysages et des peuplements, les photos aériennes, la dendrochronologie et les données de plusieurs types d'archives représentent des outils intéressants (Crumley 1994). La dendrochronologie permet la reconstruction des conditions climatiques passées, du régime de perturbation, et de la structure d'âge des peuplements (Lorimer 1980, Abrams et al. 1995, Bergeron et al. 2001, Guyette et al. 2002). En Amérique du Nord, les cartes historiques généralement réalisées par des compagnies forestières permettent de reconstituer le couvert forestier et l'organisation des types des peuplements (conifères, feuillus, mixtes) au niveau du paysage, mais sans précision sur les espèces individuelles présentes dans chaque type de peuplement (Lévesque 1997, Etheridge et al. 2005, Boucher et al. 2006b, Boucher et Grondin 2012). Les actes notariés du volume et essences de bois de chauffage vendu, datant de 18ème et de 19ème siècle, permettent de reconstituer la composition des espèces exploitées (Simard et Bouchard 1996, Brisson et Bouchard 2003). Finalement, les archives d'arpentage primitif datant du 17ème jusqu'au début de 20ème siècle permettent de reconstituer la composition forestière de manière spatialement explicite à l'échelle régionale (Bourdo 1956, Whitney 1994, Dupuis et al. 2011, Fortin 2018). Cependant les données de ces archives sont qualitatives (présence/absence) ou semi-quantitatives (abondance relative des taxons) et ne portent pas d'informations directe sur la structure diamétrale de la forêt.

0.4.2. Les modèles de simulation de la dynamique forestière

Les modèles de simulation de la dynamique forestière tentent de répondre à plusieurs questions de recherche, dont la prévision de l'impact des changements globaux sur la dynamique forestière. Ils permettent l'amélioration de la compréhension des processus et facteurs affectant la composition et la structure des forêts et de mieux prévoir leur développement futur (Bugmann 2001, Landsberg 2003). Ces modèles ont été développés depuis les années 1960, en parallèle avec le développement des ordinateurs, pour étudier la succession écologique au niveau des peuplements (Botkin 1993, Peng et al. 2006, Larocque 2016) et des paysages (Urban et al. 1991). Les chercheurs ont construit des modèles mathématiques complexes qui prennent en compte les effets des variables climatiques, les conditions de site, les relations de compétition inter et intraspécifiques, plusieurs mécanismes démographiques comme l'établissement des semis et leur transition au stade de jeunes arbres ou d'arbres matures ainsi que la croissance et la mortalité des arbres individuels (Bugmann 2001). Cependant, en raison de la complexité des écosystèmes forestiers, ces modèles sont encore à améliorer. Plusieurs études discutent du niveau de détail à inclure dans les modèles pour la simulation des processus spécifiques (Bonan et Sirois 1992, Pacala et al. 1993, Bugmann et Martin 1995, Fischlin et al. 1995, Loehle et LeBlanc 1996, Schenk 1996).

Les modèles de simulation de la dynamique forestière (par trouées) sont des modèles semi-mécanistiques qui présentent un compromis entre les modèles de croissance et de rendement de la productivité des arbres et des peuplements (Mohren et Bukhart 1994) et ceux entièrement basés sur les processus écophysiologiques (Peng et al. 2002). Plusieurs modèles de simulation de la dynamique forestière basés sur JABOWA (Botkin et al. 1972) ont été développés pour des analyses de dynamique forestière depuis le milieu des années 1970s (Gullison et Bourque 2001, He et al. 2002, Song et Woodcock 2003). Chaque modèle est adaptable à un type forestier donné pour répondre à des questions spécifiques (Bugmann 2001).

ZELIG (Urban 1990, Urban et al. 1991, Urban 2000) est un modèle de simulation de la dynamique forestière applicable à l'échelle des sites. Une grille définit la surface potentielle occupée par les arbres. La taille des pixels correspond à la zone d’influence et représente la taille typique d’une trouée causée par la mort d’un arbre dominant (Urban et Shugart 1992). Chaque arbre affecte l’environnement dans sa zone d’influence et l’agrégation des zones d’influences définit les relations de compétition entre les individus. D’autres processus importants simulés par ZELIG sont l’interception de la lumière, la mortalité ajustée par une fonction stochastique du stress et par la probabilité annuelle de mortalité de chaque espèce, l’établissement de la régénération en tant qu’événement stochastique influencé par les conditions du site et la croissance radiale des arbres, ajusté par les contraintes environnementales comme le changement dans les conditions de lumière, d’humidité du sol et des nutriments. ZELIG requiert pour chaque espèce des informations sur l’âge maximal, le diamètre à hauteur de poitrine (DHP), la hauteur, la quantité minimale et maximale de degrés-jours de croissance dans l'aire de répartition géographique de chaque espèce ainsi que leur classe de tolérance à l'ombre et au stress hydrique.

Ce modèle a été adapté à plusieurs types de forêts : ZELIG ++ (Burton and Cumming 1995) a été développé pour étudier la réponse des changements climatiques dans les forêts boréales de la Colombie Britannique. ZELIG a aussi été adapté pour étudier l'impact du feu et de l'altitude sur les patrons du paysage des forêts mixtes en Californie (Miller and Urban 1999). Finalement, ZELIG-CFS est une version de ZELIG mise à jour par le Service Canadien des forêts (Larocque et al. 2011). Elle a été conçue suite à la validation de ZELIG par des données d'inventaires historiques dans deux forêts mixtes du Québec (Larocque et al. 2006). Certaines modifications étaient nécessaires pour augmenter la capacité prédictive de modèle. Les modifications apportées concernent les fonctions de l'interception de la lumière par la cime, le taux de survie et la régénération.

Une des difficultés pour l'amélioration et la validation des modèles de simulation de la dynamique forestière est la rareté des données historiques indépendantes à long-terme sur un vaste territoire (Botkin et al. 1972, Smith et Urban 1988, Shugart et Smith 1996, Lindner et al. 1997, Bugmann 2001, Larocque 2016). Très peu d'études ont validé les modèles de simulation de la dynamique forestière par des données historiques (Lindner et al. 1997, Makela et al. 2000, Yaussy 2000, Badeck et al. 2001, Risch et al. 2005, Larocque et al. 2006, Pabst et al. 2008, Didion et al. 2009, Larocque et al. 2011). Il est également difficile de valider le rôle des perturbations anthropiques dans les modèles à cause de manque de données spatialement explicites.

0.5. Aire d'Étude et archives de la compagnie Price Brothers

La forêt mixte de la région administrative de Bas Saint Laurent dans l'Est du Québec constitue un exemple intéressant pour étudier l'impact des changements globaux sur les écosystèmes forestiers. Cette zone est située à la limite nord des forêts mixtes de Grands Lacs (Rowe 1972), à la transition entre la forêt boréale au nord et la forêt décidue au sud. Comme pour la plupart des forêts tempérées nordiques de l'Amérique du nord, elle a été intensivement exploitée par l'industrie forestière et impactée par les feux de colonisation depuis l'arrivée des européens (Fortin et al. 1993, Boucher 2007, Boucher et al. 2009b, Terrail 2013). De plus, la compagnie forestière Price Brothers, qui a opéré dans la région pendant les 19ème et 20ème siècles, a laissé des archives qui représentent une source de données historiques exceptionnelles pour décrire l'état de la forêt au début du 20ème siècle à travers les territoires qu'elle a exploité dans cette région.

Selon le système de classification écologique du Québec (Figure 0-1), l'aire d'étude est située dans le domaine bioclimatique de la sapinière à bouleau jaune et dans le domaine de la sapinière à bouleau blanc pour sa partie la plus orientale (Robitaille et Saucier 1998). Le climat est de type tempéré avec une température moyenne annuelle de 3,9°C et des précipitations moyennes annuelles de 915 mm, dont 30% tombent sous forme de neige (Environment Canada 2019). Il existe différents types de couvert forestiers dans la zone d'étude. Ces types de couvert peuvent être classifiés en peuplements résineux, feuillus, mélangés à dominance feuillue, mélangé à dominance résineuse, et des couverts en régénération. L'analyse des archives d'arpentage primitif et des anciennes cartes de couvert forestier a montré que la forêt préindustrielle du Bas-Saint-Laurent était principalement dominée par les résineux dans les basses terres, alors que des peuplements mixtes et parfois feuillus occupaient les haut-versants et les sommets de collines d'élévation moyenne (Boucher et al. 2006a, Boucher et al. 2009b, Dupuis et al. 2011). Un des changements les plus notoire révélé par ces données est l'enfeuillement récent par les érables (Dupuis et al. 2011, Terrail 2013).

L'occupation européenne de la région du Bas Saint Laurent a débuté au 17ème siècle. Au 20ème siècle, la région était alors soumise à une pression anthropique accrue par les coupes forestières et les feux de colonisation (Fortin et al. 1993). C'est au début de 19$^{\text{ème}}$ siècle que l'industrie forestière a débuté ses activités. Depuis plus de 100 ans, ces forêts ont été exploitées intensivement pour la production du bois (Boucher et al. 2009a, Boucher et al. 2009b, Boucher et Grondin 2012). La compagnie Price Brothers, ainsi que d'autres compagnies forestières, ont commencé par exploiter les épinettes et les pins de gros diamètres pour l'industrie du sciage (Price Brothers & Company Limited 1944). À l'époque, le transport du bois se faisant par la drave et l'exploitation à proximité des cours d'eau (Proulx 1985, Fortin et al. 1993). À partir de la deuxième moitié du 20$^{\text{ème}}$ siècle, en parallèle avec la mécanisation, l'ouverture des routes forestières, et le développement de l'industrie forestière pour la production de pâte à papiers, Price Brothers a préconisée la récolte de tous les peuplements matures le plus rapidement possible, puis la récolte des peuplements plus jeunes (Price Brothers & Company Limited 1944). L'aire d'étude a également été soumise à des feux de colonisation de grande ampleur. Dans la première moitié du 20$^{\text{ème}}$ siècle, ces feux ont été fréquents des zones habitées (Fortin et al. 1993, Terrail 2013). Dans la deuxième moitié du 20$^{\text{ème}}$ siècle, la stabilisation de la population ainsi que les mesures effectives de suppression des feux ont diminué leur fréquence (Blanchet 2003).

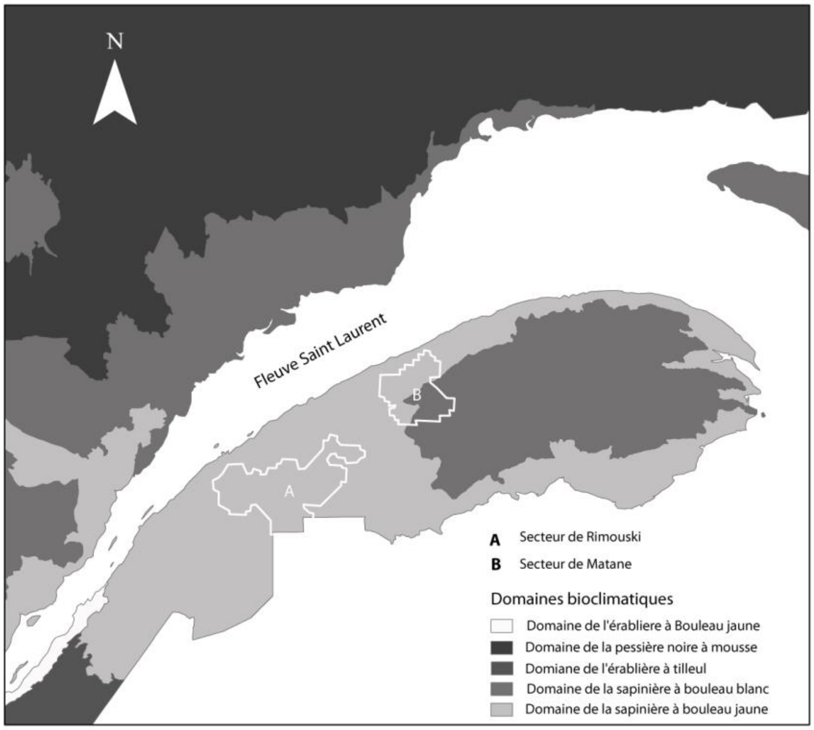


Figure 0-1: Localisation des territoires étudiés au Bas Saint Laurent. A : Secteur de Rimouski, B : Secteur de Matane

De 1928 à 1931, la compagnie forestière Price Brothers a effectué des relevés dans ses concessions du Bas Saint Laurent, dans les secteurs de Rimouski (2279 km^2) et Matane (938 km^2). Elle a constitué des cartes de végétation afin de mettre en place un plan d'exploitation. Cela comprend un réseau extrêmement dense et étendu de placettes d'inventaires (16 345 placettes sur le territoire de 4120 km^2) qui donnent la densité des tiges par classe de diamètre et par espèce alors que moins de 40% du territoire avait été coupé (Boucher et al. 2009a). La superficie de chaque placette est de 5 x 0,5 chaînes (environ 1000 m2 ; 1 chaîne ≈ 20m). Les placettes sont situées sur des virées. Elles sont distancées les unes des autres par 5 à 15 chaînes sur une virée donnée selon les secteurs. La distance entre deux virées varie entre 20 et 40 chaînes. Chaque placette présente également des informations qualitatives concernant le type de couvert forestier, la classe d'âge du peuplement, la topographie et la position des plans d'eau, ainsi que la présence de coupes ou de feux sur les virées qui séparent les placettes. Les archives de la compagnie Price Brothers comprennent aussi des cartes correspondant au même territoire qui permettent de localiser et documenter le patron spatial des coupes effectuées ainsi que les zones brûlées entre 1895 et 1960 (Price Brothers & Company Limited 1944).

0.6. Objectifs de la thèse

À partir des données d'inventaire et des cartes d'opérations des archives de la compagnie Price Brothers ainsi que des données modernes, l'objectif général de cette thèse est de décrire le changement de la composition forestière pendant le 20ème siècle et déterminer la contribution des différents agents de changement dans la définition de la composition actuelle des forêts mixtes au Bas Saint Laurent. Cet objectif principal se traduit en plusieurs objectifs plus précis, qui correspondent aux chapitres de cette thèse.

L'objectif du premier chapitre est de carctériser le régime des perturbations anthropiques du 20ème siècle et son impact sur la composition de la forêt mixte. Nous attendons que : (1) le régime des perturbations anthropiques soit caratérisé par une intensité et une superficie plus importantes que le régime des perturbations naturels, et que (2) les perturbations anthropiques aillent un effet important sur la composition forestière actuelle. Les reconstitutions et les analyses de ce chapitre ont été faites à l'échelle du paysage à l'aide des cartes forestières pour reconstituer le régime des perturbations. Afin de comparer la végétation passée des inventaires de la compagnie Price Brothers à celle des placettes modernes d'inventaires temporaires (PET) du gouvernement du Québec, nous avons utilisé des cellules de 9km^2 d'une grille étendue sur l'aire d'étude.

L’objectif du deuxième chapitre est de déterminer quels sont les effets respectifs des perturbations anthropiques, du climat, et d’environnement physique sur la composition actuelle des forêts mixtes au niveau des peuplements. Nous attendons que les espèces répondent de manière différente aux combinaisons du climat-perturbations-environnement. Les analyses de ce chapitre ont été faites avec une base de données des 743 placettes de l’inventaire de la compagnie Price Brothers systématiquement réparties sur le territoire et re-échantillonnées en 2012-2013. Ces placettes ont été couplées avec des données d’occurrence des perturbations, des données climatiques et des données environnementales.

L’objectif du troisième chapitre est d’évaluer les prédictions du modèle de simulation de la dynamique forestière (ZELIG-CFS) pour les forêts mixtes de l’est du Québec à l’aide des données historiques. Nous attendons que la probabilité de mortalité intégrée dans le modèle ne soit pas suffisante pour prendre en compte la mortalité causée par les perturbations anthropiques. Pour ce chapitre, nous avons utilisé la base de données des placettes Price re-échantillonnées en 2012-2013 ainsi que l’historique des perturbations reconstitué dans la premier chapitre.

CHAPITRE I

CHANGEMENT DU RÉGIME DE PERTURBATIONS DANS LES FORÊTS MIXTES DE L'EST CANADIEN PENDANT LE XX^{E} SIÈCLE

1.1. Résumé en français du premier article

Ce premier article, intitulé «Changement du régime de perturbations dans les forêts mixtes de l'Est Canadien pendant le 20ème siècle», est co-signé par moi-même ainsi que par les professeurs Dominique Arseneault et Luc Sirois et par le Dr. Yan Boucher. En tant que première auteure, j'ai fait l'essentiel de la recherche sur l'état de l'art, la recherche et la collecte des cartes des coupes de la compagnie Price Brothers aux archives nationales du Québec, la numérsaion des données, le développement de la méthode, l'analyse des données et la rédaction de l'article. Les professeurs Dominique Arseneault et Luc Sirois, second et troisième auteurs ont aidé à la recherche sur l'état de l'art, au développement de la méthode ainsi qu'à la révision de l'article. Le Dr. Yan Boucher, quatrième auteur, a fourni les données des placettes d'inventaire Price et a participé à la recherche de financement. Ce chapitre a été publié dans la revue «Frontiers in Ecology and Evolution» sous le référence suivante :

Elzein, T., Arseneault, D., Sirois, L., and Y. Boucher. 2020. The Changing Disturbance Regime in Eastern Canadian Mixed Forests During the 20th Century. Frontiers in Ecology and Evolution, 8(156). doi:10.3389/fevo.2020.00156

Quel a été l'impact anthropique sur le régime des perturbations des forêts mixtes de l'est de Canada pendant le 20ème siècle? Et comment a-t- il a influencé la composition des espèces arborescentes? Pour répondre à ces questions, nous avons

reconstitué le régime des perturbations anthropiques pendant le 20ème siècle et analysé son impact sur la composition moderne à travers l'utilisation des inventaires et cartes forestiers historiques et modernes. Entre 1895 et 2005, 144% de l'aire d'étude a été coupée et 19% brûlée. La période de rotation des coupes s'est raccourci de 152 ans entre 1895 et 1935 à 47 ans entre 1965 et 2005, en raison de l'amélioration de la capacité industrielle régionale. La période de rotation des feux a diminué de 1668 ans entre 1895 et 1925 à 200 ans pendant le pic d'établissement humain (1925-1955), pour ensuite augmenter à 2925 années entre 1955 et 2005. La progression géographique des perturbations anthropiques dans le paysage a reflété le contexte socio-économique. Les coupes forestières se sont déplacées des bords des cours d'eaux principaux vers l'intérieur des terres, ce qui reflète la transition du transport du bois par les rivières initialement, vers les routes forestières dans la seconde moitié de 20ème siècle. La plupart des feux ont été localisés en basse altitude, proche des terres privées, ce qui suggère des feux d'origine anthropique. Les espèces pyrophiles (peupliers) sont majoritairement trouvées à l'intérieur des zones brûlées. Malgré ces perturbations, la composition de la forêt est demeurée relativement stable, suggérant une résilience des écosystèmes forestiers régionaux.

Mots clés : perturbations anthropiques ; composition forestière ; forêt mixte ; caractéristiques des perturbations

1.2. The changing disturbance regime in eastern Canadian mixed forests during the 20th century

1.3. Abstract

How strong was the anthropogenic imprint in the disturbance regime of eastern Canadian mixed forests during the 20th century? And how did it alter the tree species composition? To answer these questions, we reconstructed the 20th century anthropogenic disturbance regime and analyzed its impact on modern forest composition using historical and modern forest inventory and map data. Between 1895 and 2005, an equivalent of 144% of the study area has been logged and 19% burned. The logging rotation period has shortened from 152 years in 1895-1935 to 47 years in 1965-2005, due to increased industrial capacity. The fire rotation period decreased from 1668 years in 1895-1925 to 200 years during the peak of human settlement (1925-1955), and then increased to 2925 years in 1955-2005. The geographical progression of anthropogenic disturbances in the landscape has reflected the socio-economic context. During the 20th century, logging moved inland from the margins of the main water courses, reflecting the shift in wood transport from log driving on rivers to the densification of the road network in the second half of the 20th century. Most fires were located at low altitude, close to private lands suggesting ignitions from anthropogenic origins. Fire prone species (poplars) are mostly found within burned areas. Despite these disturbances, forest composition remained relatively stable, suggesting resilience of regional forest ecosystems.

Key words: anthropogenic, disturbances, mixed forests, composition, disturbance characteristics

1.4. Introduction

Land use practices have become an important driver of forest ecosystem dynamics at several spatial scales since the onset of the industrial revolution. Present-day forests worldwide must cope with human related increase of disturbance frequency, intensity and extent (Foster et al. 1998, Steffen et al. 2004, Foley et al. 2005, Ellis et al. 2010; Danneyrolles et al. 2019). These anthropogenic disturbances trigger shifts in disturbance regimes (Frelich 2002), which in turn alter the composition and structure of forest communities and landscapes (Houghton 1994, White and Jentsch 2001, Foster et al. 2003, Nowacki and Abrams 2015, Trumbore et al. 2015; Danneyrolles et al. 2019). Anthropogenic fires and logging represent increased large scale mortality compared to preindustrial background levels (Trumbore et al. 2015). Thus, it is important to document how human activities have modified the disturbance regime in forest ecosystems and their consequent impact on forest composition and structure.

At the interface of boreal and deciduous biomes in eastern North America, forest landscapes have been subject to intensive industrial logging and settlement fires for more than a century (Foster et al. 1998, Lorimer 2001, Blanchet 2003, Friedman and Reich 2005b; Boucher et al. 2009b, 2014). While, the pre-industrial disturbance regime in this region was dominated by windthrows, insect outbreaks, rare natural fires, and anthropogenic fires of debated frequency and intensity (Fahey and Reiners 1981, Frelich and Lorimer 1991, Williams 2000, Lorimer and White 2003, Simard et al. 2006, Blarquez et al. 2018), logging has become one of the main causes of tree mortality in the post-industrial landscape (Canham et al. 2013). Logging creates large open sites suitable for early successional tree species colonists. As a result, it has shifted overstory tree composition from uneven aged, old growth and shade-tolerant stands to even aged, young, shade-intolerant stands (Keenan and Kimmins 1993, Foster et al. 1998, Fuller et al. 1998, Abrams 2003; Boucher et al. 2009c, Danneyrolles et al. 2019). Relative to pre-industrial conditions, post-industrial forests often show an increase in sugar maple (Acer saccharum) (Brisson and Bouchard 2003, Dupuis et al. 2011; Terrail et al. 2019), red maple (Acer rubrum) (Whitney 1994, Whitney and DeCant 2003), poplars (Populus spp.) (White and Mladenoff 1994, Foster et al. 1998, Fuller et al. 1998, Leahy and Pregitzer 2003) and white birch (Betula papyrifera) (Siccama 1971, Whitney 1994, Abrams 1998, Bürgi et al. 2000, Hall et al. 2002, Leahy and Pregitzer 2003, Dupuis et al. 2011), while shade tolerant species like white spruce (Picea glauca) and northern white cedar (Thuja occidentalis) have generally decreased (Jackson et al. 2000, Friedman and Reich 2005b, Boucher et al. 2006, Dupuis et al. 2011).

Although anthropogenic disturbances in the 19th and 20th centuries have combined with pre-industrial disturbances, their characteristics (rotation period, size, frequency, disturbance interval, and spatial pattern) are often poorly documented compared to the pre-industrial disturbance regime. Similarly, the link between anthropogenic disturbances and long term forest compositional changes has often been suggested, rather than demonstrated, because of the lack of data allowing spatially explicit reconstructions of disturbance regime and landscape composition. In this study we used archival (~1920) and modern forest maps and forest inventory plots to reconstruct the spatially explicit history of the post-industrial anthropogenic disturbance regime and parallel forest composition changes of the 20th century in a large area (3217 km2) of the eastern Canadian mixed forest. More specifically, our main objective is to quantify the main parameters (spatial pattern, rotation period and extent) of the anthropogenic disturbance regime of the 20th century and evaluate what was the relative influence of these anthropogenic disturbances on the development of present-day vegetation?

1.5. Materials and methods

1.5.1. Study area

The study area is located in the Lower Saint Lawrence Region (LSL) in the south-east of the province of Quebec, Canada (47° 92’ N to 48° 91’ N and 66° 84’ W to 68° 86’ W). It is delineated to the north by the St. Lawrence River and to the south by the province of New Brunswick and lies within the Appalachian geological formation, characterized by sedimentary bedrock. The topography generally consists of low elevation hills with moderate slopes with mean and maximum elevations of 350 m and 910 m, respectively. Surface deposits are mainly from glacial and in situ weathering origins. The meteorological data (1981-2010) of Rimouski (20 m a.s.l.), Trinité-des-Monts (260 m a.s.l.) and Saint-Jean-de-Cherbourg (320 m a.s.l.) (Figure 1-1) show mean annual temperatures of 4.4 °C, 2.5 °C and 1.9°C and annual total precipitations of 959 mm, 1100 mm and 1138 mm, respectively, 30% of which falls as snow (Environment Canada 2019).

This area is situated at the northern limit of the Great Lakes-St. Lawrence mixed forests at the transition between the temperate deciduous and the boreal coniferous forests (Rowe 1972). Up to 75% of the study area corresponds to public forest, mostly in the backcountry, whereas 25% is private land, mostly along the St. Lawrence River. The study area is composed of two former forest concessions of the Price Brothers & Company: the Rimouski (2279 km2) and Matane (938 km2) sectors. Price Brothers & Company operated in the LSL region since the 19th century until the first half of the 20th century. The two sectors belong to the balsam fir-yellow birch bioclimatic domain (temperate mixedwoods), although the south-eastern part of the Matane sector, which is higher in elevation with steeper slopes, is located in the balsam fir-white birch domain (southern boreal forest) (Robitaille and Saucier 1998, Grondin et al. 1999). Balsam fir (Abies balsamea), white spruce, and yellow birch (Betula alleghaniensis) are abundant in mesic sites in the balsam fir-yellow birch bioclimatic domain, while balsam fir, white spruce and white birch are abundant in mesic sites in the balsam fir-white birch domain. In both domains, trembling aspen (Populus tremuloides) and balsam poplar (Populus balsamifera) are also present. Sugar maple and red maple generally occupy hill tops and reach their northern range limit in the study area. Black spruce (Picea mariana) and northern white cedar generally occur on organic deposits along water courses (Robitaille and Saucier 1998).

The study area has been subject to extensive anthropogenic fires, logging practices of increasing severity and spruce plantations during the 19th and 20th centuries. Fires were frequent at the margins of inhabited areas during the early 20th century due to slash burning for land clearing and agriculture (Fortin et al. 1993, Terrail et al. 2019). In the second half of the 20th century, population stabilisation and effective fire suppression (Blanchet 2003) decreased the frequency of fires to very low values.

Logging practices during the 19th century and until the 1930s were mainly selective winter harvesting of large pine and spruce trees (Fortin et al. 1993, Boucher et al. 2009a). Logs were then transported to saw mills using water courses (Proulx 1985). Forest operations slowed down during the great economic depression of 1929-1939 and vigorously recovered following the Second World War due to the increasing demand for residential construction material. In the 1940s, the rarefaction of large diameter trees prompted a progressive transition to the pulp and paper industry exploiting smaller diameters of spruce and balsam fir (> 3 inches DBH). This phase was also marked by the progressive introduction of chainsaws and log transport by trucks (Fortin et al. 1993). In the 1970s, dramatic changes occurred over the landscape, due to mechanization and the increased cutting rate in the snow-free season (Boucher et al. 2009a). Meanwhile, a severe spruce budworm outbreak (Choristoneura fumiferana) between 1975-1992 (Boulanger and Arseneault 2004) triggered extensive salvage logging and consecutive large scale spruce plantations (Fortin et al. 1993). To our knowledge, there is no documentation of pre-European anthropogenic disturbances in the LSL region. Nevertheless, Aboriginal influence in modifying the natural fire regime has been documented elsewhere in eastern North America (Williams 2000, Blarquez et al. 2018), and could have participated in influencing pre-industrial forest composition.

1.5.2. Sources and types of maps data

We digitized and georeferenced maps from several sources (Table 1-1). In their study, Boucher et al. (2009b) digitized and analyzed maps produced during an exhaustive 1930 forest inventory by the Price Brother's & Company. Along with these data, in the present study we discovered maps of a significant extension of the 1930 inventory and digitized stand age as well as all disturbance polygons. We also georeferenced and digitized 61 maps of the Price archive fund showing logged areas, logging previsions and fire polygons for different sections of the Rimouski and Matane sectors. These historical maps were georeferenced using lakes and confined rivers from Quebec ministry of natural resources' modern maps (MFWP). In addition, we used a map of the LSL region made from a 1938 aerial survey showing fires of the ~1900-1938 period (Hébert 1938). This map was previously analyzed by Terrail (2013). Our database also included more recent fire polygons obtained as shapefiles from the fire protection agency in Quebec (SOPFEU). Finally, we used the four decadal forest inventory maps produced by the Quebec's ministry of Forests, Wildlife and Parks (MFWP) from ground surveys and aerial photographs taken in 1973-1974, 1985-1986, 1993 and 2004, respectively. We digitized disturbance polygons for the first and second decadal inventory maps, while the third and fourth decadal maps were directly obtained as digitized polygons by the MFWP.

Creating a homogenous database of all disturbance polygons was somewhat challenging, mostly due to the variable resolution of maps and the occasional repetition of some polygons in different data sources, sometimes with different dates. When a same polygon was repeated on two maps with a spatial mismatch, both polygons were merged. When dates were inconsistent for a same polygon on two different maps, the oldest date was kept, as it indicates the first mention of the occurrence of the disturbance polygon. On the maps, logging polygons between 1895 and 1965 were identified as Cut Over zones, without a precise logging type. However, these cut over zones were most likely diameter limit selective logging operations, based on written accounts of logging practices at that time (Price Brothers & Company Limited 1944, Fortin et al. 1993) as well as an analysis of forest diameter structure in survey plots in 1930-1931 of logged areas against unlogged forest (see Appendix 1-1 and 1-2). Logging polygons for the period 1965- 2005 were classified as partial cuts (25% to 75% basal area removal) or total cuts (more than 75% basal area removal) based on Quebec's department of forests decadal inventories. The 1970s Spruce budworm outbreak severity was equally categorized by Quebec's department of forests into moderate outbreaks (between 25 to 75% defoliation) and severe outbreaks (more than 75% defoliation).

The four main disturbance categories that have been considered in our analyses are (1) fire (1895-2005), (2) logging (1895-2005), (3) plantations (1955-2005), and (4) spruce budworm outbreak (1975-2005). Although the natural or anthropogenic origin of fires is not directly known, their spatial pattern indicates a predominant anthropogenic origin (Terrail 2013). In addition, even if a plantation is not a disturbance per se, plantations were included in our analysis as a human-imposed forest recovery pattern that caused important compositional difference compared to naturally regenerated stands.

The spruce budworm outbreak of 1975 -1992 and windthrows are considered natural disturbances in our database for which we have spatial information. Two additional outbreaks occurred in the region during the 20th century in 1947-1958 and 1914-1923 (Boulanger and Arseneault 2004) for which we have no spatial information. Hence, the impact of spruce budworm outbreaks during the 20th century might be under-estimated in our database. It is also important to note that Spruce Budworm outbreaks might be indirectly influenced by human activity through climate change (Gray 2008). Yet, we included the spatial data we have of the 1970s Spruce budworm outbreak to compare its extent and rotation period and to examine its interactions with previous and subsequent anthropogenic disturbances. Areas impacted by windthrows are negligible in extent compared to other disturbances and are only included for descriptive purposes of the disturbance regime. For each disturbance type, we estimated affected area (km2 and % of the study area), rate (% of the study area /year) and rotation period (i.e. the time necessary for a disturbance to cover an area equivalent to the study area; Frelich 2002). We also calculated the affected area disturbed per decade and the cumulative area disturbed for the four main disturbance types.

1.5.3. Sources and types of sampling plots data

We assessed tree composition in 1930-1931 and in 1985-2005. For the 1930 – 1931 period, we used a detailed forest inventory conducted by the Price Brothers &

Company in a total of 16 345 rectangular plots (10 x 100 m) of 0.1 ha each, systematically distributed across the Rimouski and Matane sectors (Figure 1-1). Tree taxa (> 3 inches; ~ 7.6 cm) were then tallied by 2 inches DBH classes. We georeferenced plots from their location on a 1930 map at the scale of 1: ~ 16000. Some taxa in the historical forest inventory were grouped at the genus level: Maples (Acer spp.), Spruces (Picea spp.), Pines (Pinus spp.) and Poplars. Other taxa were identified at the species level: balsam fir, yellow birch, white birch, northern white cedar, black ash (Fraxinus nigra), American larch (Larix laricina) and American elm (Ulmus Americana). Similarly, present-day forest composition (1985- 2005) was described from the sampling plots of the second, third and fourth decadal forest inventories (1985-1986, 1993 and 2004) conducted by the Quebec's ministry of Forests, Wildlife and Parks (MFWP). The first inventory was excluded because plot location is not georeferenced. During these inventories, circular sampling plots of 0.04 ha were randomly stratified according to forest stand type, excluding non-forested, unproductive and inaccessible (slope > 40%) stands. Within plots, tree taxa were tallied by 2 cm DBH classes, although DBH classes < 8 cm were excluded to match the 1930 plot database. We grouped the diametral structure (Density of stems / 10 cm diameter class) for each time period. Plots of the 1985-2005 time period were separated into 2 categories: naturally regenerated stands and plantations. We divided the study area into 333 grid cells of 3 km by 3 km. The cells contained at least four (4) inventory plots per period. We calculated the mean basal area per taxa for redundancy analysis (RDA). The study area division in 3 km by 3 km grid cells should attenuate the bias associated with the uncertainty of historical inventory sampling plots position and the variable resolution of maps used to reconstruct disturbance history. The historical inventory sampling plots position uncertainty range from 0 to 340 m and the resolution of maps used range from 1: 16 000 to 1: 190 000 (Table 1-1).

1.5.4. Redundancy analysis

Two redundancy analyses (RDA) were performed. First, we used RDA in order to examine the effect of environment and vegetation composition in 1930-1931 on subsequent occurrence of disturbances. Second, we performed a partial RDA after controlling for environment and pre-industrial vegetation in order to examine the influence of disturbances on present-day forest composition. A grid of 333 cells of 3 km by 3 km covering the study area was generated to calculate, within each cell, disturbance cover percentage, environmental variables and basal area of tree taxa in 1930-1931 and 1985-2005. We calculated the cover percentage of Fire (1895-2005), Cut Over (1895-1935), Cut Over (1935-1965), Partial Cut (1965-2005), Total Cut (1965-2005), Plantations (1955-2005), and Spruce Budworm Outbreak (1975-2005). For environmental variables (Table 1-2), we used the mean value of 10 random points per grid cell to calculate altitude (m), slope (°), aspect (°), closest distance from main rivers (m), closest distance from secondary rivers and lakes (m) and closest distance from private lands (m). Cells located inside private lands have a distance of 0 m. We also calculated soil deposit types and drainage classes cover per cell. For the two RDAs, we selected only significant variables using forward selection with the package vegan in R (Tables 1-4 and 1-5). Disturbances, taxa basal area of 1930-1931 and 1985-2005 variables were Hellinger transformed while environmental variables were standardized to zero mean and unit variance. The variation explained was reported using the adjusted R2, which takes the number of predictor variables and sample size into account to prevent the inflation of R2 values. A permutation test was applied to test for the significance of the models and axes. Partial RDAs were also performed to calculate the individual adjusted R2 for each variable in environmental and forest composition of 1930-1931 and 1985-2005 datasets. These analyses were performed using the R 3.0.3. software (R Development Core Team 2016).

1.6. Results

1.6.1. Description of the 20th century disturbance regime

During the 20th century, logging was the most widespread disturbance type, followed by fire, the 1970s spruce budworm outbreak and plantations. Windthrows were negligible compared to other considered disturbances, with a rotation period of 3000 years (Table 1-3; Figures 1-2 and 1-3). The cumulative area logged between 1895 and 2005 attained 144% of the study area (Figure 1-4.B). This indicates the some zones were logged more than once over the last 110 years. In total, 84% of the study area has been subjected to partial and/or total cut: 39% has been logged once, 34% twice, 10% thrice, and 1% logged four times. 16% of the study area has not been logged in our database. Approximately a third of the non-logged area has burned during the last century (Figure 1-2.D). The unlogged, unburned area might have been subjected to non-documented anthropogenic disturbances absent from our data base, is located in inaccessible areas for logging, or reflects the bias associated to maps variable scales in our database. Logging rotation period in the study area between 1895 and 2005 corresponds to 76 years. However, logging rotation period has continuously shortened throughout the 20th century, due to increasing industrial capacity, from 152 years in 1895-1935, to 79 years in 1935-1965, and 47 years in 1965-2005 (Table 1-3). Fire events were clustered around 1925-1955 (Figure 1-4.A), in conjunction with the population increased in the study region (Figure 1-4.E). Between 1895 and 2005, fires burned 19% of the study area (Figure 1-4.A), corresponding to a rotation period of 594 years. The fire rotation period decreased from 1668 years in 1895-1925 to 200 years in 1925-1955. Following the peak of settlement in the late 1950s, the fire rotation period increased to 2925 years (Table 1-3). Large scale plantations are relatively recent in the region and have covered 17.8% of the study area between 1955 and 2005 with a peak of 362 km2 between 1985 and 1995 (Figure 1-4.C). Spruce budworm outbreak data are available only for the recent time (1965 to 2005) and show a peak of 486 km2 area affected between 1974 and 1986. The total area affected by the outbreak is 31.7% (Figure 1-4.D) corresponding to a rotation period of 95 years (Table 1-3).

1.6.2. Spatial structure of anthropogenic disturbances

The RDA model indicates that the anthropogenic disturbances regime of the 20th century has been spatially structured by environmental variables and by the 1930-1931 tree composition (Adjusted R2 = 32%; Figure 1-5). This structure reflects human settlement and land-use history during the 20th century. The first RDA axis (20% of constrained variance) mostly expresses increasing distance from main rivers to the left (Individual R2adj = 0.084; Table 1-4) as well as the basal area of spruces in 1930 (Pic30; Individual R2adj = 0.076). The second axis (6% of constrained variance) shows a gradient from high Pines basal area in 1930 (Pin30, Individual R2adj = 0.017), steep slope (Individual R2adj = 0.009) and weathering deposit (Individual R2adj = 0.013) up to Glacial deposit (Individual R2adj = 0.012) and high birch basal area in 1930 (Bea30 and Bep30, respectively with Individual R2adj = 0.030 and 0.014). Distance from private lands (PR; Individual R2adj =0.067) and altitude (alt, Individual R2adj = 0.007) are explained by both the first and second axis of the RDA. Cut over zones between 1895 and 1935 (CO35) are situated next to main rivers. Between 1935 and 1965, logging activities (CO65) moved away from main rivers (situated in the opposite direction of CO35 in the multivariate space) towards areas where spruces were still abundant. Between 1965 and 2005 logged areas (CP05 and CT05) became diffuse across the study region and showed no specific spatial location in the multivariate space. Plantations (1955-2005; PL) occurred in flat zones, while spruce budworm outbreak (SBW) is observed in steep zones. Finally, fires (1895-2005) occurred in low altitude areas close to private lands.

1.6.3. Modern taxa composition and diameter structure

According to the partial RDA, the 20th century disturbance regime explained 6% of the modern basal area (1985-2005) in the landscape (Figure 1-6). The first RDA axis mostly express a gradient of partial cut (1965-2005) (CP05; Individual R2adj = 0.021; Table 1-5) while the second axis shows a gradient from fire (FIRE; Individual R2adj = 0.014) to spruce budworm outbreak (SBW; Individual R2adj =0.008). The third axis shows a gradient of plantation (PL; Individual R2adj = 0.011). Partial cuts between 1965 and 2005, fires and plantations explain 4.6% out of the 6% of the variance among disturbance variables. Trembling aspen (Pot) is correlated to burned areas. Sugar maple (Acs) and yellow birch (Bea) are correlated to partial cuts between 1965 and 2005. Black spruce (Pim) is associated with plantations. Northern white cedar (Tho) is not explained by any studied disturbance type as it is perpendicular to all disturbances in the multivariate space.

Between historical (1930-1931) and present-day (1985-2005) periods, we observed a change in basal area and diameter structure of tree taxa. Total basal area increased noticeably by 5.1 m2/ha in naturally regenerating stands, while it decreased by 2.8 m2/ha in plantations (Table 1-6). Most plantations were likely thinned at the time of sampling. The increase in basal area in naturally regenerating stands is largely due to a threefold increase of northern white cedar by 2.7 m2/ha and a nine fold increase in maples by 1.5 m2/ha. This increase was accompanied by an increase in the density of northern white cedar in all diameter classes and an increase in maples density for small diameter classes (Figures 1-7 and 1-8). A slight increase in basal area for spruces, balsam fir and poplars and a decrease in yellow birch and white birch also occurred (Figure 1-8), although an increased density of stems in small diameter classes occurred for these species in naturally regenerated stands (Figure 1-7). In plantations, 41% (7.1 m2/ha) of the mean basal area is represented by Spruces (Table 1-6) with a significant increase in stem density in the smallest diameter class for this taxa compared to historical and modern naturally regenerated stands values (Figure 1-7). The mean basal area of secondary natural regeneration of balsam fir (fir has not been planted) in plantations represent 44% (7.6 m2/ha). Balsam fir density has slightly increased in the smallest diameter class compared to historical and modern naturally regenerated stands values (Figure 1-7).

1.7. Discussion

1.7.1. Anthropogenic disturbance regime of the 20th century

During the 20th century, anthropogenic disturbances were omnipresent in the landscape, as for other regions of the eastern North American mixed forests (Foster 1992, Whitney 1994, Friedman and Reich 2005b). Fire activity was concentrated at low elevation during the settlement period, close to private lands suggesting ignitions from anthropogenic origins (Figures 1-3.A and 1-5). Logging activities expanded from around main rivers during the first half of the 20th century towards inland areas and higher altitude by the second half of the century (Figures 1-2 and 1-5), marking the transition from log transport by watercourses to the use of forest roads and trucks. Moreover, 18% of these logged zones have been subsequently transformed into plantations, mostly between 1985 and 1995, during the last Spruce budworm outbreak (1975 – 1990). Planted zones were chosen in backcountry accessible sectors and mostly planted with insect resistant black spruce (Pim), while the less accessible sectors on steeper slopes were disturbed by the SBW outbreak (Figures 1-5 and 1-6).

Before European settlement, the pre-industrial disturbance regime of south-eastern Quebec and northern New England was dominated by secondary disturbances like windthrows and insect outbreaks (Blais 1961, Lorimer 1977, Bormann and Likens 1979, Payette et al. 1990, Frelich 2002, Lorimer and White 2003). For the LSL region, this can be inferred from the old-growth, uneven aged forest structure of the pre-settlement forest, which was also dominated by fire-sensitive species (balsam fir, white spruce, eastern white cedar) (Etheridge et al. 2005, Boucher et al. 2009b, Dupuis et al. 2011). The very long rotation period we estimated for windthrows in the study area over the 20th century (about 3000 years; less than 1% of the landscape affected; Table 1-3) is considerably longer than the value of 1150 years estimated by Lorimer (1977) for Northern Maine between 1793 and 1827. This discrepancy may emphasize a relatively low occurrence of large windthrows in the study area. Indeed, wind storms that create large canopy openings are known to be infrequent in this type of mixed forests (Frelich and Lorimer 1991, Lorimer and White 2003). Although tree ring evidence indicate a time interval of 40 years between successive spruce budworm outbreaks in the LSL region over the past 450 years (Boulanger and Arseneault 2004), the rotation period for presettlement Spruce budworm outbreaks is hard to calculate due to the lack of spatial data.

Escaped-settlement fires and extensive logging during the 20th century have strongly altered the type, rotation period, severity and extent of disturbance events (Table 1-3). Compared to a fire rotation period of 200 years at the peak of human settlement in the region (1925-1955), the value of 1668 years calculated for the 1895-1925 interval is closer to values suggested elsewhere for pre-industrial landscapes of the temperate zone. Natural fires were documented to be rare in the presettlement land surveys in the temperate forests of eastern North America (Siccama 1971, Lorimer 1977, Foster et al. 1998). For example, recently burned areas covered 10% of the landscape in Northern Maine shortly before settlement, with a rotation period estimated to be 800 years (Lorimer 1977). An even longer fire rotation period of 1240 was reported for spruce-fir forests in Maine (Fahey and Reiners 1981). At the same time logging evolved from partial cutting diameter-limit management, associated to the saw mill industry, at the beginning of the century to total cutting, associated to the pulp and paper industry, by the end of the century (Fortin et al. 1993, Boucher et al. 2009a, Boucher et al. 2009c). Overall, logging covered 144% of the study area between 1895 and 2005, with 45% of the study area logged more than once.

1.7.2. 20th century anthropogenic disturbances impact on present day forest composition

Mixed forests in our study area showed resilience in terms of composition, despite the omnipresence of anthropogenic disturbances during the 20th century. There is a correlation between tree taxa basal area in 1930-1931 and present-day taxa basal area (Figure 1-8). At the beginning of the century, diameter limit selective logging was conducted in winter and with minimal machinery (Fortin et al. 1993). This might have protected coniferous regeneration and limited the expansion of early successional deciduous tree species, contributing to the overall observed resilience of forests to logging operations at the beginning of the 20th century (Table 1-5). A study of Boucher et al. (2017) have used a similar database and disturbance data, as in this study, in the southern boreal forest of central Canada, and have concluded that logging have a minor impact on compositional change.

Disturbances of the 20th century explain only 6% of present-day tree composition (Figure 1-6), suggesting that they have not been an important agent of forest reorganization in our study area. This contrasts with more salient views in the literature which emphasize the impact of anthropogenic disturbances on forest composition (Whitney 1994, Foster et al. 1998, Fuller et al. 1998, Friedman and Reich 2005a, Dupuis et al. 2011, Boucher et al. 2014, Fortin 2018, Danneyrolles et al. 2019). Many of these studies use vegetation data from historical land surveys (frequency of occurrence and dominance). The difference between our study area and other studies using historical land surveys might be that our study area is mostly located in public territory, while these studies were mostly located in private lands. More severe and frequent anthropogenic disturbances are likely to occur in private lands, as in the case of anthropogenic fires in our results (Figure 1-5). Moreover, the response of vegetation to disturbances might be site specific and could have been attenuated by the use of a 9 km2 grid cells. Finally, the influence of total cuts on vegetation composition might not be fully ceased by our analysis (CT05 adj R2 =

0.005; Table 1-5). Although naturally regenerated stands originating after total cuts between 1965 and 2005 cover 25% of the study area, many of the trees in these stands are 40 years old or younger and have smaller DBH than the 7cm minimum DBH for trees measured in our database.

Despite the relatively low importance of disturbances to explain the present-day forest composition, some taxa responded to disturbances in an individualistic manner, reflecting their functional traits. The increase of early-successional trembling aspen in naturally regenerated stands compared to the 1930-1931 time period (Figure 1-6 to 1-8; Table 1-6) is correlated to the important increase in fire events. Several previous studies have linked the increase of trembling aspen with anthropogenic fires in eastern North America (Bergeron 2000, Cleland et al. 2001, Friedman and Reich 2005b, Boucher et al. 2014, Boucher et al. 2017, Terrail et al. 2020). We also found that the fire sensitive balsam-fir (Rowe 1972) is mostly abundant away from fire polygons (Figure 1-6). Species usually associated with gap dynamics, such as yellow birch and sugar maple, are correlated to partial cuts (1965-2005). These species might have benefitted from the elimination of shade tolerant competitors in partial cuts as well as in areas impacted by spruce budworm outbreak (Figure 1-6) (Palik and Pregitzer 1992, Abrams 1998). Moreover, red and sugar maples produce a large quantity of seeds and can grow rapidly when exposed to light (Fei and Steiner 2008, Nolet et al. 2008). In addition, management practices which aim at preserving yellow birch seed trees in logging operations might have favoured the abundance of this species.

Planted areas have also participated to the observed present-day forest composition at the landscape level. They are human made ecosystems which are less diverse than naturally regenerated stands (Table 1-6), as 41 % of plantations basal area is composed of spruces against 19% in natural regenerated stands (Table 1-6, Figure 1-7). Other tree species found in planted stands consist in naturally regenerated balsam fir and early successional white birch.

Surprisingly northern white cedar, a late successional shade tolerant species increased in basal area and was not correlated to disturbances (Table 1-6, Figure 1-6). This result is somewhat contrary to the general tendency of the decreased cedar abundance in eastern Canadian mixed forests, even though variable between regions (Danneyrolles et al. 2017). It's present-day increase and distribution in the landscape is probably better explained when environmental factors are considered. Northern white cedar is usually found in zones with poor drainage, organic deposit and in low altitude (Robitaille and Saucier 1998). The study area's position in public territory might have also made northern white cedar exploitation less frequent. Yet, the interaction with partial natural and human disturbances (insect outbreaks and partial cuts) combined with an abundant advanced regeneration of northern white cedar was suggested to explain the dominance of this species (Heitzman et al. 1997, Ruel et al. 2014, Danneyrolles et al. 2017).

Determining the contribution of anthropogenic disturbances on forest composition should be studied along with other agents and their interactions at various spatial and temporal scales (Krankina et al. 2005, Gimmi et al. 2010, Landhäusser et al. 2010, Fisichelli et al. 2014, Nowacki and Abrams 2015, Plieninger et al. 2016, Vayreda et al. 2016, Danneyrolles et al. 2019). For example, Boisvert-Marsh et al. (2019) have suggested that disturbance of the last 40 years have been less important than climate change to explain present-day forest composition, whereas Danneyrolles et al. (2019) concluded the contrary at the scale of the last century. Moreover, the characteristics of disturbances themselves (extent, frequency, intensity, type, return interval) and their combination might also have different influences on vegetation composition (Turner 2010). In the present study, the conjugated analysis of disturbance history and associated compositional change over the transition period encompassing the early settlement of the population and the deployment of industrial forestry suggest moderate change in forest cover composition despite extensive anthropogenic disturbances in this representative eastern Canadian mixed forest.

Our study supports the recommendations of forest ecosystem management practices to use partial cutting to maintain the forest in its natural range of variability (Landres et al. 1999). On the other hand, further investigation is needed to study the impact of clear cutting as the duration and data of our study don't permit the estimation of the impact of this stand replacing disturbance. Paleoecological studies which could encompass longer time-frames could present precious complementary information on forest composition and natural disturbance history at the millennial scale.

1.8. References

Abrams, M. D. 1998. The red maple paradox: What explains the widespread expansion of red maple in eastern forests ? Bioscience, 48(5), 355-364.

Abrams, M. D. 2003. Where has all the white oak gone? Bioscience, 53(10), 927-939.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology, 81(6), 1500-1516.

Blais, J. R. 1961. Spruce budworm outbreaks in the Lower St. Lawrence and Gaspé regions. The Forestry Chronicle, 37(3), 192-202.

Blanchet, P. 2003. Feux de forêt : l'histoire d'une guerre. Montréal: Trait d'union.

Blarquez, O., Talbot, J., Paillard, J., Lapointe-Elmrabti, L., Pelletier, N., and Gates St-Pierre, C. 2018. Late Holocene influence of societies on the fire regime in southern Québec temperate forests. Quaternary Science Reviews, 180, 63-74. doi:https://doi.org/10.1016/j.quascirev.2017.11.022.

Boisvert-Marsh, L., Périé, C., and de Blois, S. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology, 1-14. https://doi.org/10.1111/1365-2745.13149

Bormann, F. H., and Likens, G. E. 1979. Catastrophic Disturbance and the Steady State in Northern Hardwood Forests: A new look at the role of disturbance in the development of forest ecosystems suggests important implications for land-use policies. American Scientist, 67(6), 660-669. doi:10.2307/27849531

Boucher, Y., Arseneault, D., and Sirois, L. 2006. Logging-induced change (1930-2002) of a preindustrial landscape at the northern range limit of northern hardwoods, eastern Canada. Canadian Journal of Forest Research, 36(2), 505-517.

Boucher, Y., Arseneault, D., and Sirois, L. 2009a. Logging history (1820–2000) of a heavily exploited southern boreal forest landscape: Insights from sunken logs and forestry maps. Forest Ecology and Management, 258(7), 1359-1368. doi:10.1016/j.foreco.2009.06.037

Boucher, Y., Arseneault, D., and Sirois, L. 2009b. La forêt préindustrielle du Bas-Saint-Laurent et sa transformation (1820-2000) : implications pour l'aménagement écosystémique. Le Naturaliste Canadien, 133(2), 60-69.

Boucher, Y., Arseneault, D., Sirois, L., and Blais, L. 2009c. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. Landscape Ecology, 24(2), 171-184. doi:10.1007/s10980-008-9294-8

Boucher, Y., Auger, I., Noël, J., Grondin, P., and Arseneault, D. 2017. Fire is a stronger driver of forest composition than logging in the boreal forest of eastern Canada. Journal of Vegetation Science, 28(1), 57-68. doi:10.1111/jvs.12466

Boucher, Y., Grondin, P., and Auger, I. 2014. Land use history (1840–2005) and physiography as determinants of southern boreal forests. Landscape Ecology, 29(3), 437-450. doi:10.1007/s10980-013-9974-x

Boulanger, Y., and Arseneault, D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. Canadian Journal of Forest Research, 34(5), 1035-1043. doi:doi:10.1139/x03-269

Brisson, J., and Bouchard, A. 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Québec, Canada. Écoscience, 10(2), 236-246.

Bürgi, M., Russell, E. W. B., and Motzkin, G. 2000. Effects of postsettlement human activities on forest composition in the north-eastern United States: a comparative approach. Journal of Biogeography, 27(5), 1123-1138.

Canham, C. D., Rogers, N., and Buchholz, T. 2013. Regional variation in forest harvest regimes in the northeastern United States. Ecological Applications, 23(3), 515-522. doi:10.1890/12-0180.1

Cleland, D. T., Leefers, L. A., and Dickmann, D. I. 2000. Ecology and Management of Aspen: A Lake States Perspective. Paper presented at the Sustaining Aspen in Western Landscapes: Symposium Proceedings, Colorado, USA.

Danneyrolles, V., Dupuis, S., Arseneault, D., Terrail, R., Leroyer, M., de Römer, A., . . . Ruel, J.-C. 2017. Eastern white cedar long-term dynamics in eastern Canada: Implications for restoration in the context of ecosystem-based management. Forest Ecology and Management, 400, 502-510. doi:https://doi.org/10.1016/j.foreco.2017.06.024

Danneyrolles, V., Dupuis, S., Fortin, G., Leroyer, M., de Römer, A., Terrail, R., . . . Arseneault, D. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications, 10(1), 1265. doi:10.1038/s41467-019-09265-z

Dupuis, S., Arseneault, D., and Sirois, L. 2011. Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. Journal of Vegetation Science, 22, 564-575.

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., and Ramankutty, N. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography, 19(5), 589-606. doi:10.1111/j.1466-8238.2010.00540.x

EnvironmentCanada. 2019. Canadian Climate Normals and averages 1981-2010. Retrieved from http://climate.weather.gc.ca/climate_normals/index_e.html

Etheridge, D. A., MacLean, D. A., Wagner, R. G., and Wilson, J., S. 2006. Effects of intensive forest management on stand and landscape charateristics in northern New Brunswick, Canada (1945-2027). Landscape Ecology, 21(4), 509-524.

Fahey, T. J., and Reiners, W. A. 1981. Fire in the forests of Maine and New Hampshire. Bulletin of the Torrey botanical club, 108(3), 362-373.

Fei, S., and Steiner, K. C. 2008. Relationships between advance oak regeneration and biotic and abiotic factors. Tree Physiology, 28(7), 1111-1119. doi:10.1093/treephys/28.7.1111

Fisichelli, N. A., Frelich, L. E., and Reich, P. B. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography, 37(2), 152-161. doi:10.1111/j.1600-0587.2013.00197.x

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P. K. 2005. Global Consequences of Land Use. Science, 309(5734), 570-574. doi:10.1126/science.1111772

Fortin, G. 2018. Transformation de la composition de la forêt de la péninsule gaspésienne au cours du XXème siècle. (Doctorat en Biologie), Université du Québec à Montréal.

Fortin, J.-C., Lechasseur, A., Morin, Y., Harvey, F., Lemay, J., and Tremblay, Y. 1993. Histoire du Bas-Saint-Laurent. Québec, Québec.

Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology, 80(4), 753-772.

Foster, D. R., Motzkin, G., and Slater, B. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems, 1(1), 96-119.

Foster, D. R., Swanson, F. J., Aber, J. D., Burke, I., Brokaw, N. V. L., Tilman, D., and Knapp, A. 2003. The importance of land-use legacies to ecology and conservation. Bioscience, 53(1), 77-88.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. New York: Cambridge University Press.

Frelich, L. E., and Lorimer, C. G. 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes region. Ecological Monographs, 61(2), 145-164.

Friedman, S. K., and Reich, P. B. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological Applications, 15(2), 726-744.

Fuller, J. L., Foster, D. R., McLachlan, J. S., and Drake, N. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems, 1(1), 76-95.

Gimmi, U., Wohlgemuth, T., Rigling, A., Hoffmann, C. W., and Bürgi, M. 2010. Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. Annals of Forest Science, 67(7), 701-701. doi:10.1051/forest/2010026

Gray, D. R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Climatic Change, 87(3), 361-383. doi:10.1007/s10584-007-9317-5

Grondin, P., Blouin, J., and Racine, P. 1999. Rapport de classification écologique du sous-domaine bioclimatique de la sapinière à bouleau jaune de l'est: Ministère des Ressources Naturelles du Québec, Direction des inventaires forestiers.

Hall, B., Motzkin, G., Foster, D. R., Syfer, M., and Burk, J. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography, 29(10-11), 1319-1335.

Harvey, B. D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management, 155(1-3), 369-385.

Hébert, A. D. 1938. Rapport concernant les opérations aériennes de Val Brillant - Comté de Matapédia. Bibliothèque et Archives nationales du Québec.

Heitzman, E., Pregitzer, K. S., and Miller, R. O. 1997. Origin and Early Development of Northern White-Cedar Stands in Northern Michigan. Canadian Journal of Forest Research, 27(12), 1953-1961.

Houghton, R. A. 1994. The worldwide extend of land-use change. Bioscience, 44(5), 305-313.

Jackson, S. M., Pinto, F., Malcolm, J. R., and Wilson, E. R. 2000. A comparison of pre-European settlement (1857) and current (1981-1995) forest composition in central Ontario. Canadian Journal of Forest Research, 30(4), 605-612.

Keenan, R. J., and Kimmins, J. P. 1993. The ecological effects of clear-cutting. Environmental Reviews, 1(2), 121-144. doi:10.1139/a93-010

Krankina, O. N., Houghton, R. A., Harmon, M. E., Hogg, E., Butman, D., Yatskov, M., Huso, M., Treyfeld, R.F., Razuvaev, V.N., Spycher, G. 2005. Effects of climate, disturbance, and species on forest biomass across Russia. Canadian Journal of Forest Research, 35(9), 2281-2293. doi:10.1139/x05-151

Landhäusser, S. M., Deshaies, D., and Lieffers, V. J. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography, 37(1), 68-76. doi:10.1111/j.1365-2699.2009.02182.x

Landres, P. B., Morgan, P., and Swanson, F. J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications, 9(1179-1188).

Leahy, M. J., and Pregitzer, K. S. 2003. A comparison of presettlement and present-day forest in northeastern lower Michigan. American Midland Naturalist, 149(1), 71-89.

Lindenmayer, D. B., and Franklin, J. F. 2002. Conserving forest biodiversity. Washington, DC: Island Press.

Lorimer, C. G. 1977. The Presettlement Forest and Natural Disturbance Cycle of Northeastern Maine. Ecology, 58(1), 139-148.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin, 29(2), 425-439.

Lorimer, C. G., and White, A. S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management, 185(1-2), 41-64.

Montoro Girona, M., Morin, H., Lussier, J.-M., and Ruel, J.-C. 2019. Post-cutting Mortality Following Experimental Silvicultural Treatments in Unmanaged Boreal Forest Stands. Frontiers in Forests and Global Change, 2(4). doi:10.3389/ffgc.2019.00004

Nie, Z., MacLean, D. A., and Taylor, A. R. 2018. Forest overstory composition and seedling height influence defoliation of understory regeneration by spruce budworm. Forest Ecology and Management, 409, 353-360. doi:https://doi.org/10.1016/j.foreco.2017.11.033

Nolet, P., Delagrange, S., Bouffard, D., Doyon, F., and Forget, E. 2008. The successional status of sugar maple (Acer saccharum), revisited. Annals of Forest Science, 65(2), 208-208. doi:10.1051/forest:2007091

Nowacki, G. J., and Abrams, M. D. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology, 21(1), 314-334. doi:10.1111/gcb.12663

Palik, B. J., and Pregitzer, K. S. 1992. A comparison of presettlement and present-day forests on two Bigtooth aspen-dominated landscape in northern lower Michigan. American midland naturalist, 127(2), 327-338.

Payette, S., Filion, L., and Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré ecological reserve, Quebec. Canadian Journal of Forest Research, 20(8), 1228-1241.

Plieninger, T., Draux, H., Fagerholm, N., Bieling, C., Bürgi, M., Kizos, T., Kuemmerle, T., Primdahl, J., Verburg, P. H. 2016. The driving forces of landscape change in Europe: A systematic review of the evidence. Land Use Policy, 57, 204-214. doi:https://doi.org/10.1016/j.landusepol.2016.04.040

Price Brothers and Company Limited, S. W. D. 1944. Working - plan report for Rimouski establishment. Archives Nationales du Québec - Chicoutimi.

Proulx, L. 1985. Les chantiers forestiers de la Rimouski (1930 - 1940), Techniques traditionnelles et culture matérielle. Université du Québec à Rimouski (UQAR).

R Development Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing.

Robitaille, A., and Saucier, J.-P. 1998. Paysage régionaux du Québec méridional, Direction de la gestion des stock forestiers et Direction des relations publiques, Ministère des Ressources naturelles du Québec. Québec: Publication du Québec.

Rowe, J. S. 1972. Forest regions of Canada. Ottawa: Information Canada.

Ruel, J.-C., Lussier, J.-M., Morissette, S., and Ricodeau, N. 2014. Growth Response of Northern White-Cedar (Thuja occidentalis) to Natural Disturbances and Partial Cuts in Mixedwood Stands of Quebec, Canada. Forests, 5(6), 1194.

Siccama, T. G. 1971. Presettlement and present forest vegetation in northern Vermont with special reference to Chittenden county. American midland naturalist, 85(1), 153-172.

Simard, I., Morin, H., and Lavoie, C. 2006. A millennial-scale reconstruction of spruce budworm abundance in Saguenay, Quéebec, Canada. The Holocene, 16(1), 31-37. doi:10.1191/0959683606hl904rp

Steffen, W., Sanderson, R. A., Tyson, P. D., Jäger, J., Matson, P. A., Moore, B., Oldfield, F., Richardson, K., Schellnhuber, H.J., Turner, B.L.,Wasson, R. J. 2004. Global Change and the Earth System - A planet under pressure: Springer-Verlag Berlin Heidelberg.

Terrail, R. 2013. Influence de la colonisation sur les transformations du paysage forestier depuis l'époque préindustrielle dans l'Est du Québec (Canada). (Doctoral thesis), Université du Québec a Rimouski (UQAR). Retrieved from http://labdendrodev.uqar.ca/wp-content/uploads/2015/02/RTerrail_PhD.pdf

Terrail, R., Morin-Rival, J., Fortin, M. J., and Arseneault, D. 2019. Effects of 20th century settlement fires on landscape structure and forest composition in Eastern Quebec, Canada. Journal of Vegetation Science.

Trumbore, S., Brando, P., and Hartmann, H. 2015. Forest health and global change. Science, 349(6250), 814-818. doi:10.1126/science.aac6759

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology, 91(10), 2833-2849. doi:10.1890/10-0097.1

Vayreda, J., Martinez-Vilalta, J., Gracia, M., Canadell, J. G., and Retana, J. 2016. Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. Global Change Biology, 22(12), 3984-3995. doi:10.1111/gcb.13394

White, M. A., and Mladenoff, D. J. 1994. Old-growth forest landscape transition from pre-European settlement to present. Landscape Ecology, 9(3), 191-205.

White, P., and Jentsch, A. 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. In K. Esser, U. Lüttge, J. W. Kadereit, and W. Beyschlag (Eds.), Progress in Botany (Vol. 62, pp. 399-450): Springer Berlin Heidelberg.

Whitney, G. G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America, 1500 to the present. Cambridge: Cambridge University Press.

Whitney, G. G., and DeCant, J. P. 2003. Physical and historical determinants of the pre- and post-settlement forests of northwestern Pennsylvania. Canadian Journal of Forest Research, 33(9), 1683-1697.

Williams, G. W. 2000. Introduction to aboriginal fire use in North America. Fire Management Today, 60(3), 8-12.

1.9. Tables

Table 1-1. Historical maps of disturbance polygons in the study area

Period	Number of maps	Map scale	Category mapped	Region covered	Source
1895-1931	1	1 : ~16 000	Logging, fire, wind throw, former agricultural land	Entire Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1940-1952	2	1 : ~16 000	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1945 - 1957	9	1 : ~32 000	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1934 -1945	8	1 : ~63 000	Logging	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1923 - 1955	24	not shown	Logging, fire	Portions of Rimouski and Matane sectors	Price Fund. Québec National Archives, Chicoutimi
1923-1938	1	1 : ~190 000	Fire	Entire Rimouski and Matane sector	Inventaire des ressources naturelles du Bas saint Laurent 1938. Quebec National Archive (ANQ-E16-P5_1938), Québec
1973-2005	4	1 : 20 000	Logging, fire, spruce budworm outbreaks, plantations	Entire Rimouski and Matane sector	Forest maps of the four decadal forest inventories. Ministry of Natural Resources of Quebec (MRN)
1932-1987	-	Polygon shapefiles	Fire	Entire Rimouski and Matane sector	SOPFEU database

Table 1-2. Environmental variables used in the RDA analysis

Variables	Description
Altitude (m)	Obtained from hypsometric curves (1: 20 000 maps) of Quebec's department of forests then transformed into a 400 m^2 cell raster in ArcGIS 10.0.
Slope (°)	Calculated from the altitude raster using spatial analyst tools in ArcGIS 10.0.
Aspect (°)	Calculated from the altitude raster using spatial analyst tools in ArcGIS 10.0.
Distance from main rivers (m)	The closest distance to the four main rivers in the study area: Rimouski, petite Rimouski, Matane and petite Matane rivers. This variable was considered in the analysis due to the historical context of log transport method along the main watercourses.
Distance from secondary rivers and lakes (m)	The closest distance to secondary rivers and lakes in the study area.
Distance from private lands (m)	The closest distance from a private land. This variable was considered to test the hypothesis of the anthropogenic origin of fire polygons which are expected to be situated closer to private lands.
Superficial deposit	Cover percentage of the 7 deposit types: Alteration, fluvial, glacial, fluvio-glacial, lacustrine, marine, and organic
Drainage class	7 classes ranging from excessive to very bad according to Quebec's department of forests classification

Table 1-3. Parameters of the 20th century disturbance regime in the study area

Category	Time span	Number of years	Covered area (km^2)	Percent total landscape (%)	Rate (percent per year)	Rotation period (years)
Fire	**1895-2005**	**110**	**596**	**19**	**0.2**	**594**
	1895-1925	30	58	2	0.06	1668
	1925-1955	30	483	15	0.50	200
	1955-2005	50	55	2	0.04	2925
Logging	**1895-2005**	**110**	**4633**	**144**	**1.3**	**76**
	1895-1935	40	844	26	0.7	152
	1935-1965	30	1219	38	1.3	79
	1965-2005	40	2750	80	2	47
Plantations	**1955-2005**	**50**	**571**	**18**	**0.4**	**282**
Spruce budworm	**1975-2005**	**30**	**1019**	**32**	**1.1**	**95**
Wind throws	**1895-2005**	**110**	**11**	**0.35**	**0.003**	**3000**
All disturbances (Excluding plantations)	**1895-2005**	**110**	**6259**	**195**	**1.7**	**56**

Table 1-4. Environmental and 1930-1931 basal area variables retained by forward selection in the RDA model to explain the 20th century disturbances. Gray coloured variables are not significant

Variable	Acronym	Individual adjusted R^2	Cumulated adjusted R^2	p-value	Within group selection order
Environmental variables					
Distance from main rivers	main rivers	0.084	0.088	≤ 0.001	1
Distance from private lands	PR	0.067	0.164	≤ 0.001	2
Weathering deposit	Wthr	0.013	0.204	≤ 0.001	3
Distance from closest water course	water	0.007	0.220	≤ 0.001	4
Glacial deposit	Glac	0.012	0.233	≤ 0.001	5
Fluvial deposit	Fluv	0.004	0.240	< 0.01	6
Slope	slope	0.009	0.246	< 0.01	7
Altitude	alt	0.007	0.253	< 0.01	8
Aspect	-	-	-	> 0.05	-
Drainage	-	-	-	> 0.05	-
Fluvio-glacier deposit	-	-	-	> 0.05	-
Lacustrine deposit	-	-	-	> 0.05	-
Marine deposit	-	-	-	> 0.05	-
Organic deposit	-	-	-	> 0.05	-
Taxa basal area 1930					
***Picea* spp.**	Pic30	0.076	0.079	≤ 0.001	1
Thuja occidentalis	Tho30	0.001	0.101	≤ 0.001	2
Betula alleghaniensis	Bea30	0.030	0.117	≤ 0.001	3
***Pinus* spp.**	Pin30	0.017	0.128	< 0.01	4
Abies balsamea	Abb30	0.018	0.139	< 0.01	5
Betula papyrifera	Bep30	0.014	0.146	< 0.01	6
***Fraxinus* spp**	Frx30	0.006	0.151	< 0.05	7
***Ulmus* spp.**	Ulm30	0.009	0.156	< 0.05	8
***Acer* spp.**	Ace30	0.005	0.161	< 0.05	9
Larix laricina	-	-	-	> 0.05	-
***Populus* spp.**	-	-	-	> 0.05	-

Table 1-5. Disturbance variables retained by forward selection in the RDA model to explain taxa basal area in 1985-2005. Gray coloured variables are not significant

Disturbance Variables	Acronym	Individual adjusted R^2	Cumulated adjusted R^2	p-value	Within group selection order
Partial cut (1965-2005)	CP05	0.021	0.021	≤0.001	1
Fire (1895-2005)	FIRE	0.014	0.035	≤0.001	2
Plantations (1955-2005)	PL	0.011	0.046	≤0.001	3
Spruce Budworm outbreak (1975-2005)	SBW	0.008	0.051	≤0.001	4
Partial cut (1935-1965)	CO65	0.005	0.055	≤0.001	5
Clear cut (1965-2005)	CT05	0.005	0.059	≤0.001	6
Partial cut (1895-1935)	CO35	-	-	> 0.05	-

Table 1-6. Taxa basal area (m2/ha ± sd) in 1930-1931 (N = 16804) and 1985-2005 for the whole study area. Basal area for the 1985-2005 period is divided into 2 groups according to origin: natural regeneration (N= 3797) or plantation (N= 385)

Species: Common name	Latin name	Acronym	1930-1931	1985-2005: Natural regeneration	1985-2005: Plantations
Balsam fir	*Abies balsamea*	Abb	9.2 (±6.3)	9.8 (±9.2)	7.6 (±8.7)
American larch	*Larix laricina*	Lar	0.01 (±0.3)	0.06(±0.62)	0.00 (±0.07)
Spruces	*Picea* spp.	Pic	3.6 (±3.8)	4.7 (±5.5)	7.1 (±7.6)
Norway spruce	***Picea abies***	Pia	-	0.04 (±1.07)	0.7 (±4.3)
White spruce	***Picea glauca***	Pig	-	3.3 (±4.3)	3.2 (±5.2)
Black spruce	***Picea mariana***	Pim	-	1.2 (±3.9)	3.0 (±5.9)
Red spruce	***Picea rubens***	Pir	-	0.1 (±0.9)	0.2 (±1.5)
Pines	*Pinus* spp.	Pin	0.03 (±0.38)	0.07 (±0.74)	0.00 (±0.03)
Red pine	***Pinus resinosa***	Pinr	-	0.02 (±0.40)	0.00 (±0.03)
White pine	***Pinus strobus***	Pins	-	0.05 (±0.61)	0.00 (±0.00)
Northern white cedar	*Thuja occidentalis*	Tho	1.6 (±4.5)	4.3 (±10.6)	0.3 (±2.4)
Conifer basal area		-	14.5 (±8.5)	18.9 (±14.0)	14.9(±2.5)
Maples	*Acer* spp.	Ace	0.18 (±1.1)	1.7 (±4.5)	0.3 (±1.4)
Red maple	***Acer rubrum***	Acr	-	0.7 (±2.0)	0.1 (±0.8)
Sugar maple	***Acer saccharum***	Acs	-	1.0 (±4.0)	0.2 (1.1)
Yellow birch	*Betula alleghaniensis*	Bea	1.8 (±3.2)	1.7 (±3.3)	0.7 (±2.0)
White birch	*Betula papyrifera*	Bep	3.6 (± 3.5)	2.3 (±0.2)	1.0 (±1.9)
Black ash	*Fraxinus nigra*	Frx	0.02 (±0.3)	0.04 (±0.43)	0.00 (±0.01)
Poplars	*Populus* spp.	Pop	0.05 (±0.58)	0.8 (±3.6)	0.4 (±2.4)
Balsam poplar	***Populus balsamifera***	Pob	-	0.3 (±2.4)	0.1 (±1.3)
Trembling aspen	***Populus tremuloides***	Pot	-	0.5 (±2.6)	0.3 (±2.0)
American elm	*Ulmus americana*	Ulm	0.01 (±0.22)	0	0
Deciduous basal area		-	5.7 (±5.0)	6.4 (±7.2)	2.5 (±4.3)
Total		-	20.2 (± 9.3)	25.3 (±12.4)	17.4 (±10.7)

1.10. Figures

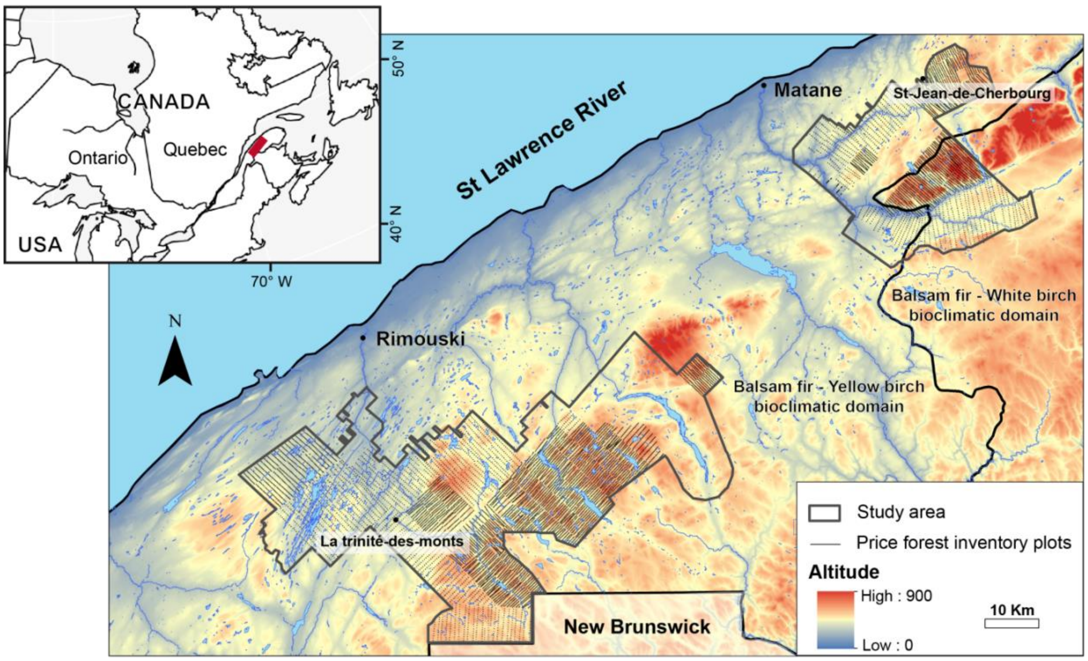


Figure 1-1. Location of the Rimouski and Matane sectors and distribution of Price forest inventory plots in eastern Canada

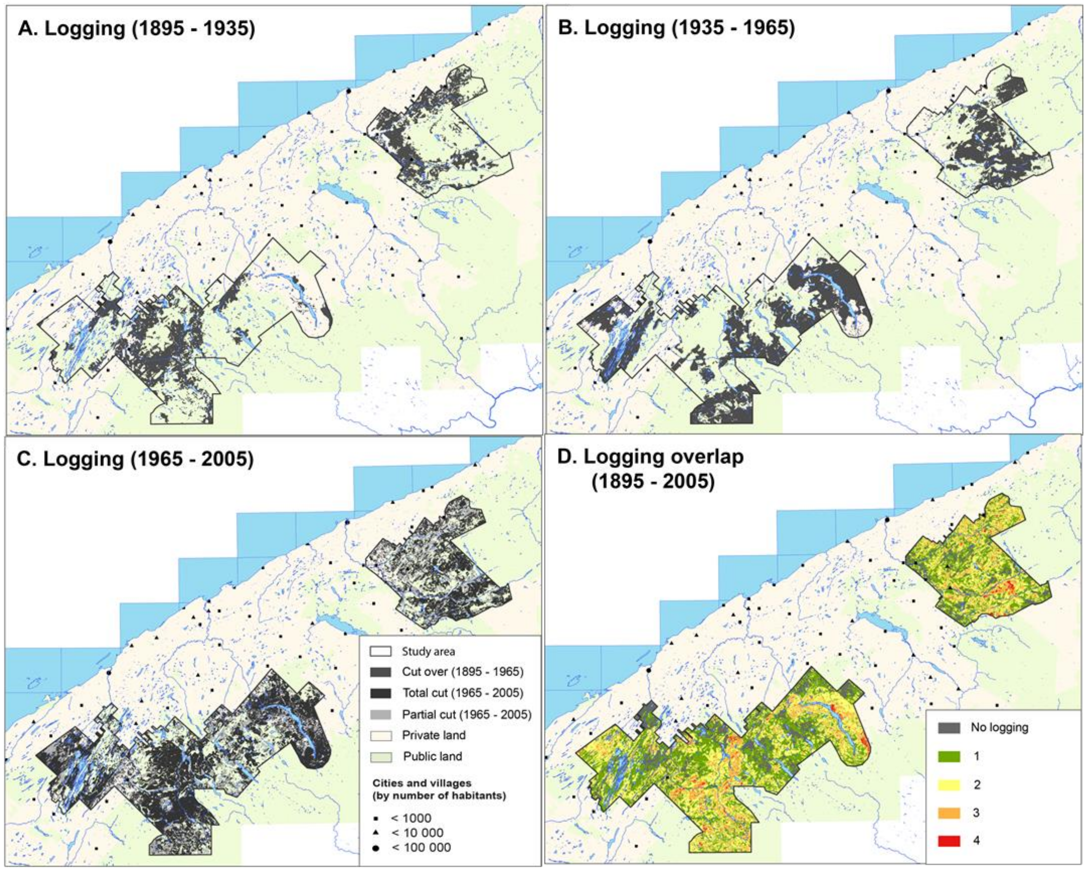


Figure 1-2. Logged areas during the periods 1895-1935 (A), 1935 - 1965 (B), and 1965 - 2005 (C); D: Number of times each patch has been logged over the 1895 - 2005 study period

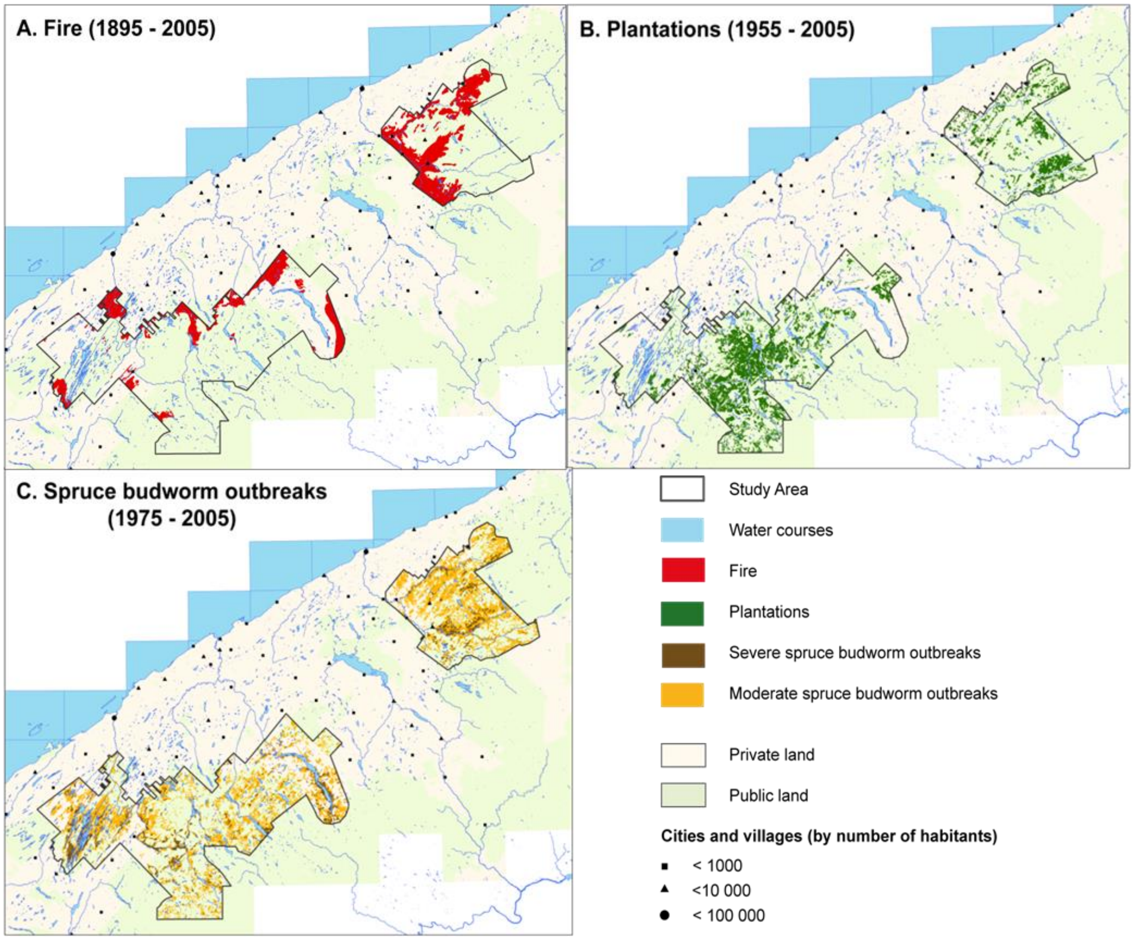
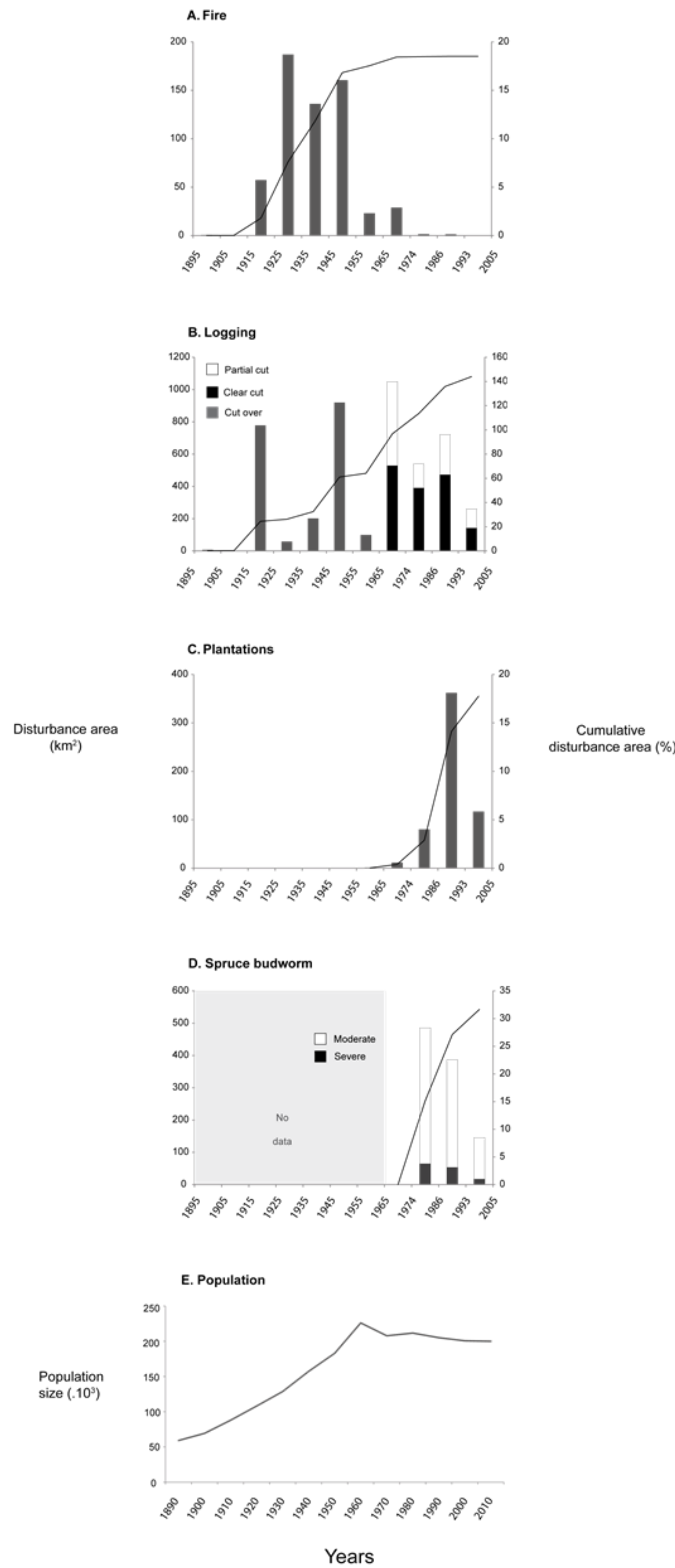


Figure 1-3. Maps of fires (A), plantations (B) and spruce budworm outbreaks (C) disturbances in the Rimouski and Matane sectors

Figure 1-4. Disturbances area (bars) and cumulative disturbance area (lines) per decade for: A. Fire, B. Logging, C. Plantations and D. Spruce budworm outbreaks. Logging type is divided into partial and clear cuts between 1975 and 2005. Areas of spruce budworm outbreaks are divided into moderate and severe outbreaks. E. Trend in human population in the LSL administrative region (Census Canada in Fortin, 1993).



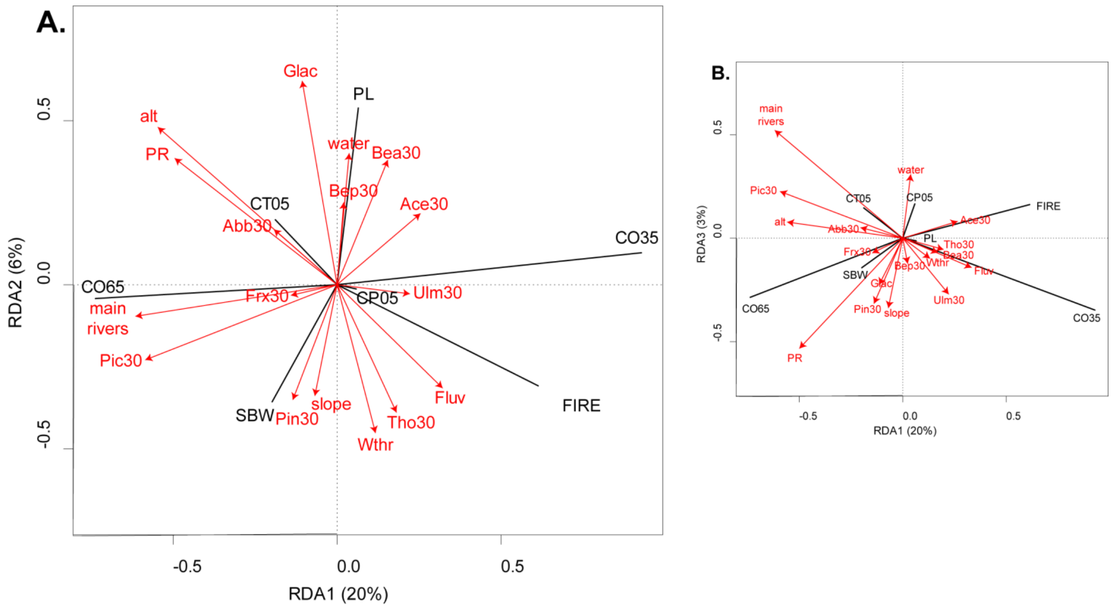


Figure 1-5. Redundancy analysis (model adjusted R2 = 32%) of the 20th century disturbances (black lines) correlated to 17 explanatory variables (red vectors) in two driver sets (environmental variables and taxa basal area in 1930). Projections showed using A. first and second ordination axes, and B. first and third ordination axes. N=333 cells of 3×3 km. FIRE: Fire (1895-2005), PL: Plantations (1955-2005), SBW: Spruce Budworm outbreaks (1975-2005), CO35: Cut over (1895-1935), CO65: Cut over (1935-1965), CP05: Partial cut (1965-2005), CT05: Clear cut (1965-2005). Acronyms of explanatory variables are indicated in the Table 1-3.

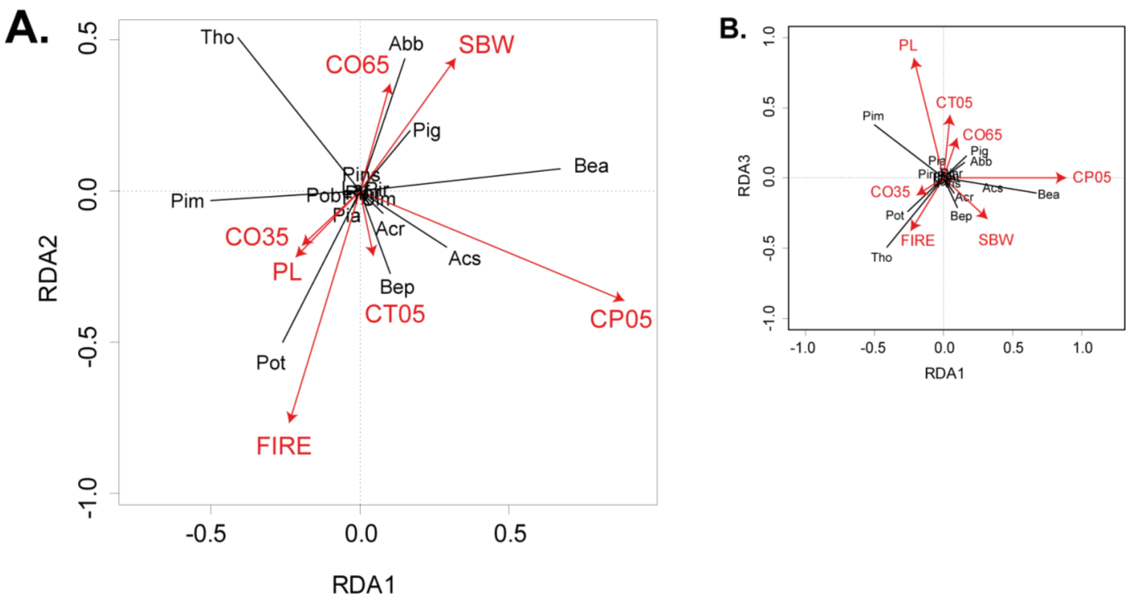


Figure 1-6. Redundancy analysis (model Adjusted R2 = 6%) of taxa basal area in 2005 (black lines) correlated to 7 disturbance explanatory variables (red vectors). Projections showed using A. first and second ordination axes and B. first and third ordination axes. N= 4573 temporary plots of the 2nd, 3rd and 4th government decennial inventories. Frx: Ash, Abb: Balsam fir, Tho: Northern white cedar, Ulm: American elm, Lar: American larch, Acr: Red maple, Acs: Sugar maple, Pob: Balsam poplar, Pot: Trembling aspen, Pins: White pine, Pinr: Red pine, Pim: Black spruce, Pia: Norway spruce, Pir: Red spruce, Pig: White spruce, Bea: Yellow birch, Bep: White birch. Acronyms of explanatory variables are indicated in the Table 1-4.

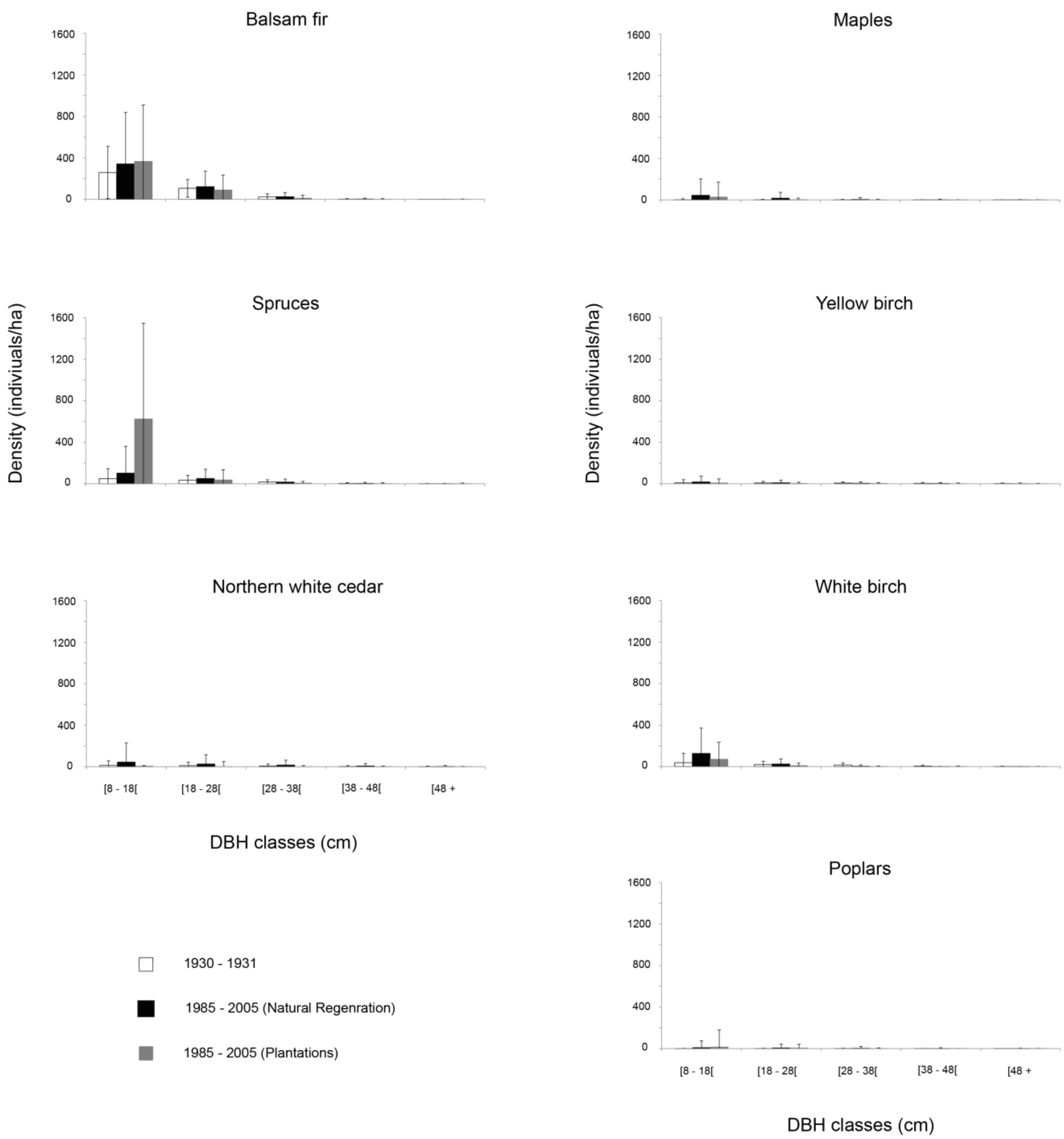


Figure 1-7. Diameter structure between 1930-1931 (N = 16345), 1985-2005 natural regenerated stands (N = 3795) and 1985 – 2005 plantations (N = 385). Bars represent standard deviation.

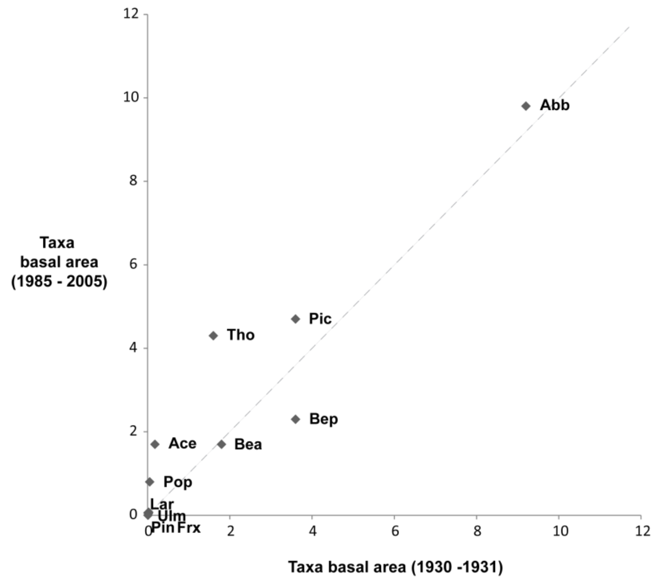


Figure 1-8. Taxa basal area (m2.ha-1) in 1930-1931 and 1985-2005 in naturally regenerated stands. Frx: Ash, Abb: Balsam fir, Tho: Northern white cedar, Ulm: American elm, Lar: American larch, Ace: Maple, Pop: Poplar, Pin: Pine, Pic: Spruce, Bea: Yellow birch, Bep: White birch.

1.11. Appendix

Table 1-S1. Disturbance area (km2) per decade

Date	Fire	Logging	Plantations	SBW
1895-1905	0.56	6.39	0	No data
1905-1915	0	2.03	0	No data
1915-1925	57.31	777.88	0	No data
1925-1935	186.99	57.87	0	No data
1935-1945	135.92	201.14	0	No data
1945-1955	160.50	919.07	0	No data
1955-1965	23.01	98.57	1.06	No data
1965-1975	28.84	1049.71	11.42	0
1975-1985	1.37	539.03	80.06	485.88
1985-1995	1.21	721.07	362.01	386.80
1995-2005	0.02	260.71	116.89	145.87

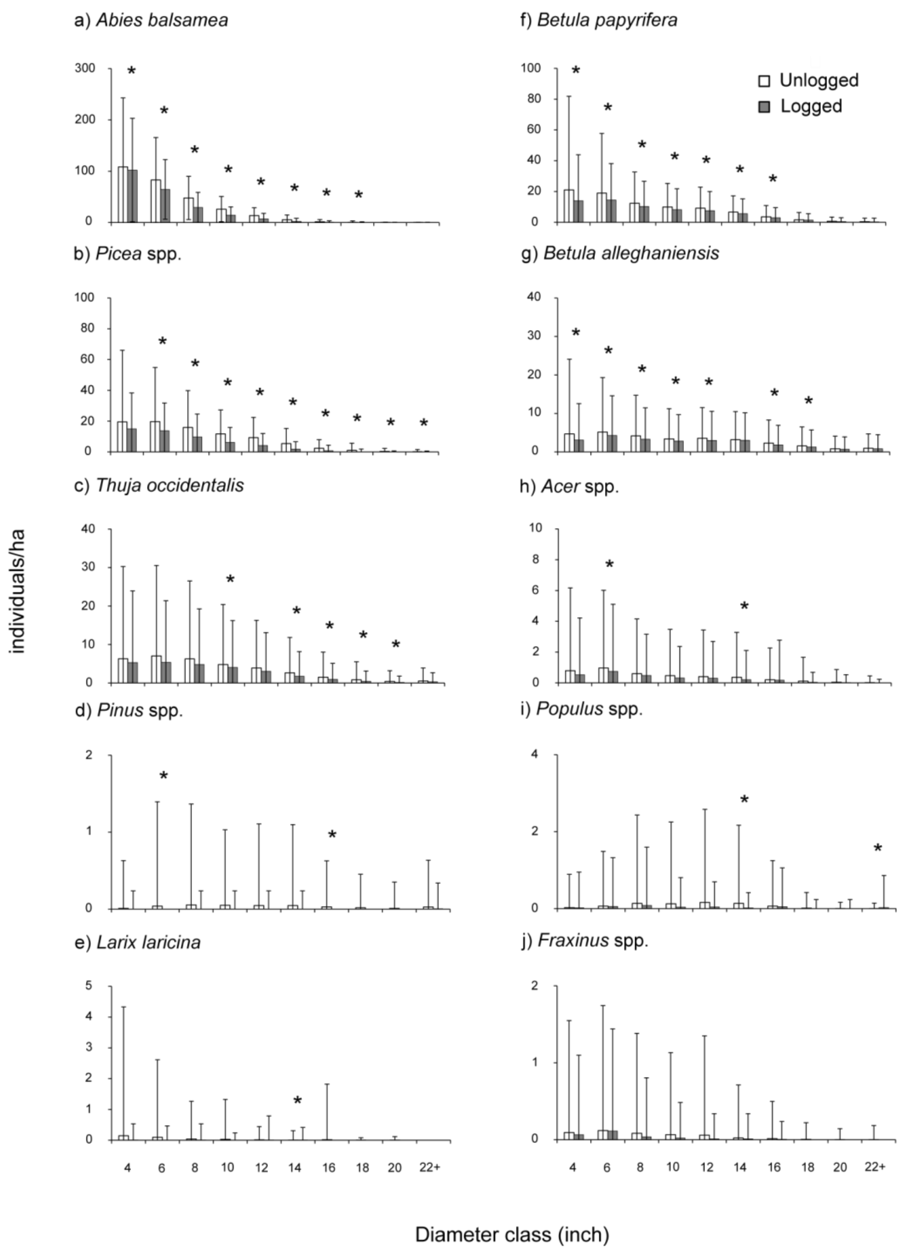


Figure 1-S1. Stem density per diameter class per species in previously unlogged (N = 14 634) versus logged plots (N = 1 822) in 1930. Bars represent standard deviation, Asterisks (*) indicate a statistically significant difference in stem density between unlogged and logged plots for a given diameter class (Wilcoxon test; $p < 0.05$).

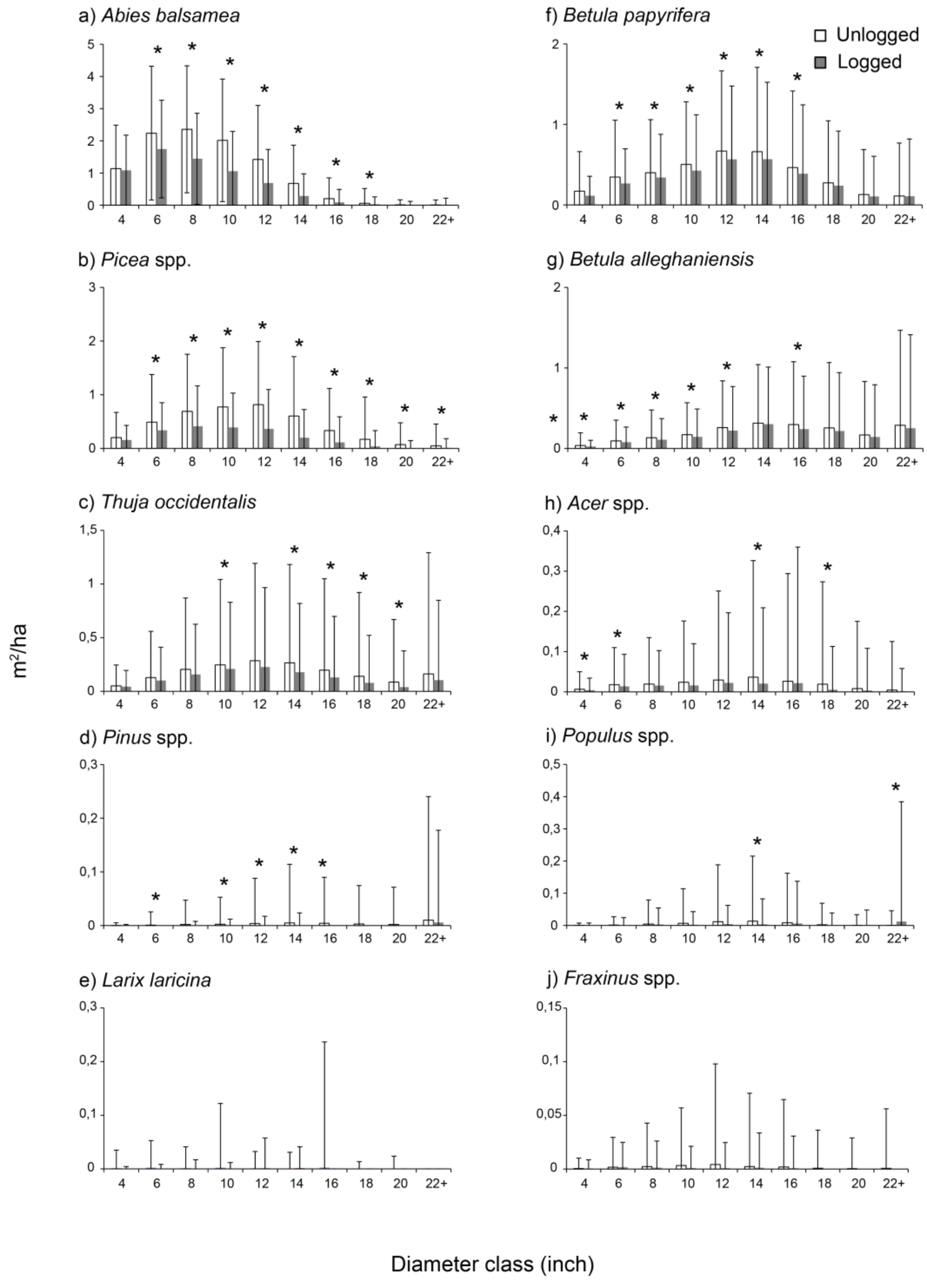


Figure 1-S2. Basal area per diameter class per species in previously unlogged (N = 14 634) versus logged plots (N = 1 822). Bars represent standard deviation, Asterisks (*) indicate a statistically significant difference in basal area (m2/ha) between unlogged and logged plots in a given diameter class (Wilcoxon test; $p < 0.05$).

CHAPITRE II
INFLUENCE DU CLIMAT ET DES PERTURBATIONS SUR LE CHANGEMENT DE LA COMPOSITION FORESTIÈRE (1930-2012) DANS L'EST DU CANADA COMME RÉVÉLÉ PAR LE RE-ÉCHANTILLONNAGE DES PLACETTES D'INVENTAIRE HISTORIQUE

2.1. Résumé en français du deuxième article

Ce deuxième article, intitulé «Influence du climat et des perturbations sur le changement de la composition forestière (1930-2012) dans l'est du Canada comme révélé par le re-échantillonnage des placettes d'inventaire historique», fut corédigé par moi-même ainsi que par les professeurs Dominique Arseneault et Luc Sirois. En tant que première auteure, ma contribution à ce travail fut l'essentiel de la recherche sur l'état de l'art, le développement de la méthode, la collecte des données sur le terrain, l'analyse des données et la rédaction de l'article. Les professeurs Dominique Arseneault et Luc Sirois, second et troisième auteurs ont aidé à la recherche sur l'état de l'art, au développement de la méthode ainsi qu'à la révision de l'article.

La contribution relative du climat et des perturbations anthropiques sur la composition actuelle des forêts mixtes de l'est de l'Amérique du Nord reste encore un objet de débat. Dans cette étude, nous avons re-échantillonné 743 placettes d'inventaire forestier établies dans les années 1930 afin de décrire le changement de la composition forestière entre 1930 et 2012. Nous avons ensuite utilisé des données spatialement explicites des perturbations ainsi que des données du climat, et de l'environnement pour identifier les variables explicatives principales responsables de la composition forestière actuelle. Nos résultats montrent qu'il existe une expansion et une densification des taxons décidus comme les érables et les peupliers, ainsi qu'une densification du bouleau blanc. Le bouleau jaune ainsi que les taxons de conifères (sapin baumier, épinettes, et thuya) sont restés constant ou ont légèrement augmenté. La surface terrière actuelle des taxons étudiés a été expliquée par la surface terrière en 1930 (21.9%), l'environnement (15.4%), le climat (12.6%), et les perturbations anthropiques du $20^{\text{ème}}$ siècle (5.1%). L'effet du climat s'est particulièrement traduit par la distribution de la surface terrière des érables rouges et des érables à sucre dans le paysage, tandis que l'effet des perturbations anthropiques du $20^{\text{ème}}$ s'est traduit par la corrélation entre les peupliers et l'occurrence des feux et par une corrélation entre le bouleau jaune et les coupes partielles survenues entre 1965 et 2005. De plus, les perturbations anthropiques du $20^{\text{ème}}$ siècle ont interagit avec le climat (0.8%) et ont avantagé encore plus l'augmentation des érables. Avec le renforcement attendu de l'effet climatique dans le futur, l'expansion des érables va probablement continuer.

Mots clés : forêts mixtes ; climat ; perturbations anthropiques ; changement de composition ; environnement physique

2.2. Influence of climate and disturbances on forest compositional changes (1930-2012) in eastern Canada as revealed from the resurvey of an early forest inventory

2.3. Abstract

The relative contribution of climate and anthropogenic disturbances in present-day composition of mixed forests of eastern North America are still a subject of debate. In this study, we re-sampled 743 forest inventory plots established in the 1930's to describe the forest compositional change between 1930 and 2012. We then used a spatially explicit disturbance data as well as climate, and environment data to identify the main explanatory variables responsible for the present-day forest composition. Our results show an expansion and densification of deciduous maples and poplars and a densification of white birch. Yellow birch and coniferous taxa (balsam fir, spruces, and northern white cedar) stayed constant or slightly increased. Present-day taxa basal area was explained by taxa basal area in 1930 (21.9%), Environment (15.4%), Climate (12.6%) and 20th century Disturbances (5.1%). The effect of climate was particularly translated by the distribution of sugar maple and red maple basal area in the landscape, while the effect of the 20th century anthropogenic disturbances was translated by the correlation between poplars and fire events, and the correlation between yellow birch and partial cuts between 1965 and 2005. Moreover, 20th century disturbances have interacted with climate (0.8%) and likely favoured the increase in deciduous maples. With the expected increase in climatic forcing, the expansion of deciduous maples is likely to continue.

Key words: mixed forests; climate; anthropogenic disturbances; compositional change; physical environment

2.4. Introduction

The impact of human activities on natural ecosystems has intensified since the onset of the industrial revolution indirectly through climate change and directly through land-use (Ellis et al. 2010, Steffen et al. 2011, Grimm et al. 2013). As such, mixed forests of eastern North America have witnessed compositional changes, compared to the pre-industrial period, mainly the increase of deciduous maples, early successional poplars and white birch, as well as the decrease in coniferous spruces and northern white cedar (Foster et al. 1998, White and Jentsch 2001, Nowacki and Abrams 2015, Danneyrolles et al. 2017). However, there is still an ongoing debate on the respective contributions of anthropogenic disturbances and climate change as the main drivers of these changes (Nowacki and Abrams 2015, Pederson et al. 2015, Danneyrolles et al. 2019).

Mixed forests represent a transitional zone where many coniferous and deciduous tree species attain their southern and northern range limits, respectively (Pastor and Mladenoff 1992, Goldblum and Rigg 2010) and are sensitive to small variations in climate (Iverson and Prasad 1998, Scheller and Mladenoff 2005, Frelich and Reich 2009). Thus, transitional zones are one of the most likely areas to detect early signs of climate-mediated community shifts (di Castri et al. 1988, Parmesan et al. 2005). The 20th century has been characterized by increasing temperatures and has been warmer than the 19th century globaly and in eastern North America in particular (Anchukaitis et al. 2017, Gennaretti et al. 2017). Simulation studies also suggest that climate forcing over the coming decades will continue to alter mixed forests composition and age structure (Iverson and Prasad 1998, Scheller and Mladenoff 2005, Duveneck et al. 2014, Boulanger et al. 2019).

Mixed forests also represent a zone that witnessed intensive land exploitation since the European settlement. Forest disturbance regimes have shifted from being dominated by natural secondary disturbances (wind throws and insect outbreaks) and rare natural fires (Fahey and Reiners 1981, Frelich and Lorimer 1991, Lorimer and White 2003) to chronic anthropogenic disturbances such as settlement fires and logging activities (Foster et al. 1998, Lorimer 2001, Blanchet 2003, Friedman and Reich 2005, Canham et al. 2013, Boucher et al. 2017, Elzein et al. 2020). This anthropogenic disturbance regime led, according to some authors, to regional homogenization of vegetation and decoupling of long-standing climate– vegetation relations in some cases (Fuller et al. 1998, Schulte et al. 2007, Thompson et al. 2013, Danneyrolles et al. 2019).

Understanding the respective impacts of climate and anthropogenic disturbances on forest ecosystems is important to assess future ecosystem development under sustained global change pressures. Nevertheless, this task is difficult due to the rarity of spatially explicit long term data on climate, disturbances and forest composition. In this study we re-sampled 743 forest inventory plots established in the 1930's and used a spatially explicit disturbance data base and climate data to explore the relative contribution of disturbance and climate change on the stand level forest composition during the preindustrial and modern times in a mixed forest of southeastern Canada. More precisely, our specific objectives were to: 1) compare basal area and density of tree taxa at the stand level between preindustrial and present day forests, 2) identify the main explanatory variables that influenced tree taxa composition for both epochs, and 3) assess the degree of variation explained and shared among driver sets.

2.5. Material and methods

2.5.1. Study area

The study area (2564 km^2) is located in the Lower Saint Lawrence region (LSL) in south-eastern Quebec (47° 92’ to 48° 91’ N and 66° 84’ to 68° 86’ W). The area is limited to the north by the St. Lawrence River and to the south by the province of New Brunswick (Canada). The study area is localized at the northern limit of the

Great Lakes-St. Lawrence mixed forests, and is part of the transition zone between the temperate deciduous forest to the south and the boreal coniferous forest to the north (Rowe 1972). It lies within the Appalachian geological formation, characterized by sedimentary bedrock. Surface deposits are largely from glacial and weathering origins. The topography generally consists of low elevation hills with moderate slopes. The mean and maximum elevations are 350 m and 910 m, respectively. The meteorological data (1981-2010) of Rimouski, Trinité-des-Monts and Saint-Jean-de-Cherbourg (Fig. 2-1) show mean annual temperatures of 4.4 °C, 2.5 °C and 1.9°C and mean annual total precipitations of 959 mm, 1100 mm and 1138 mm, respectively, 30% of which falls as snow (Environment Canada 2019). Mean annual temperature and total annual precipitation in the study region have increased between 1950 and 2011 (Ouranos 2015).

The study area consists in two former timber concessions of the Price Brothers & Company: Rimouski (1751 km^2) and Matane (813 km^2) sectors. The Price Brothers & Company operated in the LSL region from the early 19th century until the 1970s (Price Brothers & Company Limited 1944, Fortin et al. 1993). Indeed, the LSL region has been subject to extensive logging activity during the 20th century (Boucher et al. 2009a). Anthropogenic fires (Terrail et al. 2019) and spruce budworm (*Choristoneura fumiferana*) outbreaks (Boulanger and Arseneault, 2004) have also affected the region during this period.

These two sectors are situated in the Balsam fir-Yellow birch and Balsam fir – White birch bioclimatic domains (Robitaille and Saucier 1998, Grondin et al. 1999). Balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), yellow birch (*Betula alleghaniensis*), white birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*) are abundant in mesic sites. Sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*), are at their northern range limit, and generally occupy hill tops. Black spruce (*Picea mariana*) and northern white cedar (*Thuja occidentalis*) generally occupy organic deposits mostly next to water courses (Robitaille and Saucier 1998). Up to 75% of the study area corresponds to public forest, mostly in the backcountry, whereas 25% is private land, mostly along the St. Lawrence River.

2.5.2. Sampling plots and data sets

We selected a total of 743 plots from a pool of 16345 detailed plots initially surveyed by the Price Brothers & Company in 1930-1931 (hereafter referred to as the 1930 inventory). Plots cover about 10 m x 100 m (0.1 ha) and are systematically distributed across the study area (Figure 2-1). Tree species were tallied in two-inch classes of diameter at breast height (DBH) from a minimum of 3 inches (1 inch = 2.54 cm). Plots were georeferenced using ArcGIS software (ESRI 2010) from their location on a 1930 map made by Price Brothers & Company at the scale of 1: ~ 16000. The 1930 map was georeferenced using lakes and confined rivers from Quebec ministry of natural resources' modern maps. The spatial uncertainty of georeferenced plots varies between 0 to 340 m. According to Kopecký and Macek (2015), the resurvey of historical vegetation plots represents a robust way to infer temporal vegetation changes despite the uncertainty in their original location. For practical reasons, the 743 plots were re-sampled in groups of 3 to 4 consecutive plots chosen randomly in each 9 km^2 cell of a grid covering the study area. The re-sampling campaign took place during the summers of 2012 and 2013 (hereafter the 2012 inventory) using the same protocol as in 1930, including the grouping of tree taxa at the genus level (*Acer* spp., *Picea* spp. and *Populus* spp). The remaining taxa were considered at the species level: *Abies balsamea*, *Betula alleghaniensis*, *Betula papyrifera* and *Thuja occidentalis*.

Central points of plots were used to construct three datasets of explanatory variables describing the 20th century disturbance history, the physical environment, and the climate, respectively. The 20th century disturbance history was reconstructed using several historical and modern maps (Elzein et al.2020). Binary variables (presence/absence) of the disturbances dataset included: Cut over (1895-1935), Cut over (1935-1965), Partial cuts (1965 – 2005), Total cuts (1965 – 2005), Fire (1895 - 2005), and Spruce Budworm outbreaks (1975 – 2005). The fire database prior to 1920 is probably incomplete (Terrail 2013). Logging activity between 1895 and 1965 is referred to as Cut over with no mention of logging severity. Logging for the period 1965- 2005 was classified as partial cuts (25% to 75% basal area removal) or total cuts (more than 75% basal area removal) based on Quebec's department of forests decadal inventories. For the physical environment dataset, several continuous and discrete variables were considered, including altitude (m) obtained from hypsometric curves (1: 20 000 maps) of the Quebec's department of forests and transformed to 400 m^2 cell raster. Aspect and slope were then calculated from the altitude raster using the spatial analyst tools (ESRI 2010). Distance from water courses (m) was the closest distance from all rivers and lakes in the study area. Distance from private lands (m) was the closest distance from a private land. Water courses (rivers and lakes) and public/private lands polygons for the study area were obtained from the fourth decadal forest inventory map made by the Quebec's department of forests. Three soil deposit types, *in situ* weathering, glacial and organic and six drainage classes ranging from excessive to very bad were considered. For the climatic data set, variables were interpolated using BioSim 11 (https://cfs.nrcan.gc.ca/projects/133). Interpolations where based on nearby weather stations, adjusted for elevation and location differentials with regional gradients. The climatic data base used in BioSim 11 is the Canada-USA daily climatic data and daily climatic normals for the periods of 1951-1980 and 1981-2013; the former period is the only one available in the study area as a proxy of thermal condition in 1930. For each plot, mean annual temperature (°C), minimum annual temperature (°C), maximum annual temperature (°C), and mean annual precipitation (mm) were calculated from generated monthly data while growing degree days (GDD) were calculated from generated mean daily temperatures using the following formula:

$$GDD = \sum (\text{Mean Daily Temprature} - 5.56)^*$$

*: only Mean Daily Temperatures > 5.56 are considered

To give an overall description of taxa composition in the landscape in 1930 and 2012, relative basal area and relative density (Figures 2-4 and 2-5) were calculated for naturaly regenerated plots and plots situated in plantations (n = 745). For graphic visibility, these parameters were calculated as the mean of each group of 3 to 4 consecutive plots (n=187). Basal area, density, and prevalence (frequency of occurrence of taxa in sampling plots) were calculated for naturaly regenerated plots only (n = 457), while plots currently situated in plantation zones were omitted. Naturaly regenerated plots (n=457) were also used in redundancy analysis.

2.5.3. Redundancy analysis

Redundancy analysis (RDA) (Legendre and Legendre 2012) was used to examine the effect of environment, disturbances and climate on tree taxa basal area using the following models (Figures 2-6 and 2-8).

a) Taxa 1930 ~ environment + disturbances (1895 – 1935) + climate (1951 – 1980)

b) Taxa 2012 ~ taxa 1930 + environment + disturbances (1935 – 2005) + climate (1951 – 2013)

For the two RDAs, we selected only significant variables using forward selection with the package packfor in the R statistical software (V. 3.3.0, R Development Core Team 2016) (Tables 2-1 and 2-2). Taxa basal area in 1930 and 2013 was Hellinger transformed while environmental variables were standardized to zero mean and unit variance. The variation explained was reported using the adjusted R^2, which takes the number of predictor variables and sample size into account to prevent the inflation of R^2 values. A permutation test was applied to test for the significance of the models and axes. For the RDA model a, we expect that the climatic conditions for the 1930 forest to be colder than what is observed in 1951-1980 period, but earlier complete and representative climatic databases are not available for the LSL region.

2.6. Results

2.6.1. Vegetation composition and structure change between 1930 and 2012

Results show that forest composition and structure have changed between 1930 and 2012. Total basal area has significantly increased by 23% and total density by 35% (p-value ≤ 0.05; Wilcoxon test) (Figure 2-2.a and b). Hardwood maple and poplar have noticeably increased in basal area, density, and prevalence in sampled stands (Figure 2-2 and 2-3). White birch was present in more than 80% of plots during both periods; a significant decrease in its basal area and a significant increase in its density suggest numerous younger white birch individuals with smaller diameters in 2012 as compared to 1930. Yellow birch, has maintained its basal area, density, and prevalence between the two surveys. Softwood tree species (balsam fir, spruces and northern white cedar) slightly increased in basal area and density and decreased in prevalence in 2012 forests as compared to early 20th century.

Change in relative basal area and density of taxa have been spatially heterogeneous between the two surveys (Figures 2-4 and 2-5). Maples have mostly increased in the northern and western parts of the Rimouski sector. Northern white cedar has noticeably increased in the southwestern part of Rimouski sector and decreased elsewhere.

2.6.2. Variables explaining Tree taxa basal area in 1930

The RDA model explains 17.4% of constrained variance in the 1930 taxa basal area. Tree taxa basal area was then spatially structured by environmental and climatic variables (Figures 2-6). Variation partitioning (Figure 2-7) shows that environment, climate and anthropogenic disturbances explains 13.1%, 10.2%, and 1.8% of the total variance, respectively. Climate and environment data sets interaction represent 7.2% of this variation. In figure 2-6, the first RDA axis (10% of constrained variance) expresses increasing distance from water courses (Individual R^2adj =0.002; Table 2-1) and high altitude (Individual R^2adj = 0.063; Table 2-1) to the right and organic deposit (Individual R^2adj = 0.031; Table 2-1), poor drainage (Individual R^2adj = 0.010; Table 2-1) and high mean temperature (1951-1980) (Individual R^2adj = 0.74; Table 2-1) to the left. The second RDA axis (4% of constrained variance) expresses a gradient of growing degree days (1951-1980) (Individual R^2adj = 0.024; Table 2-1), glacial deposit (Individual R^2adj = 0.018; Table 2-1), and steep slope (Individual R^2adj = 0.003; Table 2-1) and in the opposite direction Fires (1895 – 1935) (Individual R^2adj = 0.010; Table 2-1). In 1930, northern white cedar and spruces occurred at low altitude close to rivers and lakes, mostly on organic deposit and poorly drained soils. Balsam fir and white birch were situated in high altitude, away from water courses. Poplars were associated with fires and maples with high growing degree days and high mean temperature. Yellow birch occurred on glacial deposit and steep slope areas.

2.6.3. Variables explaining tree taxa basal area in 2012

The RDA model explains 32.5% of constrained variance in the 2012 taxa basal area. The effect of environment and climate on basal area is reinforced compared to 1930. Disturbance effect is also more important, probably reflecting their intensification as well as their more exhaustive mapping during the 20th century. Indeed, the 2012 taxa basal area is spatially structured by the 1930 basal area, as well as by environmental, climatic variables and 20th century disturbances (Figures 2-8 and 2-9). Variation partitioning (Figure 2-9) shows that taxa basal area in 1930, environmental variables, climatic variables, and 20th century disturbances explain 21.9%, 15.4%, 12.6%, and 5.1%, respectively of the 2012 basal area. The first RDA axis (15% of constrained variance; figure 2-8) expresses the abundance of spruces (Individual R^2adj = 0.007; Table 2-2) and northern white cedar (Individual R^2adj = 0.039; Table 2-2) in 1930, poor drainage (Individual R^2adj = 0.057; Table 2-2) and organic deposit (Individual R^2adj = 0.006; Table 2-2) to the right, and yellow birch (Individual R^2adj = 0.110; Table 2-2) and partial cuts (Individual R^2adj = 0.011; Table 2-2) to the left. The second RDA axis (10% of constrained variance) expresses a gradient of high growing degree days (1951-2010) (Individual R^2adj = 0.025; Table 2-2) , mean annual temperature (Individual R^2adj = 0.025; Table 2-2), minimum annual temperature (Individual R^2adj = 0.069; Table 2-2), and maples basal area in 1930 (Individual R^2adj = 0.039; Table 2-2), opposite to increased precipitation (Individual R^2adj = 0.004; Table 2-2), distance from private lands (Individual R^2adj = 0.018; Table 2-2), high altitude (Individual R^2adj = 0.039; Table 2-2), white birch basal area in 1930 (Individual R^2adj = 0.002; Table 2-2) and balsam fir basal area in 1930 (Individual R^2adj = 0.016; Table 2-2). Most of 2012 taxa occurred in the surrounding of their original position in 1930, with slight changes. Northern white cedar has densified in zones where it was already present in 1930. Sugar maple and red maple basal areas are concentrated in zones where maples were present in 1930, which were also the warmest at that time. Yellow birch is also associated with its position in 1930, especially on sites with glacial deposit and steep slopes and partial cuts. Balsam fir and white birch, as in 1930, are today situated in high altitudes, far from water courses and far from private lands.

2.7. Discussion

In this study we assessed the relative role of site conditions, climate, and anthropogenic disturbances on the pre-industrial and the modern forest composition in a mixed forest landscape of eastern North America. Climate and environment have played an important role in taxa composition in 1930, while anthropogenic disturbances between 1895 and 1935 had a minor impact (Figure 2-7). The importance of the environmental effect (Barnes et al. 1997, Robitaille and Saucier 1998, Boucher 2007) and the role of climate (Fisichelli et al. 2014, Boisvert-Marsh et al. 2019) on vegetation distribution have been documented across mixed forests of eastern North America. The relatively weak impact of anthropogenic disturbances in 1930 is likely due to their rare occurrence and mitigated intensity at the beginning of the 20th century. Indeed, 75% of the study area was still dominated by old growth forest communities, older than 100 years, in 1930 (Boucher 2007). Environment and climate continued to play a major role in modern composition of the forests, along with the important effect of the original taxa distribution in 1930 (Figure 2-9). The important increase in anthropogenic disturbances during the 20th century has been translated by an increased influence on tree taxa distribution (from 1.8% in 1930 to 5.1% in 2012). The role of anthropogenic disturbances of the 20th century in the modern landscape was also suggested by other studies (Duchesne and Ouimet 2008, Gimmi et al. 2010, Nowacki and Abrams 2015, Fortin 2018, Danneyrolles et al. 2019). Yet, they remain less important thanpre-industrial forest composition, environmental and climatic variables in determining modern taxa composition.

Our study shows that forest compositional changes between the pre and post-industrial periods follow the same tendencies as in other parts of eastern North American mixed forests (Oosting and Reed 1944, Fuller et al. 1998, Cogbill et al. 2002, Friedman and Reich 2005, Pinto et al. 2008, Dupuis et al. 2011, Thompson et al. 2013, Nowacki and Abrams 2015, Boucher et al. 2017). The main trend enlightened by this study is an expansion, densification and increase in basal area of hardwood tree species such as maples and early successional poplars, as well as a densification of early successional white birch. Today, maples are present in 47% of sampled plots compared to 15% in 1930, and poplars are present in 21% of sampled plots compared to 3% in 1930. Moreover, early successional white birch has almost doubled in terms of density, although its prevalence and basal area slightly decreased (Figure 2-2). This suggests an increase in young, small diameter white birch individuals compared to fewer, older and large diameter individuals regenerated in the gaps of the pre-industrial forests. On the other hand, yellow birch and softwood taxa (balsam fir, spruces, northern white cedar) basal area, density and prevalence stayed constant or slightly increased (Figure 2-2).

Tree taxa basal area distribution related to changes in climate and the disturbance regime of the 20th century are variable according to the auto-ecological characteristics of species. While some taxa have stayed stable throughout the 20th century or have reacted little to climate and disturbances (e.g. balsam fir, spruces, and northern white cedar), other taxa were more stongly influence by the 20th century anthropogenic disturbances without evidence of a climatic influence (e.g. poplars and yellow birch) and some taxa depended on a combination of climatic conditions and disturbances (e.g. maples).

For instance balsam fir, spruces, and northern white cedar showed little difference in their basal area and prevalence between 1930 and 2012 (Figure 2-2) and seemed more associated with site conditions. Balsam fir, the most abundant species of the study area, is a resilient species with an optimal growth rate in southeastern Canada; it grows in a wide variety of mineral and organic soils, and it has a strong ability to grow under the shade of larger trees as well as in openings (Burns and Honkala 1990). It has maintained its presence in more than 80% of sampled plots in 1930 and 2012, and its density and basal area have slightly increased in 2012. Spruces have followed the same trend as balsam fir although with less important density and basal area in both epochs. The modern distribution of black spruce and white spruce are closely associated with edaphic and topographic factors (Figure 2-8). White spruce is more abundant in well-drained upland sites exposed to higher rate of precipitation while black spruce is more abundant in poorly drained, low altitude sites as it is generally distributed in the boreal forest (Wirth et al. 2008). The case of northern white cedar also expresses the important environmental control on its distribution as it is concentrated in low altitude poorly drained sites, close to water courses. Despite its decrease in other parts of mixed forests of eastern Canada (Danneyrolles et al. 2017) northern white cedar has slightly increased in our study area, although today it is present in fewer plots compared to 1930 (Figure 2-2).

The change in the basal area of some taxa between 1930 and 2012 has been correlated to particular anthropogenic disturbances. Poplars are correlated with the occurrence of fire events in 1930 and 2012 (Adjusted R^2 = 0.010 and 0.011.; Tables 2-1 and 2-2, Figures 2-6 and 2-8). Many studies have already shown the association between poplars and fire, as well as the important role of anthropogenic fires in structuring modern vegetation landscapes with high poplar prevalence (Bergeron 2000, Boucher et al. 2017, Terrail et al. 2019). Moreover, our results show a correlation between partial cuts between 1965 and 2005 (CP05) and the abundance of yellow birch in 2012 (adjusted R^2 = 0.11; Table 2-2). Yellow birch is known for having a good regeneration rate in a secondary disturbance gap dynamics and have likely benefitted from the elimination of shade tolerant competitors in partially cut zones (Palik and Pregitzer 1992, Abrams 1998).

The combination of the effect of climate and disturbances is mainly translated by the increase of sugar maple and red maple in the landscape (Figures 2-6 and 2-8). In 1930, maples were mostly distributed in the north western part of Rimouski sector, a low altitude zone with the highest growing degree days between 1951 and 1980 (Figures 2-10, 2-6, and 2-8). In 2012, sugar maple and red maple have densified and expanded from their position in 1930 (Figures 2-4, 2-6, and 2-8). Moreover, sugar maple and red maple basal areas in 2012 were correlated to Partial cuts between 1965 and 2005 (CP05). Logging is thus an important factor partially explaining the increase of maples (Nowacki and Abrams 2015, Fortin 2018, Danneyrolles et al. 2019) as both species can grow rapidly when exposed to light (Fei and Steiner 2008, Nolet et al. 2008), especially where climate is suitable, but their original distribution was mostly explained by climate. Both species reach their northern range limits in our study area, and are sensitive to temperature. These species are expected to migrate northward (Beckage et al. 2008, Jump et al. 2009) and several studies suggested that their increase in mixed forests is a consequence of a warming climate (Abrams 1998, Tremblay et al. 2002, Goldblum and Rigg 2005, Fisichelli et al. 2014, Boisvert-Marsh et al. 2019). Higher growing degree days suitable to maple recruitment and growth are observed in the majority of plots in 1980-2013 compared to 1951-1980 (Figure 2-10). The confinement of maples expansion primarily around sites where they were already present in 1930 emphasized the delayed response of the forest ecosystems to sustained climate warming (Beckage et al. 2008, Lenoir et al. 2009, Woodall et al. 2009). Our study suggests that the expansion of these species was triggered by partial cuts in a context of warming that enhanced their habitat.

Increasing climatic forcing is expected to overtake the impact of anthropogenic disturbances on mixed forests composition in the coming decades (Steenberg et al. 2013, Duveneck et al. 2014, Boulanger et al. 2019) and stand replacing anthropogenic disturbances like logging may accelerate the ongoing mixed forests vegetation change mainly by favouring the recruitment and growth of maples. The interaction between climate change and anthropogenic disturbances can affect complex ecosystem processes like competition and succession (Gustafson et al. 2010) and some species wouldn't have yielded changes in their distribution based on climate alone (Lo et al. 2010). High rates of stand-replacing disturbance are known to decrease forest ecosystem inertia to climate change by creating environmental conditions favouring, and thus accelerating, the colonization of pioneer species, including invaders already adapted to a warmer climate (Landhäusser et al. 2010, Steenberg et al. 2013).

2.8. References

Abrams, M. D. 1998. The red maple paradox: What explains the widespread expansion of red maple in eastern forests ? Bioscience 48:355-364.

Anchukaitis, K. J., R. Wilson, K. R. Briffa, U. Büntgen, E. R. Cook, R. D'Arrigo, N. Davi, J. Esper, D. Frank, B. E. Gunnarson, G. Hegerl, S. Helama, S. Klesse, P. J. Krusic, H. W. Linderholm, V. Myglan, T. J. Osborn, P. Zhang, M. Rydval, L. Schneider, A. Schurer, G. Wiles, and E. Zorita. 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163:1-22.

Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1997. Forest ecology. John Wiley and Sons, New York.

Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences 105:4197-4202.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81:1500-1516.

Blanchet, P. 2003. Feux de forêt : l'histoire d'une guerre. Trait d'union, Montréal.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology.

Boucher, Y. 2007. Impact des coupes du XXe siècle sur la structure et la composition du paysage forestier de l'est du Canada. These. Université du Québec à Rimouski, Rimouski.

Boucher, Y., D. Arseneault, and L. Sirois. 2009a. Logging history (1820–2000) of a heavily exploited southern boreal forest landscape: Insights from sunken logs and forestry maps. Forest Ecology and Management 258:1359-1368.

Boucher, Y., I. Auger, J. Noël, P. Grondin, and D. Arseneault. 2017. Fire is a stronger driver of forest composition than logging in the boreal forest of eastern Canada. Journal of Vegetation Science 28:57-68.

Boulanger, Y. and D. Arseneault (2004). "Spruce budworm outbreaks in eastern Quebec over the last 450 years." Canadian Journal of Forest Research 34(5): 1035-1043.

Boulanger, Y., D. Arseneault, Y. Boucher, S. Gauthier, D. Cyr, A. R. Taylor, D. T. Price, and S. Dupuis. 2019. Climate change will affect the ability of forest management to reduce gaps between current and presettlement forest composition in southeastern Canada. Landscape Ecology.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, DC, USA.

Canham, C. D., N. Rogers, and T. Buchholz. 2013. Regional variation in forest harvest regimes in the northeastern United States. Ecological Applications 23:515-522.

Cogbill, C. V., J. Burk, and G. Motzkin. 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. Journal of Biogeography 29:1279-1304.

Danneyrolles, V., S. Dupuis, D. Arseneault, R. Terrail, M. Leroyer, A. de Römer, G. Fortin, Y. Boucher, and J.-C. Ruel. 2017. Eastern white cedar long-term dynamics in eastern Canada: Implications for restoration in the context of ecosystem-based management. Forest Ecology and Management 400:502-510.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. de Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, and D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications 10:1265.

di Castri, F., A. J. Hansen, and M. M. Holland. 1988. A new look at ecotones: emerging international projects on landscape boundaries. Biology International 17:1-163.

Duchesne, L., and R. Ouimet. 2008. Population dynamics of tree species in southern Quebec, Canada: 1970–2005. Forest Ecology and Management 255:3001-3012.

Dupuis, S., D. Arseneault, and L. Sirois. 2011. Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. Journal of Vegetation Science 22:564-575.

Duveneck, M. J., R. M. Scheller, M. A. White, S. D. Handler, and C. Ravenscroft. 2014. Climate change effects on northern Great Lake (USA) forests: A case for preserving diversity. Ecosphere 5:art23.

Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589-606.

Elzein, T., Arseneault, D., Sirois, L., and Y. Boucher. 2020. The Changing Disturbance Regime in Eastern Canadian Mixed Forests During the 20th Century. Frontiers in Ecology and Evolution, 8

Environment Canada. 2019. Canadian Climate Normals and averages 1981-2010.

ESRI. 2010. Redlands, California.

Fahey, T. J., and W. A. Reiners. 1981. Fire in the forests of Maine and New Hampshire. Bulletin of the Torrey Botanical Club 108:362-373.

Fei, S., and K. C. Steiner. 2008. Relationships between advance oak regeneration and biotic and abiotic factors. Tree Physiology 28:1111-1119.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography 37:152-161.

Fortin, G. 2018. Transformation de la composition de la forêt de la péninsule gaspésienne au cours du XXème siècle. Université du Québec à Montréal.

Fortin, J.-C., A. Lechasseur, Y. Morin, F. Harvey, J. Lemay, and Y. Tremblay. 1993. Histoire du Bas-Saint-Laurent. Page 861 in Institut québécois de recherche sur la culture, editor. Québec, Québec.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems 1:96-119.

Frelich, L. E., and C. G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes region. Ecological Monographs 61:145-164.

Frelich, L. E., and P. B. Reich. 2009. Wilderness Conservation in an Era of Global Warming and Invasive Species: A case study from Minnesota's Boundary Waters Canoe Area Wilderness. Natural Areas Journal 29:385-393.

Friedman, S. K., and P. B. Reich. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological Applications 15:726-744.

Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1:76-95.

Gennaretti, F., D. Huard, M. Naulier, M. Savard, C. Bégin, D. Arseneault, and J. Guiot. 2017. Bayesian multiproxy temperature reconstruction with black spruce ring widths and stable isotopes from the northern Quebec taiga. Climate Dynamics 49:4107-4119.

Gimmi, U., T. Wohlgemuth, A. Rigling, C. W. Hoffmann, and M. Bürgi. 2010. Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. Annals of Forest Science 67:701-701.

Goldblum, D., and L. S. Rigg. 2005. Tree growth response to climate change at the deciduous–boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research 35:2709-2718.

Goldblum, D., and L. S. Rigg. 2010. The Deciduous Forest – Boreal Forest Ecotone. Geography Compass 4:701-717.

Grimm, N. B., F. S. Chapin, B. Bierwagen, P. Gonzalez, P. M. Groffman, Y. Luo, F. Melton, K. Nadelhoffer, A. Pairis, P. A. Raymond, J. Schimel, and C. E. Williamson. 2013. The impacts of climate change on ecosystem structure and function. Frontiers in Ecology and the Environment 11:474-482.

Grondin, P., J. Blouin, and P. Racine. 1999. Rapport de classification écologique du sous-domaine bioclimatique de la sapinière à bouleau jaune de l'est. Ministère des Ressources Naturelles du Québec, Direction des inventaires forestiers.

Gustafson, E. J., A. Z. Shvidenko, B. R. Sturtevant, and R. M. Scheller. 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. Ecological Applications 20:700-715.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465-485.

Jump, A. S., C. Mátyás, and J. Peñuelas. 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends in Ecology & Evolution 24:694-701.

Kopecký, M., and M. Macek. 2015. Vegetation resurvey is robust to plot location uncertainty. Diversity and Distributions 21:322-330.

Landhäusser, S. M., D. Deshaies, and V. J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography 37:68-76.

Legendre, P., and L. Legendre. 2012. Numerical ecology. 3rd English edition. Elsevier, Amsterdam ; New York.

Lenoir, J., J.-C. Gégout, J.-C. Pierrat, J.-D. Bontemps, and J.-F. Dhôte. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). Ecography 32:765-777.

Lo, Y.-H., J. A. Blanco, B. Seely, C. Welham, and J. P. Kimmins. 2010. Relationships between climate and tree radial growth in interior British Columbia, Canada. Forest Ecology and Management 259:932-942.

Lorimer, C. G., 1977. The presettlement forest and natural Disturbance cycle of Northeastern Maine. Ecology 58(1): 139-148.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin 29:425-439.

Lorimer, C. G., and A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185:41-64.

Nolet, P., S. Delagrange, D. Bouffard, F. Doyon, and É. Forget. 2008. The successional status of sugar maple (*Acer saccharum*), revisited. Annals of Forest Science 65.

Nowacki, G. J., and M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology 21:314-334.

Oosting, H. J., and J. F. Reed. 1944. Ecological composition of pulpwood forests in northwestern Maine. American Midland Naturalist 31:182-210.

Ouranos. 2015. Vers l'adaptation. Synthèse des connaissances sur le changements climatiques au Québec. Montréal, Québec.

Palik, B. J., and K. S. Pregitzer. 1992. A comparison of presettlement and present-day forests on two Bigtooth aspen-dominated landscape in northern lower Michigan. American Midland Naturalist 127:327-338.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. Townsend Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58-75.

Pastor, J., and D. J. Mladenoff. 1992. The southern boreal-northern hardwood forest border. Pages 216-240 in R. L. H. H. Shugart, and G. B. Bonan, editors, editor. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.

Pederson, N., A. W. D'Amato, J. M. Dyer, D. R. Foster, D. Goldblum, J. L. Hart, A. E. Hessl, L. R. Iverson, S. T. Jackson, D. Martin-Benito, B. C. McCarthy, R. W. McEwan, D. J. Mladenoff, A. J. Parker, B. Shuman, and J. W. Williams. 2015. Climate remains an important driver of post-European vegetation change in the eastern United States. Global Change Biology 21:2105-2110.

Pinto, F. P., S. R. Romaniuk, and M. F. Ferguson. 2008. Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada. Canadian Journal of Forest Research 38:1842-1854.

Price Brothers & Company Limited, S. W. D. 1944. Working - plan report for Rimouski establishment. Archives Nationales du Québec - Chicoutimi.

Robitaille, A., and J.-P. Saucier. 1998. Paysage régionaux du Québec méridional, Direction de la gestion des stock forestiers et Direction des relations publiques, Ministère des Ressources naturelles du Québec. Publication du Québec, Québec.

Rowe, J. S. 1972. Forest regions of Canada. Information Canada, Canadian Forest Service publication number 1300, Ottawa.

Scheller, R. M., and D. J. Mladenoff. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biology 11:307-321.

Schulte, L., D. Mladenoff, T. Crow, L. Merrick, and D. Cleland. 2007. Homogenization of northern U.S. Great Lakes forests due to land use. Landscape Ecology 22:1089-1103.

Steenberg, J. N., P. Duinker, and P. Bush. 2013. Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. Annals of Forest Science 70:61-73.

Steffen, W., J. Grinevald, P. Crutzen, and J. McNeill. 2011. The Anthropocene: conceptual and historical perspectives. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 369:842-867.

Terrail, R. 2013. Influence de la colonisation sur les transformations du paysage forestier depuis l'époque préindustrielle dans l'Est du Québec (Canada). Doctoral thesis. Université du Québec a Rimouski (UQAR).

Terrail R., J. Morin-Rival, G. de Lafontaine, M.J. Fortin and D. Arseneault. 2020. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. Journal of Vegetation Science, https://doi.org/10.1111/jvs.12832

Thompson, J. R., D. N. Carpenter, C. V. Cogbill, and D. R. Foster. 2013. Four Centuries of Change in Northeastern United States Forests. PLoS ONE 8:e72540.

Tremblay, M. F., Y. Bergeron, D. Lalonde, and Y. Mauffette. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (Acer rubrum L.) populations at the northern limit of the species range. Journal of Biogeography 29:365-373.

White, P., and A. Jentsch. 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. Pages 399-450 in K. Esser, U. Lüttge, J. W. Kadereit, and W. Beyschlag, editors. Progress in Botany. Springer Berlin Heidelberg.

Wirth, C., J. W. Lichstein, J. Dushoff, A. Chen, and F. S. Chapin. 2008. White spruce meets black spruce: dispersal, postfire, establishment, and growth in a warming climate. Ecological Monographs 78:489-505.

Woodall, C. W., C. M. Oswalt, J. A. Westfall, C. H. Perry, M. D. Nelson, and A. O. Finley. 2009. An indicator of tree migration in forests of the eastern United States. Forest Ecology and Management 257:1434-1444.

2.9. Tables

Table 2-1. Explanatory variables within each variable set selected during forward selection procedure (in black) for 1930 tree taxa basal area variation partitioning and RDA models

Variable	Acronym	Individual adjusted R^2	p-value	Within group selection order
Environnement				
Altitude	Altitude	0.063	≤ 0.001	1
Organic deposit	Orga	0.031	≤ 0.001	2
Glacier deposit	Glac	0.018	≤ 0.001	3
Drainage classes	Drain	0.010	≤ 0.001	4
Slope	Slope	0.003	< 0.05	5
Distance from water courses	Water	0.002	< 0.05	6
Distance from private lands	-	-	> 0.05	-
Slope	-	-	> 0.05	-
Aspect	-	-	> 0.05	-
Alteration deposit	-	-	> 0.05	-
Disturbances (1895 – 1935)				
Fire	BR35	0.010	≤ 0.001	1
Cut over	CO35	0.004	< 0.05	2
Climate (1951-1980)				
Mean annual temprature	Tmean51_80	0.074	≤ 0.001	1
Growing degree days	GDD51_80	0.024	≤ 0.001	2
Minimum annual temprature	Tmin51_80	-	> 0.05	-
Maximum annual temprature	Tmax51_80	-	> 0.05	-
Mean annual precipitation	Prcp51_80	-	> 0.05	-

Table 2-2. Explanatory variables within each variable set selected during forward selection procedure (in black) for 2012 variation partitioning and RDA models. In Gray variables that were removed because not significant

Variables	Acronym	Individual adjusted R^2	p-value	Within group selection order
Taxa basal area 1930				
Betula alleghaniensis	Bea 1930	0.110	≤ 0.001	1
Thuja occidentalis	Tho 1930	0.039	≤ 0.001	2
Acer spp.	Ac 1930	0.039	≤ 0.001	3
Abies balsamea	Abb 1930	0.016	≤ 0.001	4
Picea spp.	Pic 1930	0.007	≤ 0.001	5
Populus spp.	Pop 1930	0.005	< 0.05	6
Betula papyrifera	Bep 1930	0.002	< 0.05	7
Environement				
Drainage classes	Drain	0.057	≤ 0.001	1
Altitude	Altitude	0.039	≤ 0.001	2
Glacier deposit	Glac	0.018	≤ 0.001	3
Distance from private lands	Private	0.018	≤ 0.001	4
Slope	Slope	0.011	≤ 0.001	5
Organic deposit	Orga	0.006	≤ 0.001	6
Distance from water courses	Water	0.002	< 0.05	7
Aspect	-	-	> 0.05	-
Alteration deposit	-	-	> 0.05	-
Disturbances				
Spruce budworm outbreaks (1975-2005)	SBW	0.014	≤ 0.001	1
Partial cuts (1965-2005)	CP05	0.011	≤ 0.001	2
Fire (1895 - 2005)	Fire	0.011	≤ 0.001	3
Total cuts (1965-2005)	CT05	0.006	< 0.05	4
Cut over (1935-1965)	CO65	0.006	< 0.05	5
Cut over (1895-1935)	-	-	> 0.05	-
Climate (1951 – 2013)				
Minimum annual temprature	Tmin	0.069	≤ 0.001	1
Growing degree days	GDD	0.025	≤ 0.001	2
Mean annual temprature	Tmean	0.025	≤ 0.001	3
Mean annual precipitation	Prcp	0.004	< 0.05	4
Maximum annual temprature	-	-	> 0.05	-

2.10. Figures

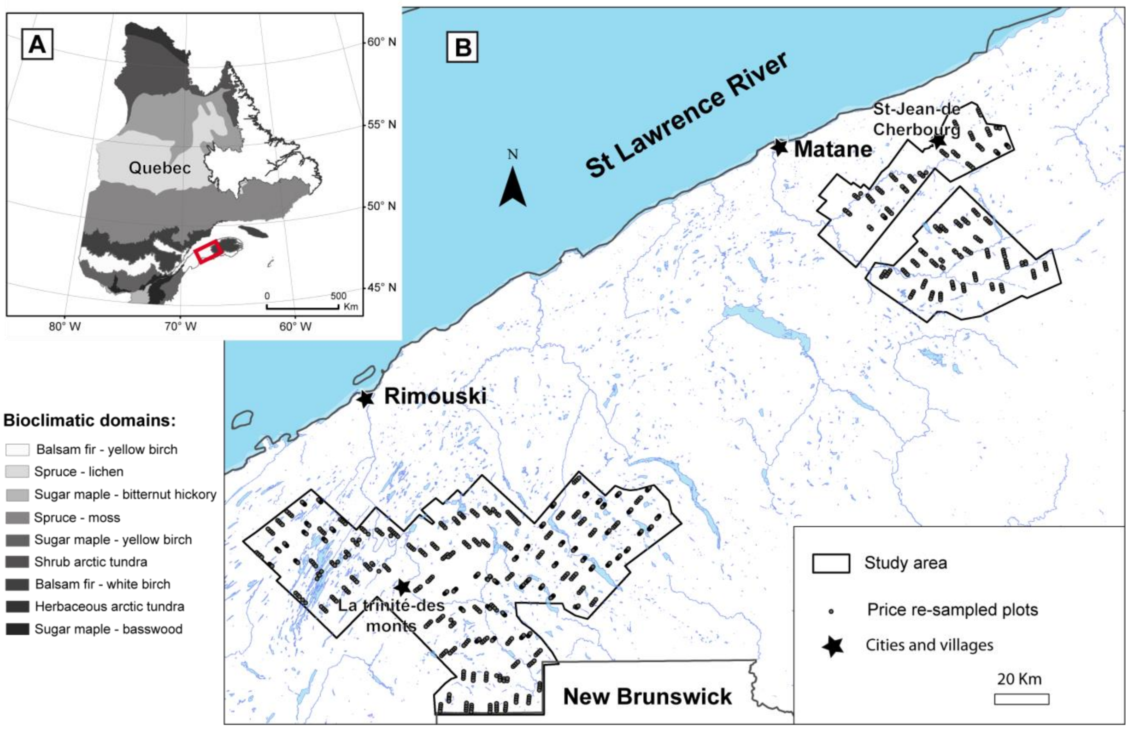


Figure 2-1. A. Quebec bioclimatic domains classification and location of the study area. B. Rimouski and Matane study areas and the distribution of Price forest inventory re-sampled plots.

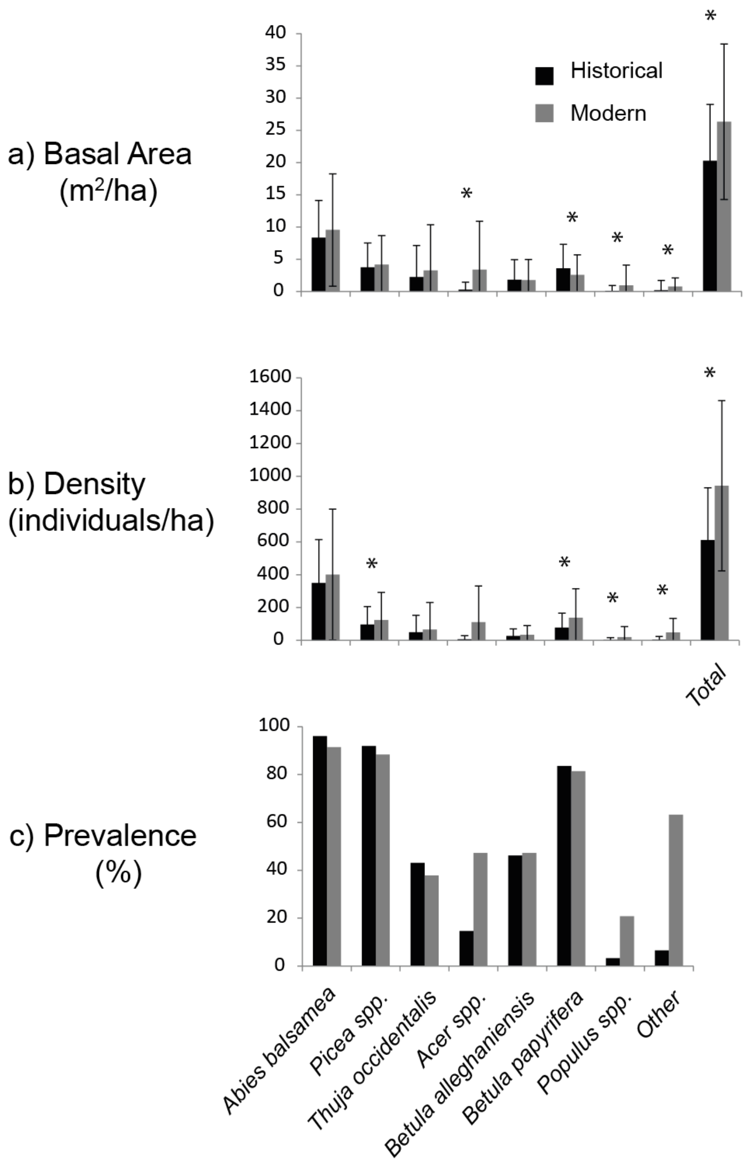


Figure 2-2. a) Basal area (m2/ha), b) Density (individuals/ha), and c) Prevalence (%) of tree taxa between historical (1930-1931) and modern data (2012-2013) in resampled plots (without plantations, N= 457). Bars represent standard deviation. Asterix (*) indicate statistically significant difference between historical and modern values using Wilcoxon test. Prevalence is the percentage of the presence of a given taxa in sampling plot.

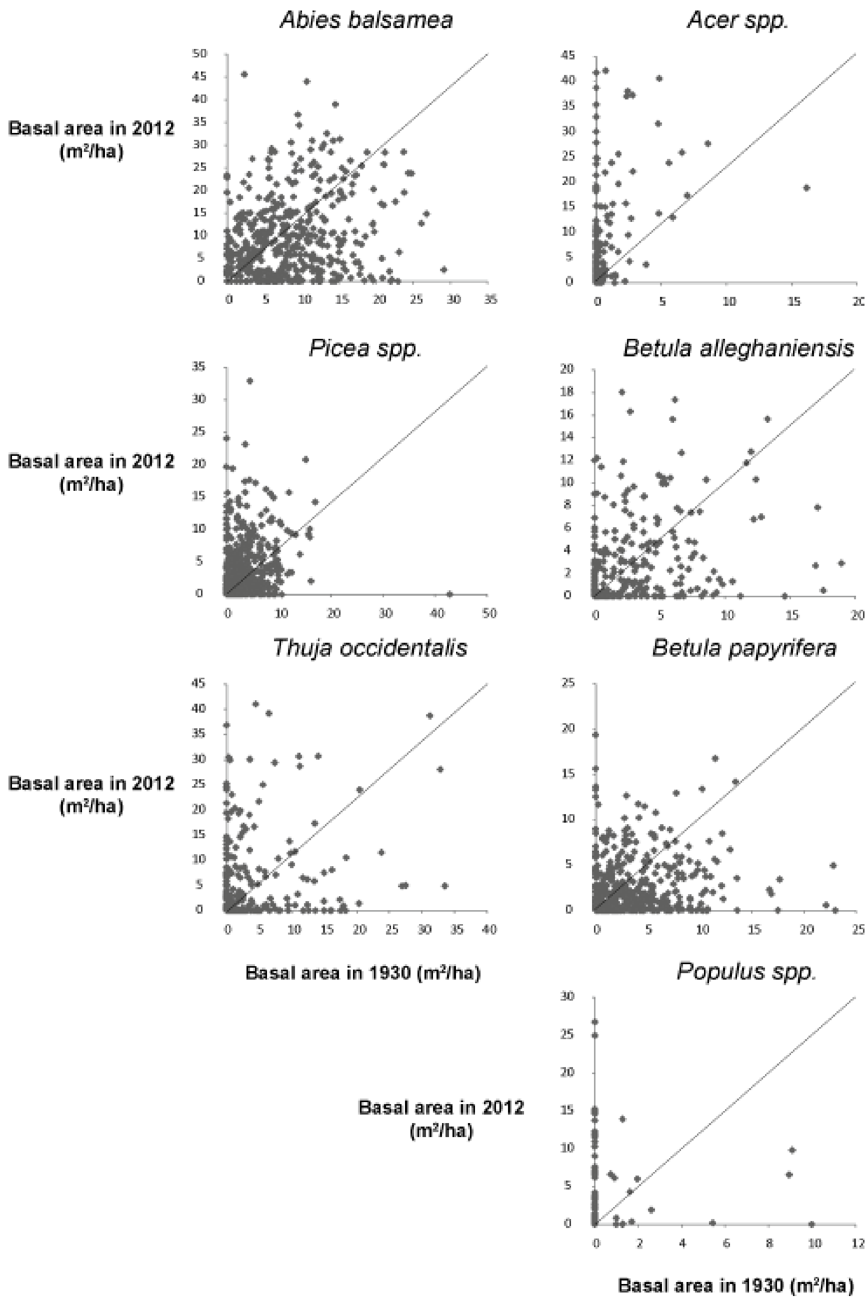


Figure 2-3. Taxa basal area (m2/ha) in 1930 and 2012. Dots represent re-samples plots in natural regenerated stands (plantations not included) (N=457).

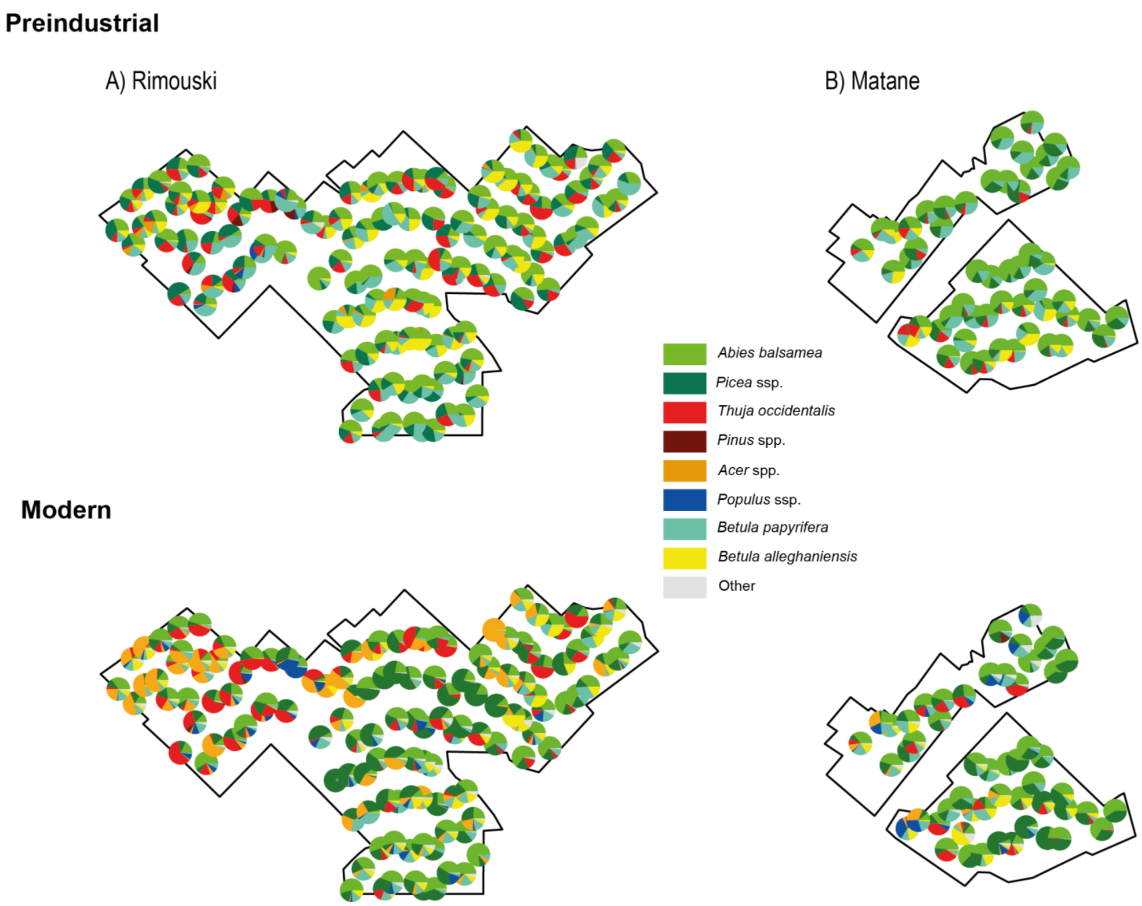


Figure 2-4. Relative basal area (%) of taxa in preindustrial and modern periods in A) Rimouski and B) Matane sectors. (n=187). Each pie represent the mean relative basal area for each species in a group of 3 to 4 inventory plots for visibility.

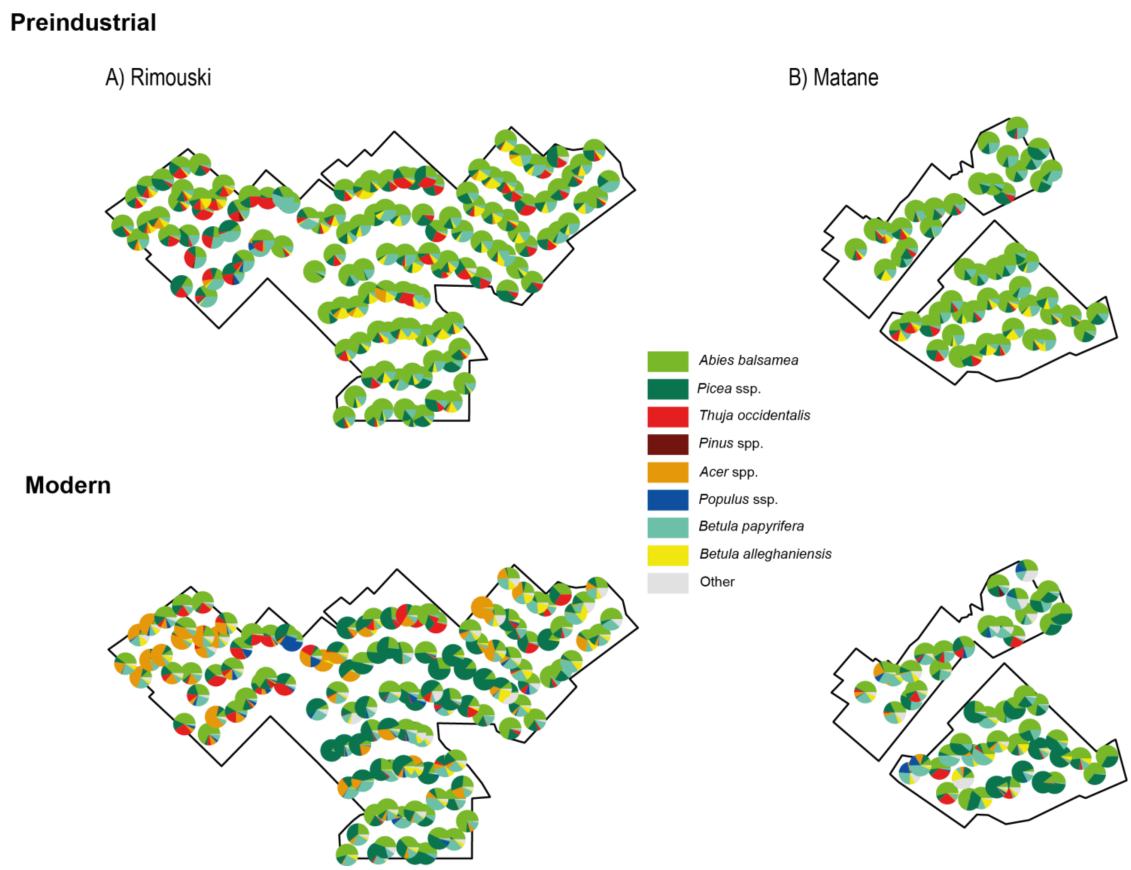


Figure 2-5. Relative density (%) of taxa in preindustrial and modern periods in A) Rimouski and B) Matane sectors (n=187). Each pie represent the mean relative basal area for each species in a group of 3 to 4 inventory plots for visibility.

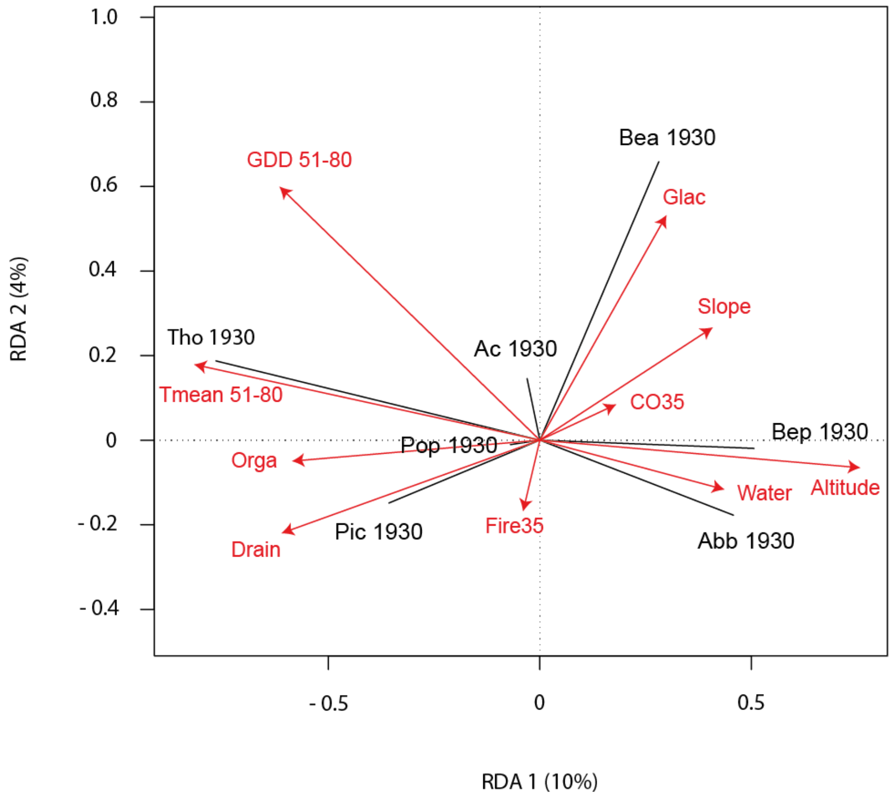


Figure 2-6. Redundancy analysis (RDA – scaling2) of 1930 taxa basal area (black lines) correlated to 10 explanatory variables (red vectors) in three driver sets (environmental variables, disturbance variables and climate variables). Projections showed using first and second ordination axes. Abb 1930: Balsam fir, Tho 1930: Northern white cedar, Ac 1930: Maples, Pop 1930: Poplars, Pic 1930: Spruces, Bea 1930: Yellow birch, Bep 1930: White birch. For explanatory variables acronyms see Table 2-2.

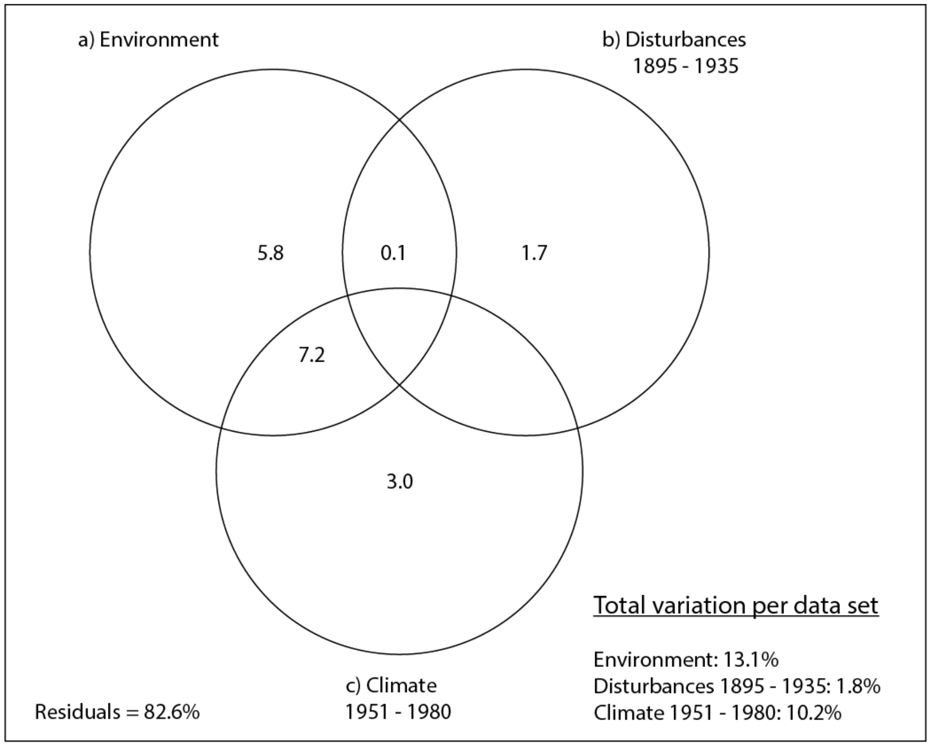


Figure 2-7. Variation partitioning model of hellinger transformed taxa basal area in 1930 explained by a) environment, b) disturbances between 1895 and 1935, and d) climate between 1951 and 1980 variables. The full variation partitioning model with all 3 driver sets explained 17.4% of variation in taxa basal area in 1930 (based on adjusted R2).

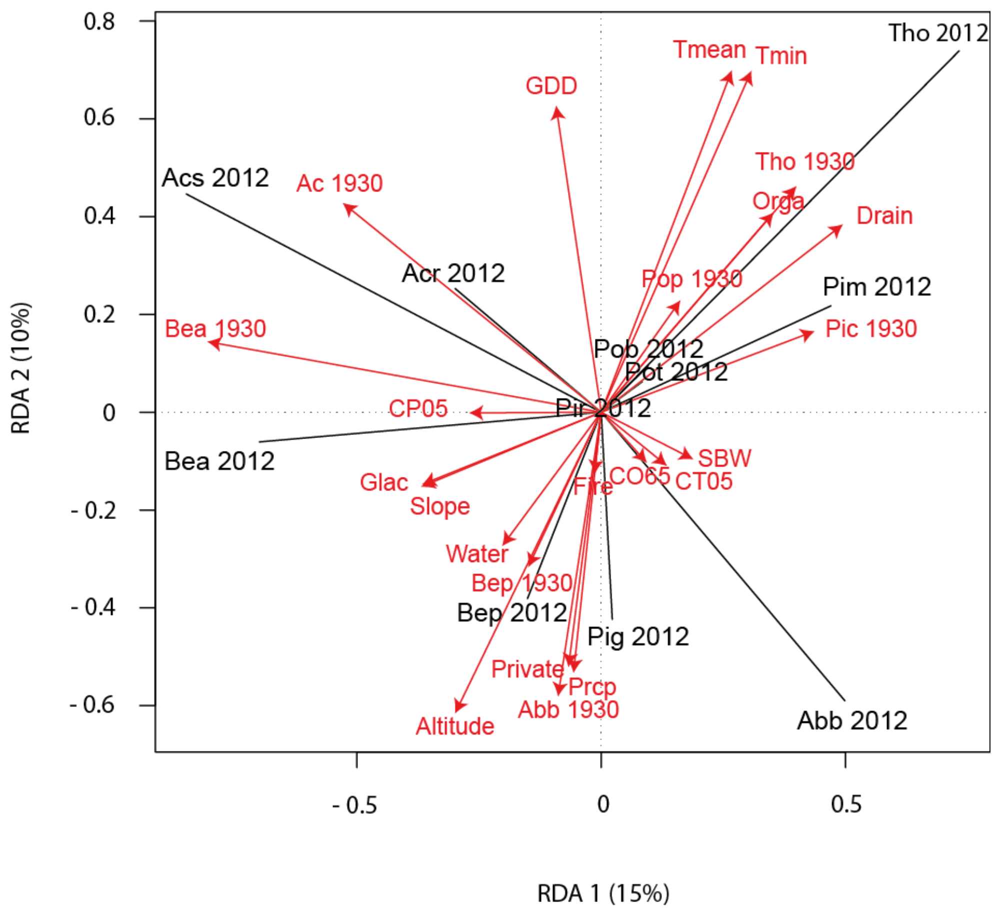


Figure 2-8. Redundancy analysis (RDA – scaling 2) of 2012 taxa basal area (black lines) correlated to 23 explanatory variables (red vectors) in four driver sets (taxa basal area in 1930, environmental variables, disturbance variables and climate variables). Projections showed using first and second ordination axes. Abb 2012: Balsam fir, Tho 2012: Northern white cedar, Acr 2012: Red maple, Acs 2012: Sugar maple, Pob 2012: Balsam poplar, Pot 2012: Trembling aspen, Pim 2012: Black spruce, Pir 2012: Red spruce, Pig 2012: White spruce, Bea 2012: Yellow birch, Bep 2012: White birch. For explanatory variables acronyms see Table 2-1.

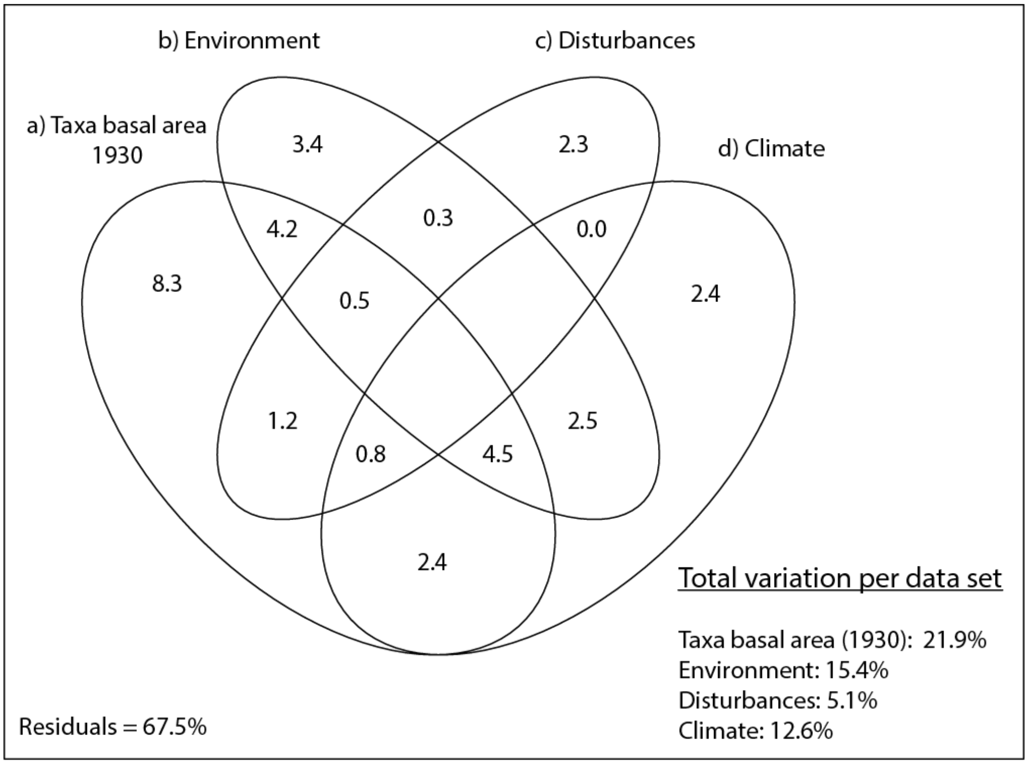


Figure 2-9. Variation partitioning model of Hellinger transformed taxa basal area in 2012 explained by a) taxa basal area in 1930, b) environment, c) disturbances, and d) climate variables. The full variation partitioning model with all 4 driver sets explained 32.5% of variation in taxa basal area in 2012 (based on adjusted R2).

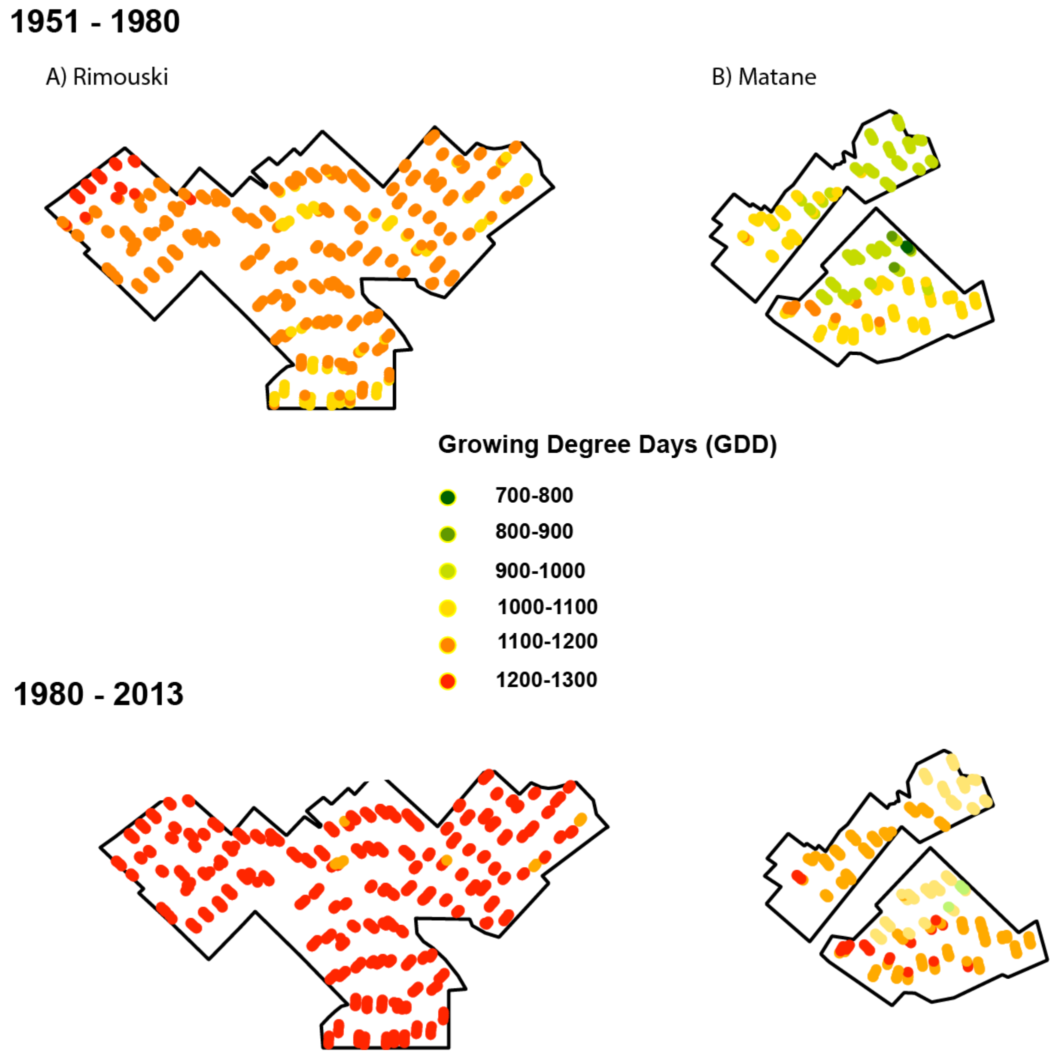


Figure 2-10. Growing Degree-Days of sampling plots in the study area (between 1951-1980 and 1980 - 2010) calculated by Biosim.

2.11. Appendix

Table 2-S1. Explanatory variables within each variable set selected during forward selection procedure (in black) for tree taxa basal area difference between 2012 and 1930 variation partitioning and RDA models

Variables	Acronym	Individual adjusted R^2	p-value	Within group selection order
Taxa basal area 1930				
Betula alleghaniensis	Bea 1930	0.054	≤ 0.001	1
Betula papyrifera	Bep 1930	0.033	≤ 0.001	2
Picea spp.	Pic 1930	0.030	≤ 0.001	3
Abies balsamea	Abb 1930	0.021	≤ 0.001	4
Acer spp.	Ac 1930	0.016	≤ 0.001	5
Thuja occidentalis	Tho 1930	0.012	≤ 0.001	6
Populus spp.	-	-	> 0.05	-
Environement				
Drainage classes	Drain	0.013	≤ 0.001	1
Distance from private lands	Private	0.011	≤ 0.001	2
Alteration deposit	Alter	0.015	≤ 0.001	3
Altitude	Altitude	0.007	< 0.05	4
Slope	Slope	0.004	< 0.05	5
Distance from water courses	Water	0.003	< 0.05	6
Aspect	-	-	> 0.05	-
Glacier deposit	-	-	> 0.05	-
Organic deposit	-	-	> 0.05	-
Disturbances				
Spruce budworm outbreaks (1975-2005)	SBW	0.018	≤ 0.001	1
Fire (1895 - 2005)	Fire	0.013	≤ 0.001	2
Cut over (1935-1965)	CO65	0.007	< 0.05	3
Total cuts (1965-2005)	CT05	0.005	< 0.05	4
Cut over (1895-1935)	CO35	0.003	< 0.05	5
Partial cuts (1965-2005)	-	-	> 0.05	-
Difference climate between the periods 1981 – 2013 and 1951-1980				
Difference in growing degree days	dif_GDD	0.013	≤ 0.001	1
Difference in mean annual precipitation	dif_prcp	0.007	< 0.05	2
Difference on maximum annual temprature	dif_Tmax	0.004	< 0.05	3
Difference in mean annual temprature	dif_Tmean	0.005	< 0.05	4
Difference in minimum annual temprature	dif_Tmin	-	> 0.05	-

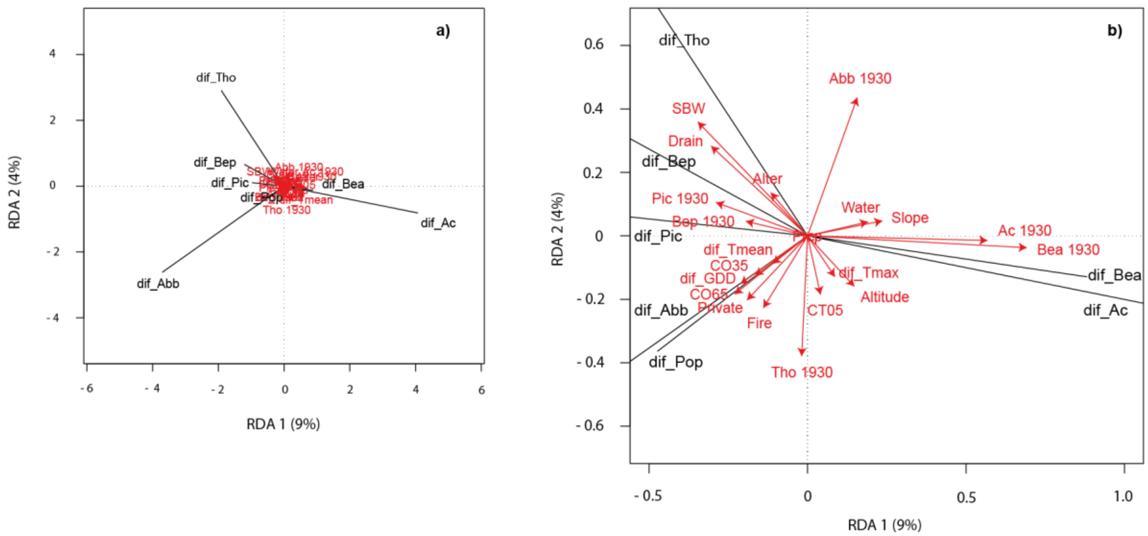


Figure 2-S1. Redundancy analysis (RDA – scaling2) of tree taxa basal area difference between 2012 and 1930 (black lines) correlated to 21 explanatory variables (red vectors) in four driver sets (taxa basal area in 1930, environmental variables, disturbance variables between 1895 and 2005 and difference in mean of climatic variables for the periods 1951 – 1980 and 1981-2013). Projections showed using first and second ordination axes. Tree taxa basal area difference between 2012 and 1930 acronyms: dif_Abb: Balsam fir, dif_Tho: Northern white cedar, dif_Ac: Maples, dif_Pop: Poplars, dif_Pic: Spruces, dif_Bea: Yellow birch, dif_Bep: White birch. For explanatory variables acronyms see Table 2-S1.

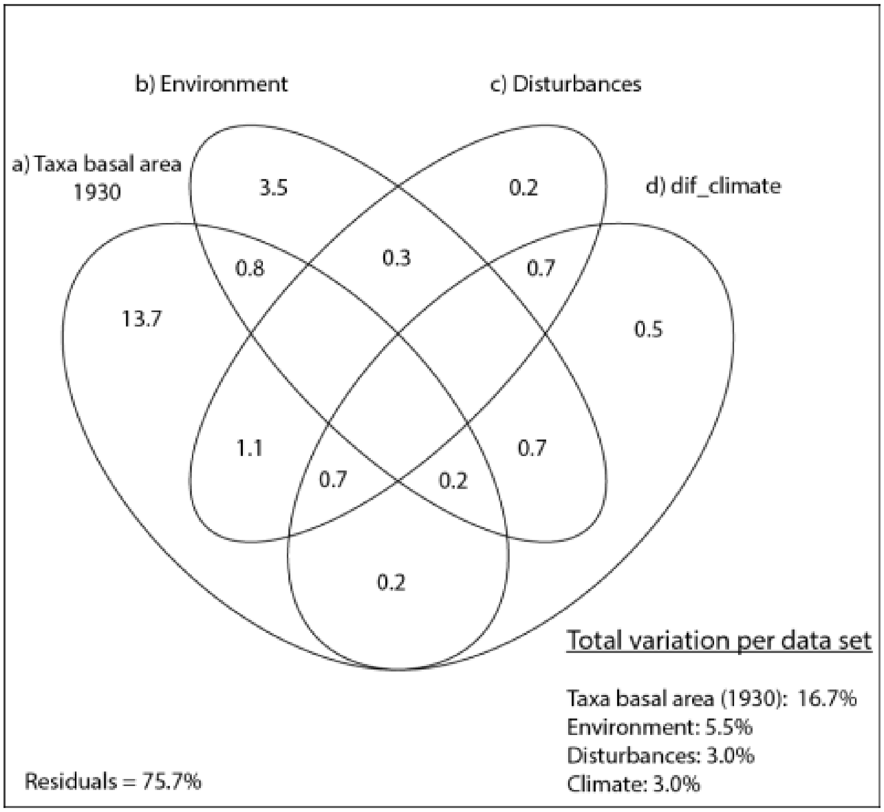


Figure 2-S2. Variation partitioning model of tree taxa basal area difference between 2012 and 1930 explained by a) taxa basal area in 1930, b) environment, c) disturbances between 1895 and 2005, and d) difference in mean of climatic variables for the periods 1951 – 1980 and 1981-2013 (dif_climate) . The full variation partitioning model with all 4 driver sets explained 24% of variation (based on adjusted R2).

CHAPITRE III

COMPARAISON DES PRÉDICTIONS D'UN MODÈLE DE SUCCESSION PAR TROUÉES AVEC DES DONNÉES DE VÉGÉTATION ET DE PERTURBATIONS DANS LES FORÊTS MIXTES DE L'EST CANADIEN

3.1. Résumé en français du troisième article

Ce troisième article, intitulé «Comparaison des prédictions d'un modèle de succession par trouées avec des données de végétation et de perturbations dans les forêts mixtes de l'Est Canadien», fut corédigé par moi-même ainsi que par le Dr. Guy Larocque et les professeurs Luc Sirois et Dominique Arseneault. En tant que première auteure, ma contribution à ce travail fut l'essentiel de la recherche sur l'état de l'art, l'exécution des analyses et la rédaction de l'article. Le Dr. Guy Larocque, le deuxième auteur et concepteur du modèle utilisé pour cet article, ainsi que les peofesseurs Luc Sirois et Dominique Arseneault, troisième et quatrième auteurs, ont aidé au développement de la méthode et à la révision de l'article. Ce chapitre a été publié dans la revue «Forest Ecology and Management» sous le référence suivante :

Elzein, T., Larocque, G. R., Sirois, L., and D. Arseneault. 2020. Comparing the predictions of gap model with vegetation and disturbance data in south-eastern Canadian mixed forests. Forest Ecology and Management, 455, 117649. doi:https://doi.org/10.1016/j.foreco.2019.117649

L'amélioration et la validation des modèles de succession par trouées (gap models) se heurtent au manque des données historiques indépendantes auxquelles on peut

comparer les résultats de simulation. Dans cette étude, nous évaluons le degré auquel le modèle de simulation de la succession ZELIG-CFS prédit le développement à long terme des forêts mixtes dans le sud-est du Québec, en considérant l'histoire des perturbations. Un inventaire forestier historique ainsi qu'une base de données des perturbations couvrant la période 1930 – 2013, ont été utilisés pour évaluer la justesse des simulations. ZELIG-CFS a bien prédit la surface terrière du sapin baumier dans les simulations avec et sans perturbations. Quand les perturbations ont été considérées, les prédictions de l'épinette blanche et le bouleau blanc ont été améliorées. En même temps, la surface terrière des espèces décidues qui ont le plus contribué au changement de composition observé (érable rouge, érable à sucre, et peuplier faux-tremble), a été systématiquement sous-estimée par le modèle. Nous suggérons plusieurs avenues d'améliorations : (1) Une meilleure intégration des stratégies de la régénération des espèces d'arbres, à partir de leur taux de germination jusqu'à leur transition aux stades de plantules. De plus, l'intégration d'une probabilité de reproduction végétative pour les espèces capables de drageonnement comme l'érable rouge, l'érable à sucre, le peuplier faux-tremble, et le thuya. (2) Le couplage du modèle de succession écologique à des modèles de risque par placette pour mieux simuler les probabilités des perturbations naturelles et anthropiques comme source de mortalité exogène.

Mots clés : modèle de succession par trouée ; ZELIG-CFS ; prédictions ; forêt mixte ; composition forestière ; perturbations anthropiques ; base de données historique

3.2. Comparing the predictions of gap model with vegetation and disturbance data in south-eastern Canadian mixed forests

3.3. Abstract

The lack of long term independent historical data constitute a major impediment to the further improvement and validation of forest simulation models. In this study, we evaluate the degree to which the gap model ZELIG-CFS realistically predicts the long term stand development of mixed forests in southeastern Quebec when disturbance history is considered. An early 1930 forest inventory and disturbance data were used to evaluate model simulation performance over the 1930-2013 period. ZELIG-CFS well predicted the basal area of balsam fir in simulations with and without disturbances. When disturbances were simulated, the predictions for white spruce and white birch were more realistic than in the simulation without disturbances. At the same time, deciduous species that contributed the most to the compositional changes observed during the 20th century in mixed forests (red maple, sugar maple, and trembling aspen) were systematically underestimated by the model. Several improvement avenues are suggested: (1) A better integration of regeneration strategies of tree species, especially the integration of a probability of vegetative reproduction for sprouting species like red maple, sugar maple, trembling aspen and northern white cedar, (2) Coupling gap models with a stand risk model to better simulate natural and human disturbance probability as a source of exogenous mortality.

Key words: gap models; ZELIG-CFS; predictions; mixed forest; forest composition; anthropogenic disturbances; historical database

3.4. Introduction

Forest gap models are a class of semi mechanistic, individual-tree forest dynamics models that have wide applications, but need further developments to improve their capacity to simulate forest ecosystem dynamics. They have been developed over the last few decades to study succession pathways in forest ecosystems (Botkin 1993, Peng et al. 2006, Larocque 2016) and landscapes (Urban et al. 1991), and have also been applied to study past vegetation dynamics using fossil pollen data (Solomon and Shugart 1984). Their strength resides in their realism at emulating basic vegetational processes which make them reliable tools to explore forest dynamics (Solomon 1986, Shugart and Smith 1996, Keane et al. 2001, Norby et al. 2001, Price et al. 2001, Wullschleger et al. 2001). Some authors have also suggested that they have the potential to replace empirical growth and yield models in policy and forest management planning (Landsberg 2003, Taylor et al. 2009). Suggested improvements of gap models concern the simulation of processes inducing mortality (Lindner et al. 1997, Keane et al. 2001, Pabst et al. 2008, Larocque et al. 2011) and regeneration (Price et al. 2001, Wehrli et al. 2007). The effects of temperature response functions on growth rate have also been discussed in several studies and reviews (Sirois et al. 1994, Loehle and LeBlanc 1996, Schenk 1996, Monserud 2003, Portner et al. 2010).

Several simulation studies emphasize the importance of the explicit consideration of natural and human forest disturbances as an exogenous source of mortality (Schumacher and Bugmann 2006, Seidl et al. 2011). Simulated species composition can differ when mortality caused by specific disturbances like fire, harvest, browsing, grazing by mammals, and insect outbreaks was taken into account (Dale et al. 1986, Kienast and Kräuchi 1991, Prentice et al. 1993, Lexer and Hönninger 1998, Jorritsma et al. 1999, Miller and Urban 1999, Keane et al. 2001, Seagle and Liang 2001, Pabst et al. 2008). Disturbances are important drivers of forest dynamics and would eventually affect the successional trajectory of a forest stand (Smith and Urban 1988, White and Jentsch 2001, Frelich 2002). For example, mixed forests in eastern North America have experienced a shift in disturbance regime following European colonisation due to settlement fires and intensive industrial logging (Foster et al. 1998, Lorimer 2001, Blanchet 2003, Friedman and Reich 2005, Terrail et al. 2020, Elzein et al. 2020). These novel disturbances represent an increasing risk of large scale mortality compared to preindustrial background levels (Canham et al. 2013, Trumbore et al. 2015). Furthermore, mortality caused by different disturbance types such as fires, insect outbreaks, and logging varies across species, size classes and vigor classes and also affect the regeneration processes through the modification of light conditions and soil humidity (Price et al. 2001, White and Jentsch 2001).

One of the difficulties that limits the further improvement and validation of gap models is the limited availability of long-term, independent historical data to evaluate the realism of models simulations (Botkin et al. 1972, Smith and Urban 1988, Shugart and Smith 1996, Lindner et al. 1997, Bugmann 2001, Larocque et al. 2016). Yet, gap models have well been tested against long-term independent historical data (Dale et al. 1986, Liu and Ashton 1995, Lindner et al. 1997, Makela et al. 2000, Yaussy 2000, Badeck et al. 2001, Risch et al. 2005, Larocque et al. 2006, Pabst et al. 2008, Didion et al. 2009, Larocque et al. 2011, Holm et al. 2012, Rasche et al. 2012, Shuman et al. 2014, Foster et al. 2017). An example of gap model validation with long-term independent data is a study conducted by Larocque et al. (2006) in the mixed forests of eastern Canada which highlighted the critical lack of knowledge on the dynamics of regeneration, which resulted in poor predictions for some species like yellow birch. In the case of this paper, the quantitative nature of the vegetation database and the spatially explicit disturbance data represent an additional opportunity to further test the predictions of gap models and validate the role of disturbances in the simulations. Furthermore, many modellers have used gap models to study forest changes over long time periods (100 – 500 years), whereas some authors suggest that their accuracy should be evaluated for time scales <100 years (Yaussy 2000).

The objective of this study was to evaluate the degree to which the gap model ZELIG-CFS (Larocque et al. 2011) realistically predicted the long term stand development of mixed forests using a detailed historical dataset of forest composition and disturbance. The observation dataset consisted of a spatially explicit 1930 stand inventory data coupled with a detailed disturbance database (1935-2005) in south eastern Canadian mixed forests. We specifically aimed at using the model in a mixed forest region and to identify biases in model performance with or without exogenous mortality caused by disturbances.

3.5. Material and methods

3.5.1. Study area

The study area (2,564 km2) is located in the Lower Saint Lawrence region (LSL) in the province of Quebec, Canada (47° 92’ to 48° 91’ N and 66° 84’ to 68° 86’ W). It is characterized by low elevation hills with moderate slopes. The mean and maximum elevations are 350 and 910 m, respectively. Underlying geology is characterized by the sedimentary bedrock of the Appalachian geological formation. Meteorological data from weather stations at Rimouski and Trinité-des-Monts between 1981 and 2010 showed that mean annual temperature varied between 4.4 and 2.5 °C, respectively, and mean annual total precipitations varied between 959 and 1100 mm, 30% of which fall as snow (Environment Canada 2019).

The vegetation zone is at the northern limit of the Great Lakes-St. Lawrence mixed forests (Rowe 1972) at the transition between the temperate deciduous and the boreal coniferous forests. Balsam fir (Abies balsamea), white spruce (Picea glauca), yellow birch (Betula alleghaniensis), white birch (Betula papyrifera) are abundant in mesic sites. Sugar maple (Acer saccharum) and red maple (Acer rubrum), are at their northern range limit and generally occupy hill tops, while Black spruce (Picea mariana) and northern white cedar (Thuja occidentalis) generally occupy organic deposits mostly next to water courses (Robitaille and Saucier 1998).

Forests in the study area have been shaped by extensive logging and anthropogenic settlement fires during the 20th century (Elzein et al. 2020). Prior to extensive industrial logging at the beginning of the century, the forest in the region was dominated by old growth (> 100 years old) coniferous stands in the lowlands, while mixed and deciduous stands represented less than 40% of the landscape and occupied hill tops (Boucher et al. 2009b). Intensive logging gave place to a fragmented landscape, that is nowadays a mosaic of plantations, regenerating deciduous stands, and young even-aged forests with a few patches of unmanaged mature forests (Boucher et al. 2009b, Dupuis et al. 2011, Elzein et al. 2020). The post-industrial landscape has been also structured by anthropogenic fires, which increased the abundance of trembling aspen (Populus tremuloides) (Terrail et al. 2020, Elzein et al. 2020).

3.5.2. ZELIG-CFS structure and function

ZELIG-CFS (Larocque et al. 2011) is a modified version of ZELIG (Urban and Shugart 1992), which has its roots in JABOWA and FORET simulation models (Urban 1990). Like ZELIG, it simulates individual-tree growth, regeneration and mortality. Individual-tree growth is computed by estimating maximum potential growth rate in an annual time step and then constrains it through limiting ecological factors based on light interception by competitors, soil moisture, a soil fertility factor and ambient temperature. The effect of temperature on species-specific growth rate is modelled by a parabolic equation constrained by the species' minimum and maximum growing degree-days within its entire geographical range (Table 3-1).

ZELIG-CFS is an advanced simulation model based on ZELIG (Smith and Urban 1988). Compared to other gap models, new algorithms for crown interaction effects and prediction of species-specific mortality rate and regeneration were developed in

ZELIG-CFS. In particular, mortality rate functions based on DBH and DBH growth rate were developed (Larocque et al. 2011). Then, a random value is computed to determine if a tree dies or not depending on its probability of survival. The consideration of species-specific crown shape allows interaction between individual trees instead of modelling the forest as a matrix of gap sized squares variably filled leaf area as in the original version of ZELIG. Modelling of the available light growing factor (ALGF) and crown recession rate influence radial growth of the stems. Mortality rate in ZELIG-CFS is computed by taking into consideration species-specific degree of tolerance to slow growth rate as a function of DBH and radial growth rate (Larocque et al. 2011), estimated from empirical data. Furthermore, ZELIG-CFS accounts for spatial heterogeneity of seedling distribution by using a species-specific stocking factor that is provided as input. The stocking factor adjusts the potential number of seedlings that can germinate under the prevailing site conditions, species ecological requirements, and competition. ZELIG-CFS randomly introduces a pre-established number of seedlings per species each year of the simulation based on empirical observations, and simulates the shade tolerance of species as the sensitivity to light conditions in the understorey. Ecological characteristics of different species are described in ZELIG-CFS using 5 shade tolerance classes, 3 stress tolerance classes in response to soil fertility, and 5 drought tolerance classes in response to soil moisture (Table 3-1).

ZELIG-CFS functioning includes several steps. Simulations are initialized with site physical data, monthly mean temperature and precipitation values, species' functional traits, potential seed establishment values and individual tree DBH data. The annual changes are then computed as follow: generation of random fluctuations of monthly climatic conditions, prediction of individual-tree mortality and growth, prediction of seedling establishment and sapling development, update of characteristics such as basal area and leaf area index, and recording of the main state variables. These computations are repeated for the number of annual cycles determined in the initialization phase (Figure 3-1). Many individually simulated forest patches can be aggregated to depict vegetation succession at the landscape level.

3.5.3. Initializing ZELIG-CFS

To initialize ZELIG-CFS, we used data from a detailed forest inventory conducted by the Price Brothers & Company between 1930 and 1931 (hereafter referred to as the 1930 inventory) in 457 rectangular plots of 0.1 ha each. Individual stems (DBH> 3 inches; ~ 7.6 cm) were then tallied by tree taxa and 2-inches DBH classes. In order to validate ZELIG-CFS simulations with observations, the same plots were re-sampled in the summers of 2012 and 2013 (2013 inventory). The plots selected for this study represent naturally regenerated stands and do not include any plantations that are commonly found in the region. In 1930 these plots were known to be mature forests that had not been disturbed between 1895 and 1935 according to our disturbance data base (Elzein et al. 2020). In the historical data base, some taxa were grouped such as birches, poplars, maples and spruces. Because some species were aggregated in genera in 1930 database, we attributed the proportional abundance of species belonging to each genera in 2013 to the 1930 database. This permitted us to identify these genera in the 1930 database to the species level, information necessary to initiate simulations in ZELIG-CFS. The simulations were made per plot. Tree DBHs in the 1930 sample plots were entered for model initialization. Regeneration density (potential number of seedlings/m2) and stocking (proportion) per species were determined using values from the literature (Table 3-2). Spatially explicit disturbance history was reconstructed for each plot per 10 year interval between 1935 and 2005 using historical and modern forest maps (Elzein et al. 2020). The reconstructed disturbances were classified as fires, logging, and a 1970s Spruce Budworm outbreak. Logging includes three categories: partial logging (1935 – 1965), partial logging (1965 – 2005), and total logging (1965 – 2005). On the Price Brothers & Company historical maps, logging polygons between 1935 and 1965 were identified as Cut Over zones, without a precise logging type. However, these cut over zones were most likely diameter limit partial logging operations, based on written accounts of logging practices at that time (Price Brothers & Company Limited 1944, Fortin et al. 1993) and an analysis of forest diameter structure in logged vs. unlogged plots subsequently surveyed in 1930-1931 (Elzein et al. 2020). Logging polygons for the period 1965-2005 were classified as partial cuts (logging severity varying from 25% to 75% of basal area) or total cuts (more than 75% basal area removal) based on Quebec's department of forests decadal inventories. Species' traits to be entered in ZELIG-CFS include maximum age (years), maximum DBH (cm), maximum height (m), growth rate scaling coefficient, minimum and maximum growing degree days in species` range, shade tolerance class, drought tolerance class, and crown shape. Site Fertility class is also parametrized in the model (Larocque et al. 2011).

We adapted ZELIG-CFS for our study area by providing the relevant environmental parameters, including longitude (°), latitude (°), altitude (m), plot area (m2), soil type (qualitative variable based on texture), soil fertility factor (mg/ha/year), and monthly mean temperatures (°C) and precipitations (mm), along with corresponding standard deviations. Soil fertility factor is expressed in terms of the maximum megagrams per hectare of aboveground biomass that a site can produce in a year and is used to determine potential competition for nutrients per forest type. Soil type per plot was inferred using drainage classes from the fourth decadal inventory map produced by the Quebec's department of forests. The Sandy soil type was attributed to drainage classes 0,1, and 2, sandy loam to class 3, loam to class 4, silt loam to class 5, and clay loam to class 6. The 457 sampled plots were classified into four compositional types (Yellow birch-Red maple, White birch-Balsam fir, Balsam fir-Spruce, and Northern white cedar-Spruce) by cluster analysis of the main species basal area in 1930. Soil fertility factor for each forest type was then calculated using DBH values from one representative plot whose total basal area was closest to the mean value of all plots belonging to a particular forest type. Finally, monthly temperatures and precipitations for each sampling plot were obtained from BioSim 11 (https://cfs.nrcan.gc.ca/projects/133), based on available Canada-USA daily climatic data for the periods 1951-1980 and 1981-2013. BioSim 11 forecasts are based on regional air temperature and precipitation interpolated from nearby weather stations, adjusted for elevation and location differentials with regional gradients. Plots adjusted growing degree days (GDD) are calculated in ZELIG-CFS from mean monthly temperatures generated per plot by BioSim 11 for the growing season (May to September) using the following formula:

$$GDD=(\text{Mean Monthly Temprature}-5.56)\times\text{Number of days in the month}$$

GDD varied between 884 and 1218 in our study area, with 15% of our plots with values greater than 1204.

3.5.4. ZELIG-CFS performance and evaluation

To evaluate the degree to which ZELIG-CFS realistically predicts the long term stand development of mixed forests two sets of simulations were performed, with and without disturbances. For each set, each plot was simulated for 80 years and outputs were generated at 5 year intervals. For simulation with disturbance, each known disturbance event was simulated in the year and plots it actually occurred (Elzein et al. 2020). During each disturbance event, randomly selected individual trees were removed to account for a determined percentage of basal area removal per species per disturbance type (Table 3-3). These percentages were estimated according to the known results of each disturbance on stand basal area in our study area. Depending on its disturbance history, each plot could be subjected to one or several disturbances in various years of the simulations. 169 out of the total 457 simulated plots have been subjected to 100% biomass removal and were grown from scratch at various stages of the simulation to account for stand replacing disturbances like clear cuts and/or fires.

ZELIG-CFS performance was evaluated by plotting the trajectory of simulated basal area per species and comparing the results of the last simulation year (year 80) to observed values in 2013. For simulations with disturbances, five groups of plots were considered depending on the presence/absence of each disturbance into each plot during the simulation period. We plotted the trajectory of simulated basal area values and compared the last simulated year value to observed values in each group. In this latter analysis, plots with more than one disturbance type were selected more than once.

3.6. Results

ZELIG-CFS is sensitive to disturbance regime. It performed better in the simulation with disturbances than without disturbance (Figures 3-2 and 3-3). It has well estimated the basal area of balsam fir, white spruce, white birch and black spruce by the end of the simulation period in the simulation with disturbances (Figure 3-2), while white spruce and white birch were overestimated in the simulation without disturbances (Figure 3-3). Relative to observations, both simulations with and without disturbances under-predicted the basal area increase for red maple, sugar maple, trembling aspen, yellow birch and northern white cedar in 2013 as compared to 1930. During the 1930-2013 time interval, relative basal area of trembling aspen, red maple and sugar maple increased from less than 1% to 3%, 4%, and 9%, respectively (Figure 3-4). Yet, at the end of simulations with or without disturbances relative basal areas of these three taxa were near 0% (Figure 3-4). Conversely, the model over-estimated the relative basal area of softwood tree species other than cedar. The basal area of these taxa decreased from 71% to 67% in plots over the 1930-2013 time interval, yet it increased to 76% and 78% in simulations with and without disturbances respectively (Figure 3-4). Differences were particularly pronounced for sugar maple, yellow birch, and northern white cedar.

When disturbance types were simulated separately, the simulated mean basal area per species was relatively similar among disturbance types, except for fire and total logging (1965-2005) (Figure 3-5). For all disturbance types, mean basal area decreased during the simulation for white spruce, white birch and northern white cedar. For balsam fir, mean basal area for fire and total logging (1965-2005) groups decreased and then started to increase again. The simulated basal areas for all disturbance types were underestimated for red maple, sugar maple, yellow birch and black spruce. Trembling aspen basal area was slightly underestimated for all disturbance types, except for fire where it was largely underestimated.

Simulated diameter distributions diverged compared to observed values for some species (Figure 3-6). In simulations with and without disturbances, white spruce and white birch simulated mean basal area at year 80 was mostly concentrated in large diameter individuals, while the observed values indicated a more homogeneous distribution across DBH classes. This indicates a lower simulated mortality rate in larger individuals compared to observations. Similarly, balsam fir diameter distribution at year 80 was mostly concentrated in small DBH while observed values were more homogenous across DBH classes. For sugar maple and yellow birch, individuals in large diameter classes were under-estimated by the model suggesting higher levels of mortality compared to observations. All diameter classes for northern white cedar were underestimated by the simulations compared to observed values.

The observed and simulated prevalence (frequency of occurrence) differed according to species. White spruce and white birch were present in 60% of simulated plots with disturbances at year 80, while observed prevalence in 2013 was 80% for white spruce and 90% for white birch (Figure 3-7). For balsam fir, prevalence was about 90% in observed and simulated plots. For sugar maple, red maple, yellow birch, and trembling aspen, prevalence showed a drastic low (near 0%) in simulated plots compared to observed values of 22%, 38%, 47%, and 16%, respectively (Figure 3-7). Northern white cedar prevalence was sensibly the same for simulated and observed plots. On the other hand, black spruce prevalence in the simulated plots is 66%, compared to the 36% observed prevalence.

Balsam fir, white spruce and white birch showed a balance between the number of plots where basal area was overestimated and under-estimated (Figure 3-8). There was a systematic under-estimation of the mean basal area in the simulated plots for red maple, sugar maple, yellow birch and trembling aspen. Black spruce and northern white cedar mean basal areas were more frequently under-estimated than over-estimated.

3.7. Discussion

In the context of the intensified 20th century anthropogenic disturbances (Foster et al. 1998, Foley et al. 2005, Elzein et al. 2020), the simulations with disturbances resulted in more realistic predictions of the dynamics of mixed forests. When disturbances were simulated (Figure 3-2), ZELIG-CFS performed well for the three most dominant species in 1930 (Balsam fir, White birch and white spruce) (Figure 3-4), while without disturbances white spruce and white birch were over estimated by the simulation (Figure 3-3). On the other hand, for deciduous species (red maple, sugar maple and trembling aspen) that had low relative basal areas in 1930 (Figure 3-4), the model could not reproduce their observed expansion and densification in 2013 (Figures 3-4 and 3-7). These expanding taxa were systematically underestimated in the simulations with and without disturbances (Figures 3-2 and 3-3). The increase of red maple, sugar maple and trembling aspen is a generalised phenomenon contributing to the observed post-industrial mixed forests compositional change in eastern North America (Whitney 1994, Foster et al. 1998, Fuller et al. 1998, Dupuis et al. 2011, Fisichelli et al. 2014, Danneyrolles et al. 2019). Many studies have discussed factors responsible of this compositional change in mixed forests, notably climate change and anthropogenic disturbances (Nowacki and Abrams 2015, Pederson et al. 2015, Danneyrolles et al. 2019).

Our study area is located at the northern range limits of sugar maple and red maple. In the simulation, the growth rate of these two species was likely reduced compared to their growth in the middle of their geographic range, thus increasing the probability of stress-related mortality (Reich et al. 2015). Indeed, the parabolic growing-degree-day function in ZELIG-CFS underlying assumption is that the minimum and maximum temperature tolerances for a species are the values observed at the northern and southern boundaries of its geographic distribution, respectively (Shugart and Smith 1996). Despite our assumption of a constant climate throughout our simulations, the 20th century has been warmer than the 19th century in North America (Anchukaitis et al. 2017, Gennaretti et al. 2017) and precipitations have increased (IPCC 2013). Many empirical studies have linked the increase in sugar and red maples in temperate forests to rising temperatures (Tremblay et al. 2002, Goldblum and Rigg 2005, Fei and Steiner 2008, Fisichelli et al. 2014, Boisvert-Marsh et al. 2019). Simulations with higher temperatures (or degree-days) would have likely improved sugar maple and red maple growth rate and survival (El-Bayoumi et al. 1984).

Anthropogenic disturbances of the 20th century are also considered as an important contributor to the observed forest compositional changes (Nowacki and Abrams 2015, Danneyrolles et al. 2019). Some processes related to anthropogenic disturbances, not simulated by ZELIG-CS, might explain the underestimation of maples and poplars. Red maple and sugar maple are often considered shade tolerant species (Table 3-1); therefore large disturbance-induced canopy openings would disfavour their recruitment (Dansereau 1944, Parker et al. 1985). Yet, these species produce a large quantity of seeds, have good germination rates, and can grow rapidly when exposed to light (Fei and Steiner 2008, Nolet et al. 2008). Their shade tolerance class in the model might have been detrimental to them when stand replacing disturbances were simulated (Table 3-3). Furthermore, vegetative reproduction is not simulated by ZELIG-CFS and the model may have underestimated the ability of sprouting and layering species, like red maple, northern white cedar and trembling aspen to recover and expand following disturbances (Oliver and Larson 1996, Price et al. 2001). Early successional trembling aspen increase (Figure 3-7) has been associated with fire activity in the study area (Boucher et al. 2017, Terrail et al. 2020, Elzein et al. 2020). Indeed, fires consume litter and modify temperature conditions and nutrient availability, favouring seedlings establishment and sprouting of fire-prone trembling aspen (Johnstone et al. 2010, Bowman et al. 2015, Johnstone et al. 2016). On the other hand, fire preventive measures (Blanchet 2003) could have favoured the expansion of maples (Hutchinson et al. 2008).

For northern white cedar, layering as well as the interaction between partial disturbances and advanced regeneration (Danneyrolles et al. 2017), might explain why its increase observed in our study region was not simulated by the model (Figure 3-7).

In the absence of disturbances, the model overestimated white spruce and white birch basal area at year 80 (Figure 3-3). Moreover, their simulated basal area is concentrated among large individuals when disturbances are removed (Figure 3-6). This may reflect the fast growth rate coefficient of these two species compared to the other species (Table 3-1) as well as the fact that they are located in the middle of their distribution range in our study area, thus, their growth is optimal.

There is considerable room for debate regarding the level of details that should be included in gap models to simulate forest processes (Bonan and Sirois 1992, Bugmann and Martin 1995, Fischlin et al. 1995, Loehle and LeBlanc 1996, Schenk 1996, Deutschman et al. 1999, Didion et al. 2009). The results of this study provide some possible avenues to improve the realism of gap models at simulating different types of disturbances: (1) A better integration of regeneration strategies of tree species, especially the integration of a probability of vegetative reproduction for sprouting and layering species like red maple, sugar maple, trembling aspen and northern white cedar, (2) Coupling gap models with a stand risk model to better simulate natural and human disturbance probability as a source of exogenous mortality across species and stem size classes, especially in the context of anthropogenic disturbance regime shift. For example, integrating the probability of presence of pyrophiles species like trembling aspen with fire activity and modifying red maple and sugar maple shade tolerance classes to better adapt fast growth in zones with stand replacing disturbances like total cuts.

3.8. References

Anchukaitis, K. J., R. Wilson, K. R. Briffa, U. Büntgen, E. R. Cook, R. D'Arrigo, N. Davi, J. Esper, D. Frank, B. E. Gunnarson, G. Hegerl, S. Helama, S. Klesse, P. J. Krusic, H. W. Linderholm, V. Myglan, T. J. Osborn, P. Zhang, M. Rydval, L. Schneider, A. Schurer, G. Wiles, and E. Zorita. 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163:1-22.

Badeck, F.-W., H. Lischke, H. Bugmann, T. Hickler, K. Hönninger, P. Lasch, M. J. Lexer, F. Mouillot, J. Schaber, and B. Smith. 2001. Tree Species Composition in European Pristine Forests: Comparison of Stand Data to Model Predictions. Climatic Change 51:307-347.

Blanchet, P. 2003. Feux de forêt : l'histoire d'une guerre. Trait d'union, Montréal.

Boisvert-Marsh, L., C. Périé, and S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology.

Bonan, G. B., and L. Sirois. 1992. Air temperature, tree growth, and the northern and southern range limits to Picea mariana. Journal of Vegetation Science 3:495-506.

Botkin, D. B. 1993. Forest dynamics: an ecological model. Oxford University Press, New York.

Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some Ecological Consequences of a Computer Model of Forest Growth. Journal of Ecology 60:849-872.

Boucher, Y., D. Arseneault, and L. Sirois. 2009b. La forêt préindustrielle du Bas-Saint-Laurent et sa transformation (1820-2000) : implications pour l’aménagement écosystémique. Le Naturaliste Canadien 133:60-69.

Boucher, Y., I. Auger, J. Noël, P. Grondin, and D. Arseneault. 2017. Fire is a stronger driver of forest composition than logging in the boreal forest of eastern Canada. Journal of Vegetation Science 28:57-68.

Bowman, D. M. J. S., G. L. W. Perry, and J. B. Marston. 2015. Feedbacks and landscape-level vegetation dynamics. Trends in Ecology & Evolution 30:255-260.

Bugmann, H. 2001. A Review of Forest Gap Models. Climatic Change 51:259-305.

Bugmann, H., and P. Martin. 1995. How physics and biology matter in forest gap models. Climatic Change 29:251–257.

Canham, C. D., N. Rogers, and T. Buchholz. 2013. Regional variation in forest harvest regimes in the northeastern United States. Ecological Applications 23:515-522.

Dale, V. H., M. Hemstrom, and J. Franklin. 1986. Modeling the long-term effects of disturbances on forest succession, Olympic Peninsula, Washington. Canadian Journal of Forest Research 16:56-67.

Danneyrolles, V., S. Dupuis, D. Arseneault, R. Terrail, M. Leroyer, A. de Römer, G. Fortin, Y. Boucher, and J.-C. Ruel. 2017. Eastern white cedar long-term dynamics in eastern Canada: Implications for restoration in the context of ecosystem-based management. Forest Ecology and Management 400:502-510.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. de Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, and D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications 10:1265.

Dansereau, P. 1944. Interpreting climaxes in Quebec. Science 99:426-427.

Deutschman, D. H., S. A. Levin, and S. W. Pacala. 1999. Error propagation in a forest succession model:The role of fine-scale heterogeneity in light. Ecology 80:1927-1943.

Didion, M., A. D. Kupferschmid, A. Zingg, L. Fahse, and H. Bugmann. 2009. Gaining local accuracy while not losing generality — extending the range of gap model applications. Canadian Journal of Forest Research 39:1092-1107.

Dupuis, S., D. Arseneault, and L. Sirois. 2011. Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. Journal of Vegetation Science 22:564-575.

El-Bayoumi, M. A., H. H. Shugart, and R. W. Wein. 1984. Modelling succession of Eastern Canadian mixedwood forest. Ecological Modelling 21:175-198.

Elzein, T., Arseneault, D., Sirois, L., and Y. Boucher. 2020. The Changing Disturbance Regime in Eastern Canadian Mixed Forests During the 20th Century. Frontiers in Ecology and Evolution, 8

EnvironmentCanada. 2019. Canadian Climate Normals and averages 1981-2010.

Fei, S., and K. C. Steiner. 2008. Relationships between advance oak regeneration and biotic and abiotic factors. Tree Physiology 28:1111-1119.

Fischlin, A., H. Bugmann, and D. Gyalistras. 1995. Sensitivity of a forest ecosystem model to climate parametrization schemes. Environmental Pollution 87:267-282.

Fisichelli, N. A., L. E. Frelich, and P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography 37:152-161.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309:570-574.

Fortin, J.-C., A. Lechasseur, Y. Morin, F. Harvey, J. Lemay, and Y. Tremblay. 1993. Histoire du Bas-Saint-Laurent. Page 861 in Institut québécois de recherche sur la culture, editor. Québec, Québec.

Foster, A. C., J. K. Shuman, H. H. Shugart, K. A. Dwire, P. J. Fornwalt, J. Sibold, and J. Negron. 2017. Validation and application of a forest gap model to the southern Rocky Mountains. Ecological Modelling 351:109-128.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems 1:96-119.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, New York.

Friedman, S. K., and P. B. Reich. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological applications 15:726-744.

Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1:76-95.

Gennaretti, F., D. Huard, M. Naulier, M. Savard, C. Bégin, D. Arseneault, and J. Guiot. 2017. Bayesian multiproxy temperature reconstruction with black spruce ring widths and stable isotopes from the northern Quebec taiga. Climate Dynamics 49:4107-4119.

Goldblum, D., and L. S. Rigg. 2005. Tree growth response to climate change at the deciduous–boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research 35:2709-2718.

Holm, J. A., H. H. Shugart, S. J. Van Bloem, and G. R. Larocque. 2012. Gap model development, validation, and application to succession of secondary subtropical dry forests of Puerto Rico. Ecological Modelling 233:70-82.

Hutchinson, T. F., R. P. Long, R. D. Ford, and E. K. Sutherland. 2008. Fire history and the establishment of oaks and maples in second-growth forests. Canadian Journal of Forest Research 38:1184-1198.

IPCC. 2013. Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14:369-378.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin III, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology 16:1281-1295.

Jorritsma, I. T. M., A. F. M. van Hees, and G. M. J. Mohren. 1999. Forest development in relation to ungulate grazing: a modeling approach. Forest Ecology and Management 120:23-34.

Keane, R. E., M. Austin, C. Field, A. Huth, M. J. Lexer, D. Peters, A. Solomon, and P. Wyckoff. 2001. Tree mortality in gap models: application to climate change. Climatic Change 51:509-540.

Kienast, F., and N. Kräuchi. 1991. Simulated successional characteristics of managed and unmanaged low-elevation forests in central Europe. Forest Ecology and Management 42:49-61.

Landsberg, J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. Canadian Journal of Forest Research 33:385-397.

Larocque, G. R. 2016. Ecological forest management handbook.

Larocque, G. R., L. Archambault, and C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecological Modelling 199:350-362.

Larocque, G. R., L. Archambault, and C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecological Modelling 222:2570-2583.

Larocque, G. R., H. H. Shugart, W. Xi, and J. A. Holm. 2016. Forest succession models. Pages 179 - 214 in G. R. Larocque, editor. Ecological Forest Management Handbook. Taylor & Francis Group, Boca Raton, FL.

Lexer, M. J., and K. Hönninger. 1998. Simulated effects of bark beetle infestations on stand dynamics in *Picea abies* stands: coupling a patch model and a stand risk model. Pages 289-308 in M. Beniston and J. L. Innes, editors. The Impacts of Climate Variability on Forests. Springer Berlin Heidelberg, Berlin, Heidelberg.

Lindner, M., R. Sievanen, and H. Pretzsch. 1997. Improving the simulation of stand structure in a forest gap model. Forest Ecology and Management 95:183-195.

Liu, J., and P. S. Ashton. 1995. Individual-based simulation models for forest succession and management. Forest Ecology and Management 73:157-175.

Loehle, C., and D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90:1-31.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin 29:425-439.

Makela, A., R. Sievanen, M. Lindner, and P. Lasch. 2000. Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. Tree Physiology 20:347-355.

Miller, C., and D. L. Urban. 1999. Forest Pattern, Fire, and Climatic Change in the Sierra Nevada. Ecosystems 2:76-87.

Monserud, R. A. 2003. Evaluating Forest Models in a sustainable forest management context. Forest Biometry, Modelling and Information Sciences 1:35-47.

Nolet, P., S. Delagrange, D. Bouffard, F. Doyon, and É. Forget. 2008. The successional status of sugar maple (*Acer saccharum*), revisited. Annals of Forest Science 65.

Norby, R. J., K. Ogle, P. S. Curtis, F.-W. Badeck, A. Huth, G. C. Hurtt, T. Kohyama, and J. Peñuelas. 2001. Aboveground growth and competition in forest gap models: an analysis for studies of climatic change. Climatic Change 51:415-447.

Nowacki, G. J., and M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology 21:314-334.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. Update edition. Wiley, New York.

Pabst, R. J., M. N. Goslin, S. L. Garman, and T. A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. Forest Ecology and Management 256:958-972.

Parker, G. R., D. J. Leopold, and J. K. Eichenberger. 1985. Tree dynamics in an old-growth, deciduous forest. Forest Ecology and Management 11:31-57.

Pederson, N., A. W. D'Amato, J. M. Dyer, D. R. Foster, D. Goldblum, J. L. Hart, A. E. Hessl, L. R. Iverson, S. T. Jackson, D. Martin-Benito, B. C. McCarthy, R. W. McEwan, D. J. Mladenoff, A. J. Parker, B. Shuman, and J. W. Williams. 2015. Climate remains an important driver of post-European vegetation change in the eastern United States. Global Change Biology 21:2105-2110.

Peng, C., X. Wen, G. Shao, and K. Reynolds. 2006. Forest simulation models: Computer Applications in Sustainable Forest Management. Pages 101-125. Springer Netherlands.

Portner, H., H. K. M. Bugmann, and A. Wolf. 2010. Temperature response functions introduce high uncertainty in modelled carbon stocks in cold temperature regimes. Biogeosciences 7:3684.

Prentice, I. C., M. T. Sykes, and W. Cramer. 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecological Modelling 65:51-70.

Price Brothers & Company Limited, S. W. D. 1944. Working - plan report for Rimouski establishment. Archives Nationales du Québec - Chicoutimi.

Price, D., N. Zimmermann, P. van der Meer, M. Lexer, P. Leadley, I. Jorritsma, J. Schaber, D. Clark, P. Lasch, S. McNulty, J. Wu, and B. Smith. 2001. Regeneration in gap models: priority issues for studying forest responses to climate change. Climatic Change 51:475-508.

Rasche, L., L. Fahse, A. Zingg, and H. Bugmann. 2012. Enhancing gap model accuracy by modeling dynamic height growth and dynamic maximum tree height. Ecological Modelling 232:133-143.

Reich, P. B., K. M. Sendall, K. Rice, R. L. Rich, A. Stefanski, S. E. Hobbie, and R. A. Montgomery. 2015. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change 5:148-152.

Risch, A. C., C. Heiri, and H. Bugmann. 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. Ecological Modelling 181:161-172.

Robitaille, A., and J.-P. Saucier. 1998. Paysage régionaux du Québec méridional, Direction de la gestion des stock forestiers et Direction des relations publiques, Ministère des Ressources naturelles du Québec. Publication du Québec, Québec.

Rowe, J. S. 1972. Forest regions of Canada. Information Canada, Canadian Forest Service publication number 1300, Ottawa.

Schenk, H. J. 1996. Modeling the effects of temperature on growth and persistence of tree species: A critical review of tree population models. Ecological Modelling 92:1-32.

Schumacher, S., and H. Bugmann. 2006. The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Global Change Biology 12:1435-1450.

Seagle, S. W., and S.-Y. Liang. 2001. Application of a forest gap model for prediction of browsing effects on riparian forest succession. Ecological Modelling 144:213-229.

Seidl, R., P. M. Fernandes, T. F. Fonseca, F. Gillet, A. M. Jönsson, K. Merganičová, S. Netherer, A. Arpaci, J.-D. Bontemps, H. Bugmann, J. R. González-Olabarria, P. Lasch, C. Meredieu, F. Moreira, M.-J. Schelhaas, and F. Mohren. 2011. Modelling natural disturbances in forest ecosystems: a review. Ecological Modelling 222:903-924.

Shugart, H. H., and T. M. Smith. 1996. A review of forest patch models and their application to global change research. Climatic Change 34:131-153.

Shuman, J. K., H. H. Shugart, and O. N. Krankina. 2014. Testing individual-based models of forest dynamics: Issues and an example from the boreal forests of Russia. Ecological Modelling 293:102-110.

Sirois, L., G. B. Bonan, and H. H. Shugart. 1994. Development of a simulation model of the forest-tundra transition zone of northeastern Canada. Canadian Journal of Forest Research 24:697-706.

Smith, T. M., and D. L. Urban. 1988. Scale and resolution of forest structural pattern. Vegetatio 74:143-150.

Solomon, A. M. 1986. Transient response of forests to CO2-induced climate change: simulation modeling experiments in eastern North America. Oecologia 68:567-579.

Solomon, A. M., and H. H. Shugart. 1984. Integrating forest-stand simulations with paleoecologiacal records to examine long-term forest dynamics. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Taylor, A. R., H. Y. H. Chen, and L. VanDamme. 2009. A Review of Forest Succession Models and Their Suitability for Forest Management Planning. Forest Science 55:23-36.

Terrail R, J. Morin-Rival, G. de Lafontaine, M.J. Fortin and D. Arseneault. 2020. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. Journal of Vegetation Science, https://doi.org/10.1111/jvs.12832

Tremblay, M. F., Y. Bergeron, D. Lalonde, and Y. Mauffette. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. Journal of Biogeography 29:365-373.

Trumbore, S., P. Brando, and H. Hartmann. 2015. Forest health and global change. Science 349:814-818.

Urban, D. L. 1990. A Versatile model to simulate forest pattern: a user's guide to ZELIG Version 1.0. University of Virginia, Charlottesville, Virginia.

Urban, D. L., G. B. Bonan, T. M. Smith, and H. H. Shugart. 1991. Spatial applications of gap models. Forest Ecology and Management 42:95-110.

Urban, D. L., and H. H. Shugart. 1992. Individual-based models of forest succession. Pages 249-292 in R. K. P. D. C. Glenn- Lewin, and T. T. Veblen, editors, editor. Plant succession: theory and prediction. Chapman and Hall, London, UK.

Wehrli, A., P. J. Weisberg, W. Schönenberger, P. Brang, and H. Bugmann. 2007. Improving the establishment submodel of a forest patch model to assess the long-term protective effect of mountain forests. European Journal of Forest Research 126:131-145.

White, P., and A. Jentsch. 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. Pages 399-450 in K. Esser, U. Lüttge, J. W. Kadereit, and W. Beyschlag, editors. Progress in Botany. Springer Berlin Heidelberg.

Whitney, G. G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America, 1500 to the present. Cambridge University Press, Cambridge.

Wullschleger, S. D., R. B. Jackson, W. S. Currie, A. D. Friend, Y. Luo, F. Mouillot, Y. Pan, and G. Shao. 2001. Below-ground processes in gap models for simulating forest response to global change. Climatic Change 51:449-473.

Yaussy, D. A. 2000. Comparison of an empirical forest growth and yield simulator and a forest gap simulator using actual 30-year growth from two even-aged forests in Kentucky. Forest Ecology and Management 126:385-398.

3.9. Tables

Table 3-1. Species characteristics in ZELIG-CF

Species	Maximum age (years)	Maximum dbh (cm)	Maximum height (m)	Growth rate scaling coefficient	Growing degree-days Minimum	Growing degree-days Maximum	Shade[a] tolerance class	Maximum[b] drought tolerance	Fertility[c] class
Abies balsamea	200	65	30	69	250	2404	1	1	3
Acer pensylvanicum	75	22	15	150	889	5500	1	2	3
Acer rubrum	150	80	30	176	1260	6601	2	3	3
Acer saccharum	300	110	44	89	1204	3200	1	2	2
Acer spicatum	50	18	9.5	150	889	5500	1	2	3
Betula alleghaniensis	250	150	45	100	1420	3084	3	2	2
Betula papyrifera	140	70	30	160	700	2500	4	3	3
Picea glauca	200	64	30	132	447	1929	2	3	3
Picea mariana	250	40	20	70	265	1929	2	3	3
Pinus strobus	450	150	37	68	1500	3183	4	2	3
Populus tremuloides	125	75	37	158	889	5556	5	3	2
Fraxinus americana	300	100	40	75	1225	2279	3	1	1
Thuja occidentalis	400	100	29	55	1000	2188	2	4	3

*Adapted from Larocque et al. 2011

a Rank: 1 = very shade-tolerant; 5 = very shade intolerant.

b Rank: 1 = very drought intolerant; 5 = very drought tolerant.

c Rank: 1 = nutrient stress intolerant; 3 = nutrient stress tolerant

Table 3-2. Regeneration density and stocking values used in the simulation

Species		density	stocking	references
Abies balsamea	**Balsam fir**	2.12	0.84	Roy, Ruel and Plamondon (2000)
Acer pensylvanicum	**Striped maple**	0.03	0.05	Larocque, Archambault and Delisle (2006)
Acer rubrum	**Red maple**	2.37	0.83	Roy et al. (2000)
Acer saccharum	**Sugar maple**	5.00	0.80	Archambault, Delisle and Larocque (2009)
Acer spicatum	**Mountain maple**	1.00	0.75	Archambault, Morissette and Bernier-Cardou (1997)
Betula alleghaniensis	**Yellow birch**	1.00	0.30	Bolton and D'Amato (2011)
Betula papyrifera	**White birch**	0.03	0.04	Archambault et al. (1997)
Picea glauca	**White spruce**	0.03	0.08	Archambault et al. (1997)
Picea mariana	**Black spruce**	0.14	0.20	Roy et al. (2000)
Pinus strobus	**White pine**	0.01	0.02	Larocque et al. (2006)
Populus tremuloides	**Trembling aspen**	1.00	0.50	Roy et al. (2000)
Fraxinus americana	**American ash**	0.02	0.05	Larocque et al. (2006)
Thuja occidentalis	**Northern white cedar**	0.30	0.44	Roy et al. (2000)

Table 3-3. Simulated percentage of basal area removed per species for each disturbance type

Disturbances	SAB	ERP	ERR	ERS	ERE	BOJ	BOP	EPB	EPN	PIB	PET	SOA	THO
Fire (1935 – 2005)	100	100	100	100	100	100	100	100	100	100	100	100	100
Partial Logging (1935 – 1965)	75	0	0	0	0	0	0	75	75	0	0	0	50
Partial Logging (1965 – 2005)	50	50	50	50	50	50	50	50	50	50	50	50	50
Total Logging (1965 – 2005)	100	100	100	100	100	100	100	100	100	100	100	100	100
Moderate spruce budworm outbreak (1975-2005)	25	0	0	0	0	0	0	25	0	0	0	0	0
Severe spruce budworm outbreak (1975 – 2005)	75	0	0	0	0	0	0	75	0	0	0	0	0

3.10. Figures

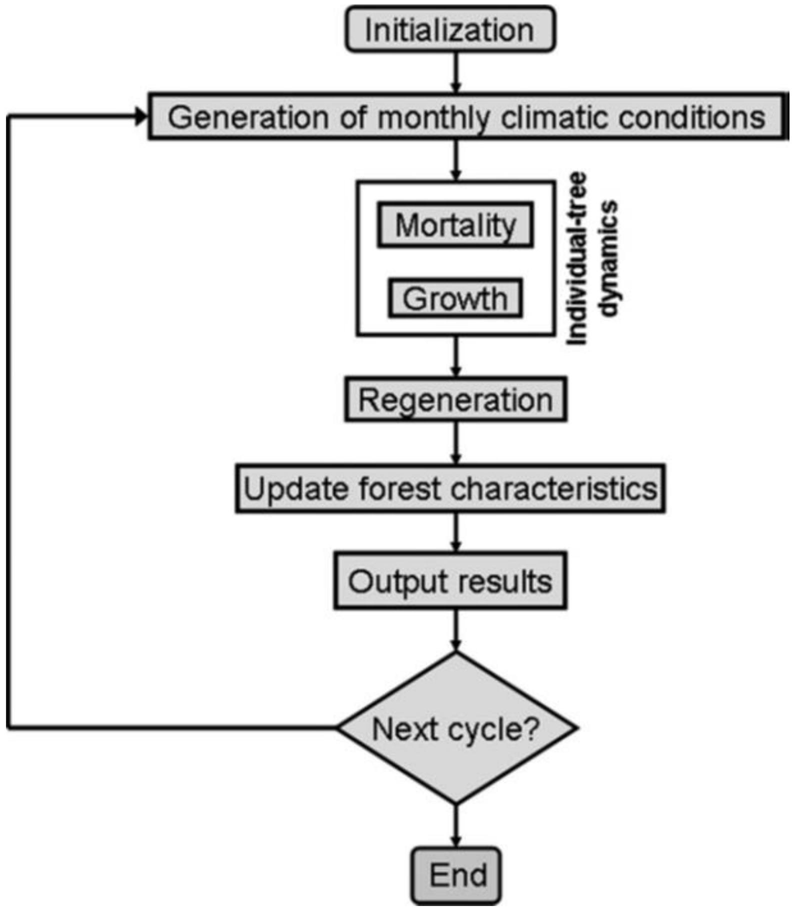


Figure 3-1. Basic conceptual diagram of ZELIG-CFS gap model (from Larocque et al. 2011).

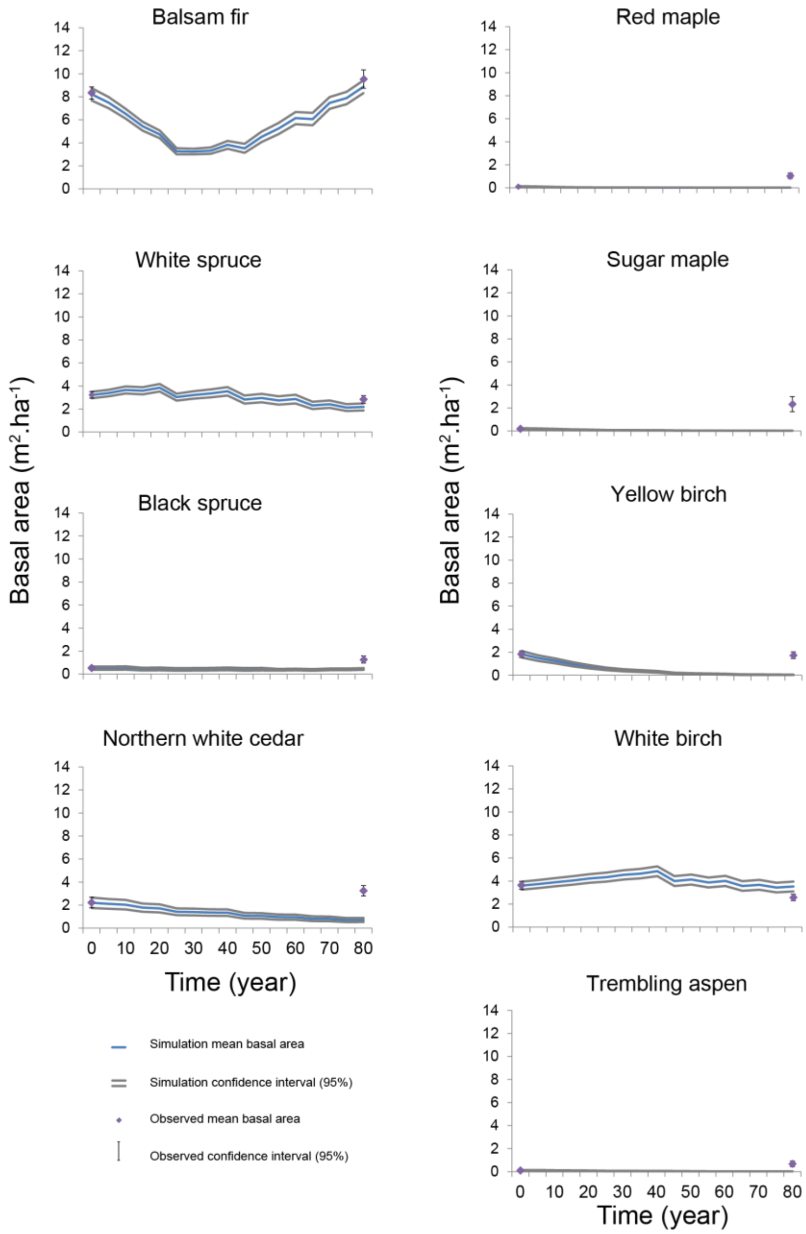


Figure 3-2. Mean simulated and observed basal area (m2.ha-1) for species using regeneration density and stocking values of table 3-1 and disturbance history for each sampling plot. N = 457.

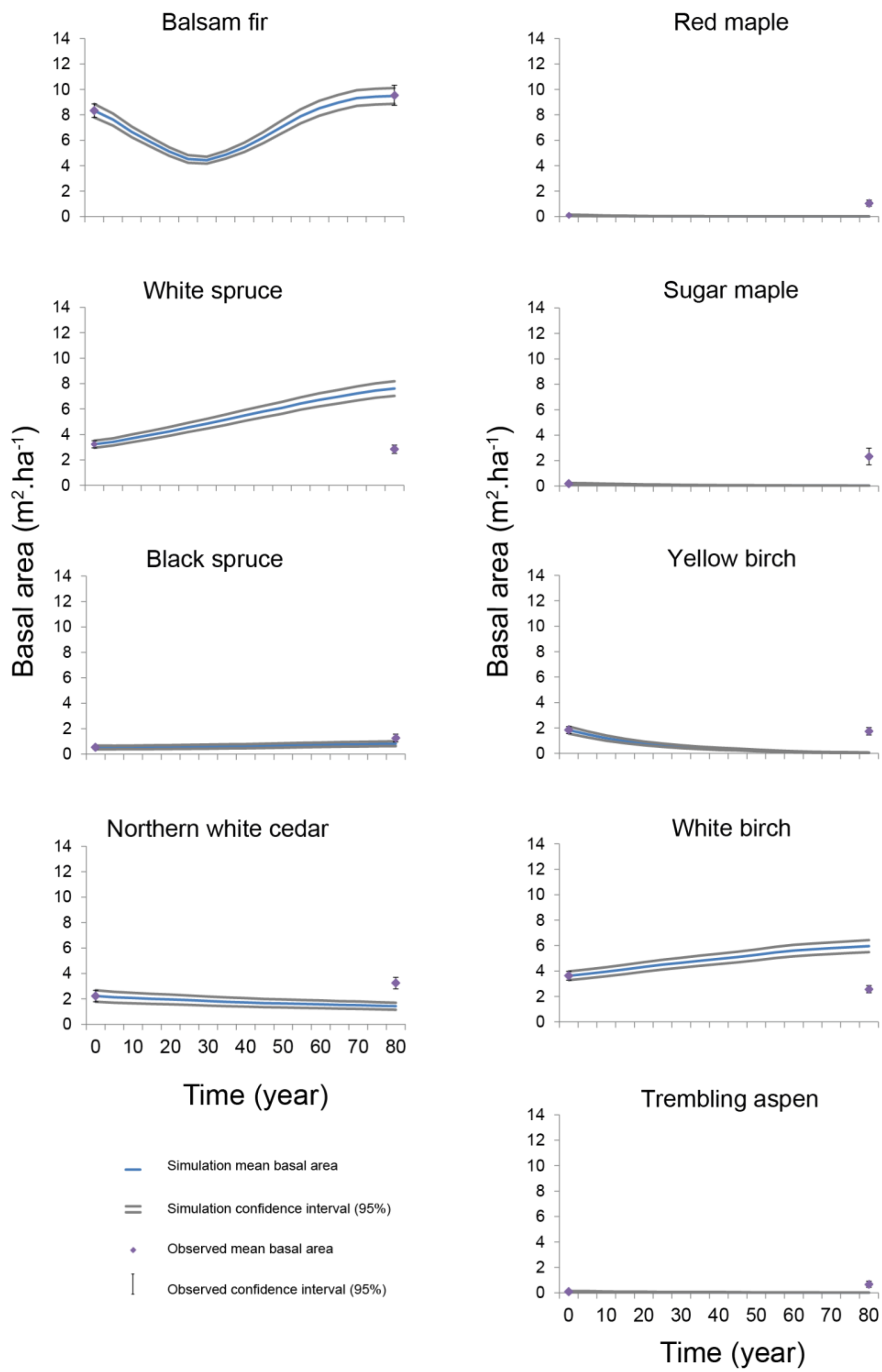


Figure 3-3. Mean simulated and observed basal area (m2.ha-1) without disturbances for species using regeneration density and stocking values of table 3-1. N = 457.

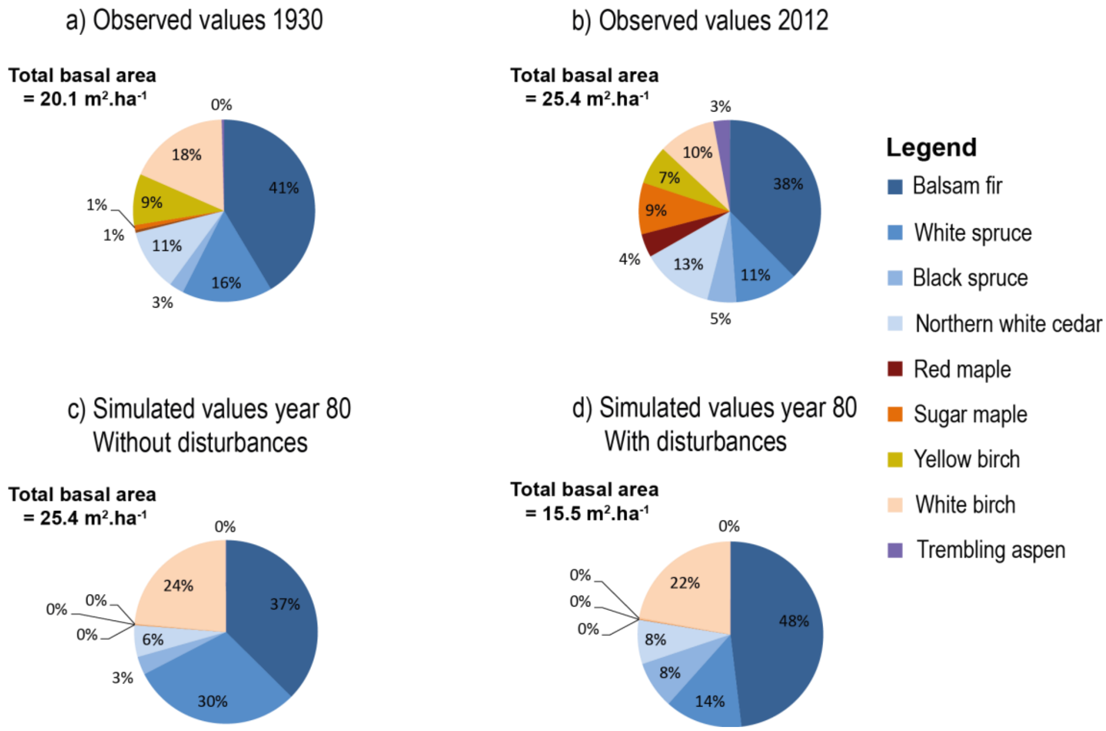


Figure 3-4. Total basal area (m2.ha-1) and species relative basal area (proportion) for a) observed values of 1930, b) observed values of 2012, c) Simulated values of year 80 without disturbances, and d) simulated values of year 80 with disturbances.

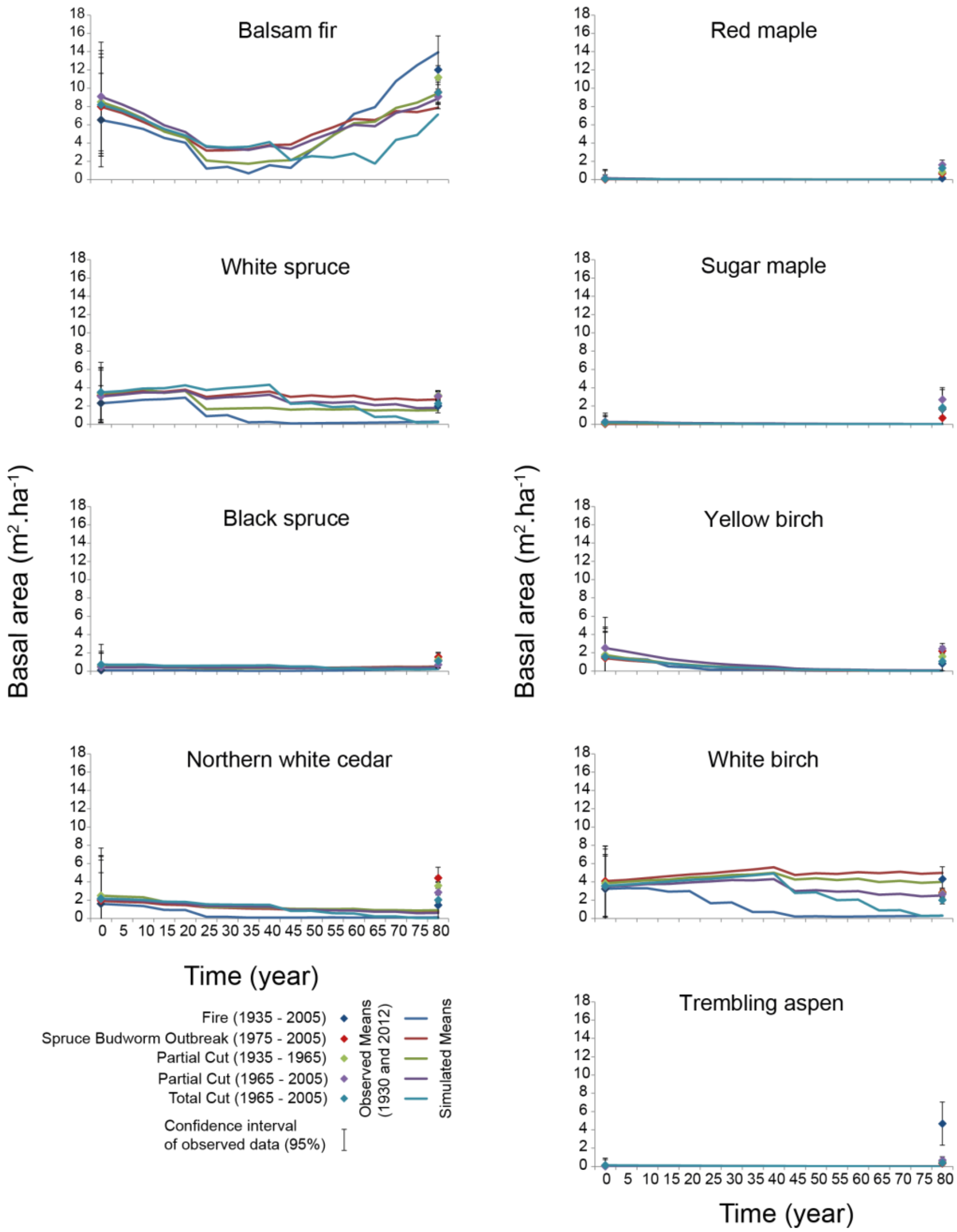


Figure 3-5. Mean simulated and observed basal area (m2.ha-1) for species per disturbance group using regeneration density and stocking values of table 3-1 and disturbance history for each sampling plot. Fire (1935 – 2005): N = 31; Spruce Budworm outbreak (1975 – 2005): N = 201; Partial logging (1935 – 1965): 201; Partial logging (1965 – 2005): N = 160; Total logging (1965 – 2005): 157.

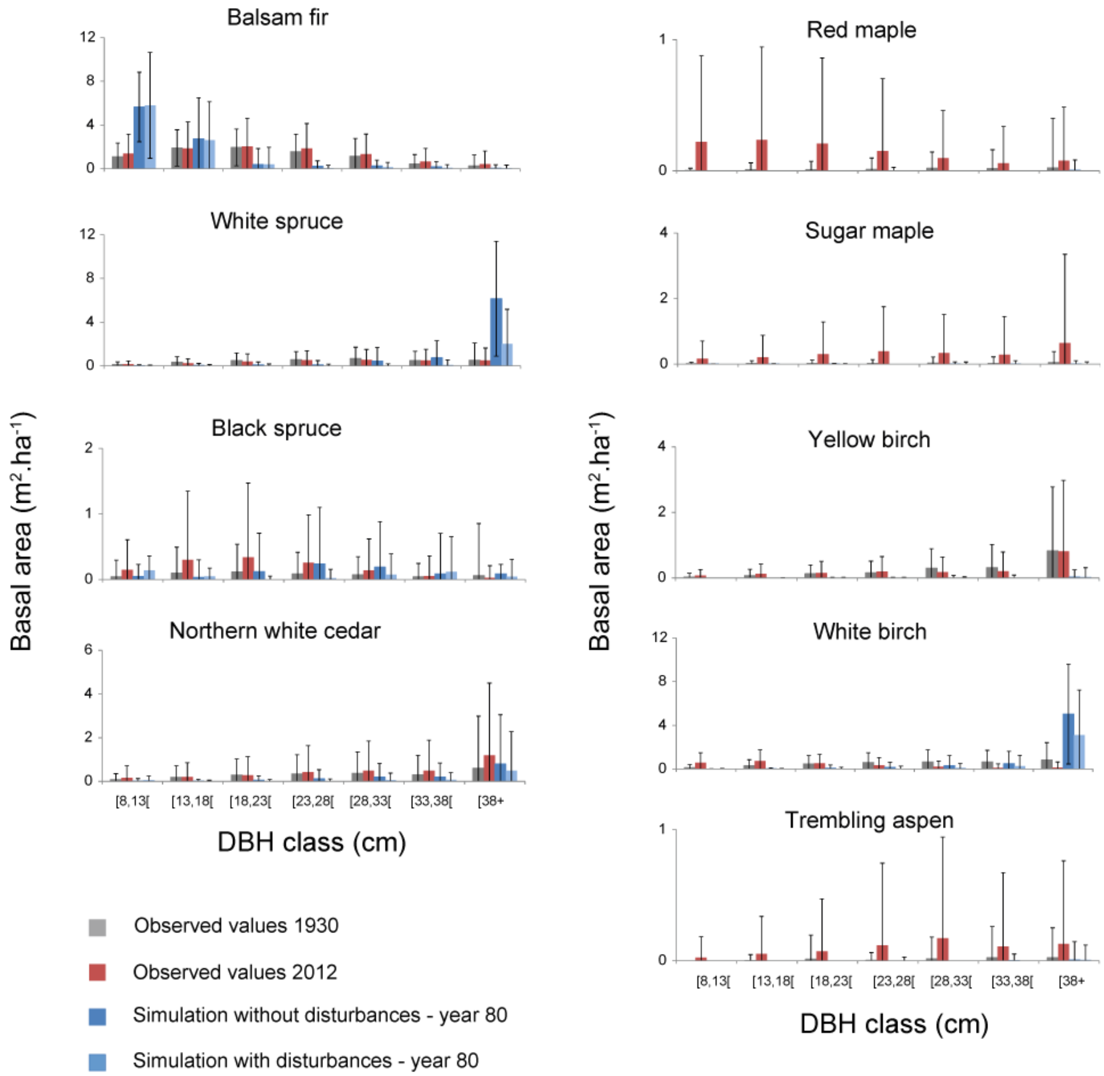


Figure 3-6. DBH structure per species for observed values (1930 and 2012) and simulated values at year 80 for simulations without and with disturbances. Bars represent standard deviation. N = 457.

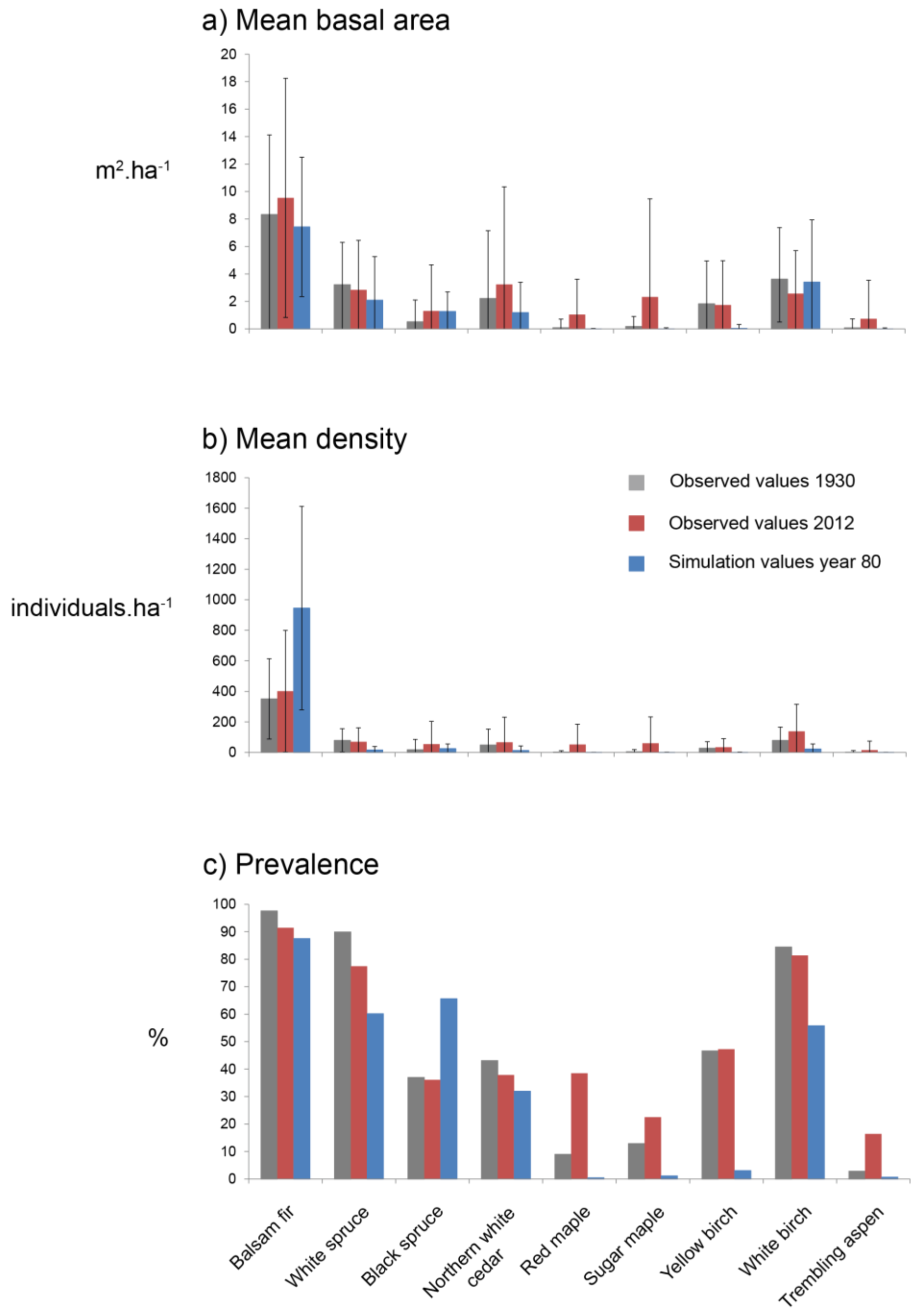


Figure 3-7. Mean basal area (m2.ha-1), mean density (individuals.ha-1) and prevalence (%) per species for observed values in 1930, 2012 and simulated values at year 80. Bars represent standard deviation. N = 457.

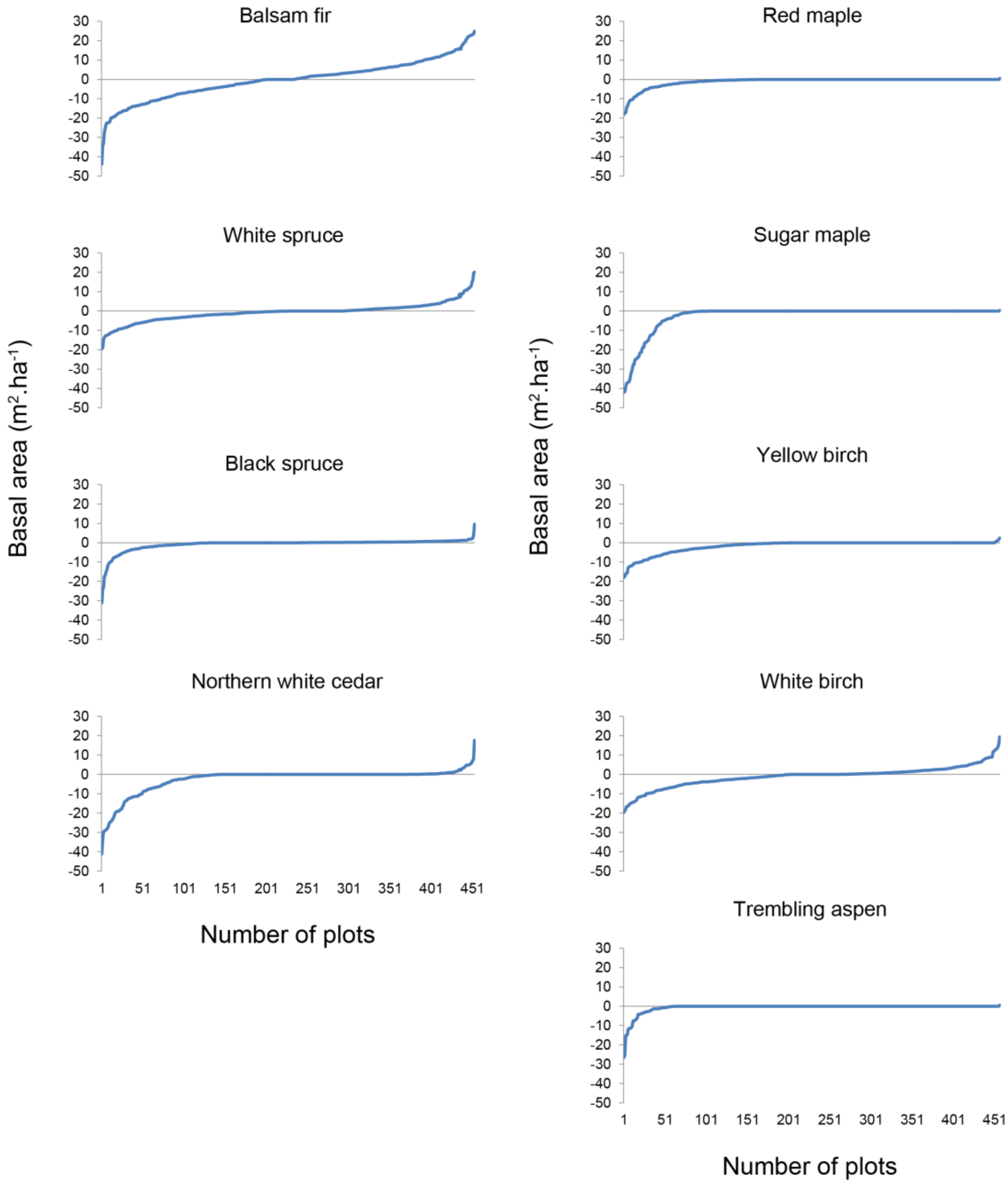


Figure 3-8. Comparaison between observed and simulated basal area values per species for each sampling plot. N = 457.

3.11. Appendix

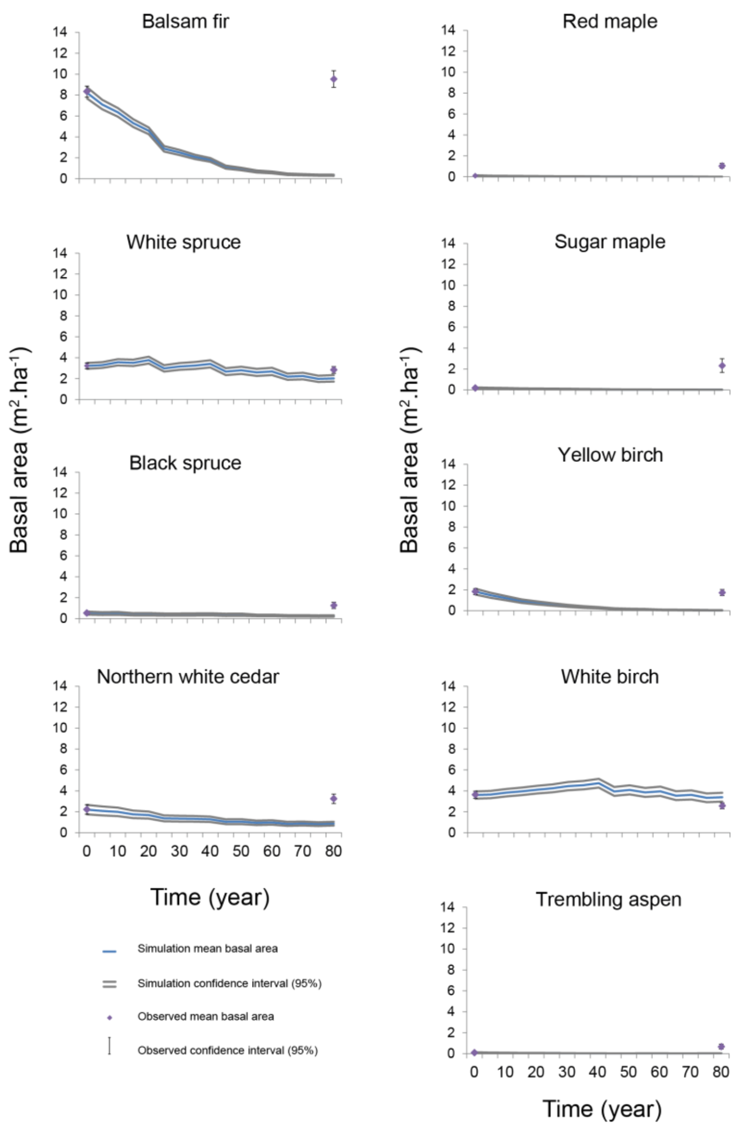


Figure 3-S1. Mean simulated and observed basal area (m2.ha-1) for species using regeneration density and stocking values of table 3-1 and disturbance history for each sampling plot. Density of 1000 individuals per m2 and stocking of 100% were modified for Sugar maple, Red maple, Yellow birch and Trembling aspen to examine the effect of regeneration values on the performance of the model for these species. N = 457.

CONCLUSION GÉNÉRALE

Les archives de la compagnie Price Brothers constituent une source de données exceptionnelle, comparée aux autres sources de données qui permettent la reconstitution de la forêt préindustrielle. Dans l'est de l'Amérique du Nord, la majorité des archives utilisées sont basées sur les travaux d'arpentages primitifs (Bourdo 1956, Clarke et Finnegan 1984, White et Mladenoff 1994, Whitney 1994, Jackson et al. 2000a, Scull et Richardson 2007, Aubé 2008, Pinto et al. 2008, Dupuis et al. 2011, Fortin 2018), qui contiennent des données moins précises que les archives de la compagnie Price Brothers. Ces dernières permettent le calcul de valeurs comme la surface terrière, la densité, et la structure diamétrale des tiges par taxon, d'une manière directement comparable avec les données issues d'échantillonnages modernes comme celles des placettes temporaires et permanentes du gouvernement du Québec réalisées à partir des années 1970s. De plus, la compagnie Price Brothers a produit des cartes d'opérations sylvicoles dans ces concessions de la région du Bas Saint Laurent. Ces cartes nous ont permis de reconstituer une histoire spatialement explicite des coupes et des feux tout au long du 20ème siècle. Les données sur les perturbations et la végétation historique ont permis des analyses quantitatives détaillées et sont à la base des avancées de cette thèse.

Les forêts tempérées nordiques sont connues pour avoir une matrice forestière parfois composée des peuplements de petites tailles, de l'ordre de quelques hectares seulement. Les deux premiers chapitres de cette thèse ont comparé la végétation pré et post industrielle en utilisant deux échelles spatiales différentes. Dans le premier chapitre, une analyse utilisant une grille avec des cellules de 9 km^2 a été effectué. Le deuxième chapitre utilise un jeu de données composé de 743 placettes mesurées dans les années 1930’ par la compagnie Price, puis re-échantillonnées pendant les étés 2012 et 2013. Une analyse comparative (Figure 4-1), montre que l’utilisation des deux échelles spatiales donnent les mêmes tendances entre les époques pour les taxons étudiés en termes de surface terrière, de densité et de fréquence d’occurrence. Cependant les proportions (en pourcentages) sont différentes entre les deux jeux de données. L’augmentation en densité et l’expansion spatiale des érables et peupliers sont plus importants quand on effectue l’analyse au niveau des placettes. De même, les matrices de transition des peuplements forestiers pré- vs post-industrielle montrent que la méthode des grilles sous-estime l’abondance des peuplements dominés par les espèces à feuillage décidu et les peuplements en régénération, car ils sont plus petits en taille que les cellules de la grille.

Nos résultats ont apporté des nouvelles informations sur les caractéristiques du régime des perturbations anthropiques du 20ème siècle dans la forêt tempérée nordique (période de rotation et superficie) ainsi que leurs patrons spatio-temporels durant le 20ème siècle. Les coupes forestières ont touché une superficie qui correspond à 144% de l’aire d’étude, montrant ainsi l’omniprésence de cette perturbation sur le territoire, tandis que 19% de l’aire d’étude a été brûlé et 18% a été transformé en plantations. La progression géographique des perturbations anthropiques dans le paysage durant le 20ème siècle a reflété le contexte socio-économique. Les coupes forestières se sont déplacé des bords des cours d’eaux principaux vers l’intérieur des terres, ce qui reflète la transition du transport du bois, initialement par flottage sur les rivières, vers les routes forestières dans la seconde moitié de 20ème siècle. La période de rotation des coupes s’est raccourcie entre le début et la fin du 20ème siècle, en raison de l'augmentation de la capacité industrielle régionale. La plupart des feux ont été localisés en basse altitude, proche des terres privées, suggérant une origine anthropique. Plusieurs auteurs ont mentionné l’importance des feux dans la structuration de la composition des espèces dans le paysage (Bergeron et al. 2002, Boucher et al. 2017, Terrail et al. 2019). La période de rotation des feux s’est raccourcie, passant de 1668 ans entre 1895 et 1925 à 200 ans pendant le pic d'établissement humain (1925-1955), pour ensuite augmenter à 2925 années après l'application des mesures de suppression des feux. Notons que la période de rotation des feux de 1668 ans, avant le pic d'établissement dans la région, est comparable au cycle naturel des feux dans d'autres parties de la forêt tempérée nordique (Siccama 1971, Lorimer 1977, Foster et al. 1998, Schauffler et Jacobson 2002). La tendance de raccourcissement du cycle de feux à cause des activités humaines a été observé ailleurs dans les forêts tempérées nordique (Cwynar 1977, Wein et Moore 1977, Bowman et al. 2011, Dupuis et al. 2011).

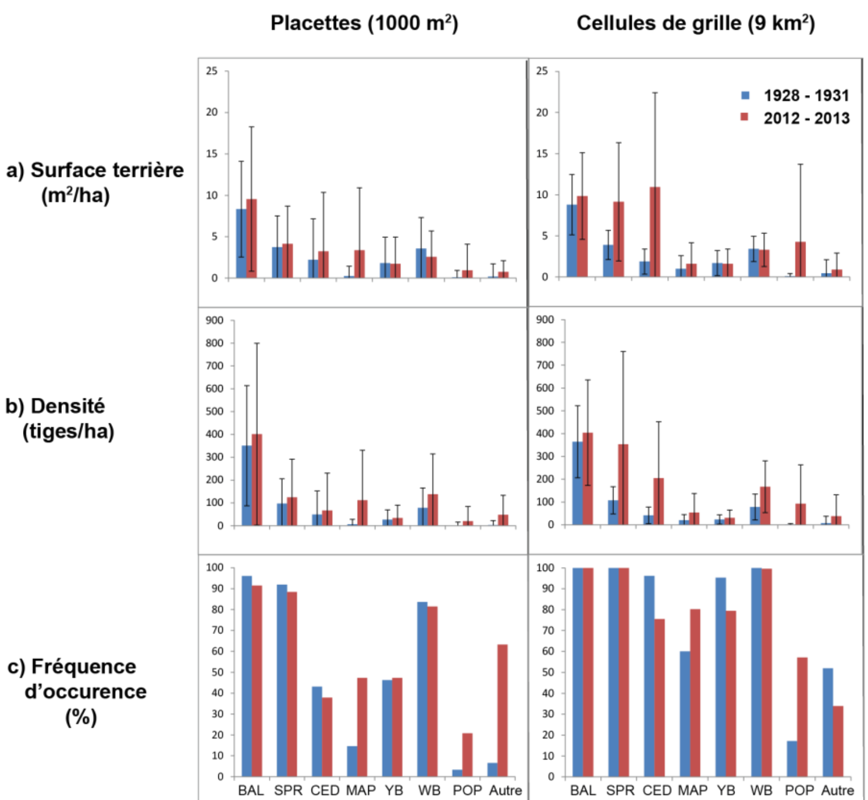
Cette étude a également permis de consolider nos connaissances sur la composition forestière pré et postindustrielle et sur les facteurs responsables de la distribution des taxons dans le paysage. Nous avons observé un changement de la composition forestière entre 1930 et 2012, notamment l'augmentation des espèces à feuillage décidus comme les érables et les peupliers. Ces changements ont déjà été observés dans la région du Bas Saint Laurent à l'aide des archives d'arpentages primitifs (Dupuis et al. 2011, Terrail 2013), ainsi qu'à travers les analyses des cartes des peuplements forestiers (Boucher 2007). La même tendance a également été observée dans les autres régions de la forêt tempérée nordique de l'est de l'Amérique du Nord (Oosting et Reed 1944, Fuller et al. 1998, Cogbill et al. 2002, Friedman et Reich 2005, Pinto et al. 2008, Thompson et al. 2013, Nowacki et Abrams 2015, Danneyrolles et al. 2016, Boucher et al. 2017). L'environnement physique et le climat ont été déterminants dans la répartition des taxons en 1930 et 2012. L'effet des perturbations anthropiques a augmenté de 1.8% en 1930 à 5.1% en 2012, à cause de l'augmentation de la fréquence et de la superficie touchée par ces perturbations. Il y a un grand nombre d'études qui ont suggéré que les perturbations anthropiques sont les principaux facteurs responsables du changement de la végétation dans la forêt tempérée nordique (Duchesne et Ouimet 2008, Gimmi et al. 2010, Nowacki et Abrams 2015, Fortin 2018, Danneyrolles et al. 2019). Cependant, dans notre étude, cet effet reste le moins important sur la végétation actuelle comparé aux autres facteurs climatiques et environnementaux. Ce résultat permet de préciser la contribution respective des différents facteurs responsables de la distribution actuelle des taxons d'arbres.

Notre analyse a donc permis de déterminer la réponse individuelle des différents taxons aux changements selon leurs caractéristiques autoécologiques. Certains taxons comme le sapin baumier, les épinettes, et le thuya sont restés stables ou ont légèrement augmenté durant le 20ème siècle. Leur distribution dans le paysage semble plus déterminée par les conditions environnementales. Le sapin baumier est une espèce capable de se régénérer dans une grande variété de substrats et de conditions de lumière. De plus, dans le sud–est du Canada, il est situé au milieu de son aire de répartition avec un taux de croissance optimal (Burns et Honkala 1990). Les répartitions géographiques de l'épinette noire et de l'épinette blanche ont été largement déterminées par les conditions topographiques et édaphiques. L'épinette blanche a été plus fréquente dans des sites en haute altitude qui sont mieux drainés et associé à un niveau de précipitation plus important que dans les basses terres. L'épinette noire, ainsi que le thuya occidental, ont été principalement localisés dans des sites de basse altitude où règne un mauvais drainage. Le thuya occidental a légèrement augmenté en surface terrière et en densité, mais est présent dans moins de sites qu'en 1930. Cette densification de thuya dans les sites humides va à l'encontre des résultats d'autres études réalisées dans la région qui ont documenté une diminution de cette espèce (Dupuis et al. 2011, Terrail 2013, Danneyrolles et al. 2017). Ces études ont utilisé les archives de l'arpentage primitif réalisé dans des zones qui se trouvent dans les terres privées, tandis que plus que 70% de notre aire d'étude se trouve présentement dans la forêt publique. Les différentes méthodes et pression d'aménagement entre les terres privées et les forêts publiques peuvent être à l'origine de ces résultats contrastés. Des taxons comme les peupliers et bouleau jaune ont été largement associés aux perturbations anthropiques du 20ème siècle sans évidence d'influence climatique. L'augmentation des peupliers a été fortement associée aux évènements des feux comme c'est le cas ailleurs dans la forêt tempérée nordique (Bergeron 2000, Boucher et al. 2017, Terrail et al. 2019). Le bouleau jaune connu pour son taux de régénération élevé dans les trouées (Palik et Pregitzer 1992, Abrams 1998) a été associé aux coupes partielles. Finalement, l'augmentation des érables a été associée à une combinaison des conditions climatiques et des coupes partielles. Les érables étaient largement distribués en 1930 dans les zones de basses collines avec une somme thermique élevée et ont augmenté en densité et en surface terrière à partir de ces zones initiales où ils étaient abondants en 2012. On a également observé une expansion de ces taxons dans le paysage de la forêt moderne avec une présence dans 47% des placettes en 2012 comparé à 15% des placettes en 1930.

Finalement, la base de données historiques de végétation et des perturbations a été utilisée afin de tester la performance d'un modèle de succession par trouée (ZELIG-CFS). Nos résultats ont montré que la prise en compte des perturbations anthropiques dans les simulations permet de faire de meilleures prédictions avec ZELIG-CFS pour des espèces qui n'ont pas montré beaucoup de changement dans leur surface terrière et leur fréquence entre les époques comme le sapin baumier, l'épinette blanche, et le bouleau blanc. Par contre, les érables et les peupliers, des taxons qui ont observé une augmentation et une expansion depuis l'époque préindustrielle, ont été systématiquement sous-estimés par le modèle. La sensibilité des érables aux changements climatiques, l'association des peupliers aux feux et la capacité de reproduction végétative des érables et peupliers ont été identifiés comme des raisons responsables de cette sous-estimation et ont permis des propositions d'améliorations du modèle.

L'impact des changements climatiques et des perturbations anthropiques continuera à affecter la végétation des forêts tempérées nordiques dans le futur. Certains auteurs s'attendent à ce que l'effet du climat surpasse celui des perturbations anthropiques dans les prochains décennies (Steenberg et al. 2013, Duveneck et al. 2014, Boulanger et al. 2019) et que les perturbations anthropiques, comme les coupes forestières, accélèreront ce changement à travers le recrutement et la croissance des espèces pionnières adaptées à un climat plus chaud comme les érables (Landhäusser et al. 2010, Steenberg et al. 2013).

Cette thèse apporte une meilleure compréhension des patrons de répartition et les raisons du changement de végétation dans la forêt tempérée nordique au cours du 20ème siècle, ce qui permet une meilleure prise de décision concernant les stratégies d'aménagement écosystémique. Des pratiques d'aménagement écosystémique qui tendent à imiter le régime des perturbations naturelles par les coupes partielles pourraient éventuellement ralentir l'enfeuillement de la forêt mixte. Par contre, plus d'études sont nécessaires pour determiner l'impact des coupes totales sur la composition forestière car notre base de données ne permet pas d'évaluer cet aspect. Des études paleoécologiques qui peuvent s'étendre sur une période de temps plus longue peuvent également ajouter des informations importantes et complémentaires sur la composition forestière et l'histoire des perturbations dans une échelle millinaire. Finalement, le choix de référer à la forêt pré industrielle comme unique cible pour la conception des stratégies d'aménagement écosystémique n'est peut-être pas définitif. D'importantes réflexions sur les mesures d'adaptation au changement de la composition forestière qui va continuer à s'opérer dans le futur (Boulanger et al. 2019) doivent être poursuivies.



d) Matrice de transition

Placettes (1000 m²) — 1928 - 1931 (lignes) / 2012 - 2013 (colonnes)

	F	M_FI	M_FT	C	Régé	%Paysage
F	32	16	42	10	0	4
M_FI	15	18	25	41	1	28
M_FT	28	14	34	20	4	16
C	12	16	13	58	1	50
Régé	11	56	33	0	0	2
% Paysage	16	18	20	45	1	100

Cellules de grille (9 km²) — 1928 - 1931 (lignes) / 2012 - 2013 (colonnes)

	F	M_FI	M_FT	C	Régé	%Paysage
F	0	0	0	0	0	0
M_FI	0	40	12	48	0	31
M_FT	1	41	27	31	0	28
C	1	32	2	65	0	41
Régé	0	0	0	0	0	0
% Paysage	1	37	12	50	0	100

Figure 4-1. Comparaison entre les résultats des deux méthodes d'analyses de végétation (au niveau des placettes et grille) entre les époques pré et post industrielle. a) Surface terrière (m2/ha), b) Densité (tiges/ha), c) Fréquence d'occurrence (%), and d) matrice de transition des types des peuplements forestiers. Les barres représentent l'écart type. BAL : Abies balsamea, SPR : Picea spp., CED : Thuja occidentalis, MAP : Acer spp., YB : Betula alleghaniensis, WB : Betula papyrifera, POP : Populus spp. F : Feuillus, M_FI : mixte avec feuillus intolérants, M_FT : mixte avec feuillus tolérants, C : Conifère.

RÉFÉRENCES BIBLIOGRAPHIQUES

Abrams, M. D. 1998. The red maple paradox: What explains the widespread expansion of red maple in eastern forests? Bioscience 48:355-364.

Abrams, M. D. 2003. Where has all the white oak gone? Bioscience 53:927-939.

Abrams, M. D., D. A. Orwig, et T. E. DeMeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine mixed-oak forest in the southern Appalachians, USA. Journal of Ecology 83:123-133.

Anchukaitis, K. J., R. Wilson, K. R. Briffa, U. Büntgen, E. R. Cook, R. D'Arrigo, N. Davi, J. Esper, D. Frank, B. E. Gunnarson, G. Hegerl, S. Helama, S. Klesse, P. J. Krusic, H. W. Linderholm, V. Myglan, T. J. Osborn, P. Zhang, M. Rydval, L. Schneider, A. Schurer, G. Wiles, et E. Zorita. 2017. Last millennium Northern Hemisphere summer temperatures from tree rings: Part II, spatially resolved reconstructions. Quaternary Science Reviews 163:1-22.

Anderson, N. J., H. Bugmann, J. A. Dearing, et M.-J. Gaillard. 2006. Linking palaeoenvironmental data and models to understand the past and to predict the future. Trends in Ecology & Evolution 21:696-704.

Aubé, M. 2008. The pre-European settlement forest composition of the Miramichi River watershed, New Brunswick, as reconstructed using witness trees from original lans surveys. Canadian Journal of Forest Research 38:1159-1183.

Badeck, F.-W., H. Lischke, H. Bugmann, T. Hickler, K. Hönninger, P. Lasch, M. J. Lexer, F. Mouillot, J. Schaber, et B. Smith. 2001. Tree species composition in european pristine forests: comparison of stand data to model predictions. Climatic Change 51:307-347.

Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, et T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of the National Academy of Sciences 105:4197-4202.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology 81:1500-1516.

Bergeron, Y., M. Flannigan, S. Gauthier, A. Leduc, et P. Lefort. 2004. Past, Current and Future Fire Frequency in the Canadian Boreal Forest: Implications for Sustainable Forest Management. AMBIO: A Journal of the Human Environment 33:356-360.

Bergeron, Y., S. Gauthier, V. Kafka, P. Lefort, et D. Lesieur. 2001. Natural fire frequency for the eastern Canadian boreal forest: Consequences for sustainable forestry. Canadian Journal of Forest Research 31:384-391.

Bergeron, Y., A. Leduc, B. D. Harvey, et S. Gauthier. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fennica 36:81-95.

Bergeron, Y., P. J. H. Richard, C. Carcaillet, S. Gauthier, M. Flannigan, et Y. T. Prairie. 1998. Variability in fire frequency and forest composition in Canada's southeastern boreal forest: A challenge for sustainable forest management. Conservation Ecology (online) 2:Article 6.

Blanchet, P. 2003. Feux de forêt : l'histoire d'une guerre. Trait d'union, Montréal.

Blarquez, O., Talbot, J., Paillard, J., Lapointe-Elmrabti, L., Pelletier, N., et C. Gates St-Pierre. 2018. Late holocene influence of societies on the fire regime in southern Québec temperate forests. Quat. Sci. Rev. 180, 63–74.

Boisvert-Marsh, L., C. Périé, et S. de Blois. 2019. Divergent responses to climate change and disturbance drive recruitment patterns underlying latitudinal shifts of tree species. Journal of Ecology.

Bonan, G. B., et L. Sirois. 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana*. Journal of Vegetation Science 3:495-506.

Botkin, D. B. 1993. Forest dynamics: an ecological model. Oxford University Press, New York.

Botkin, D. B., J. F. Janak, et J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology 60:849-872.

Bouchard, M., D. D. Kneeshaw, et Y. Bergeron. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. Forest Ecology and Management 204:297-313.

Boucher, É., D. Arseneault, et B. Hétu. 2006a. Late Holocene development of a floodplain along a small meandering stream, northern Québec, Canada. Geomorphology 80:267-281.

Boucher, Y. 2007. Impact des coupes du XXe siècle sur la structure et la composition du paysage forestier de l'est du Canada. These. Université du Québec à Rimouski, Rimouski.

Boucher, Y., D. Arseneault, et L. Sirois. 2006b. Influence des coupes forestières industruelles (1900-2000) sur la structure et la composition des paysages de la sapinière à bouleau jaune de l'Est, Québec. Université du Québec à Rimouski.

Boucher, Y., D. Arseneault, et L. Sirois. 2009a. Logging history (1820–2000) of a heavily exploited southern boreal forest landscape: Insights from sunken logs and forestry maps. Forest Ecology and Management 258:1359-1368.

Boucher, Y., D. Arseneault, et L. Sirois. 2009b. La forêt préindustrielle du Bas-Saint-Laurent et sa transformation (1820-2000) : implications pour l'aménagement écosystémique. Le Naturaliste Canadien 133:60-69.

Boucher, Y., I. Auger, J. Noël, P. Grondin, et D. Arseneault. 2017. Fire is a stronger driver of forest composition than logging in the boreal forest of eastern Canada. Journal of Vegetation Science 28:57-68.

Boucher, Y., et P. Grondin. 2012. Impact of logging and natural stand-replacing disturbances on high-elevation boreal landscape dynamics (1950–2005) in eastern Canada. Forest Ecology and Management 263:229-239.

Boulanger, Y., D. Arseneault, Y. Boucher, S. Gauthier, D. Cyr, A. R. Taylor, D. T. Price, et S. Dupuis. 2019. Climate change will affect the ability of forest management to reduce gaps between current and presettlement forest composition in southeastern Canada. Landscape Ecology.

Bourdo, E. A. J. 1956. A review of the general land office survey and of its use in quantitative studies of former forests. Ecology 37:754-768.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. DeFries, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, M. Mack, M. A. Moritz, S. Pyne, C. I. Roos, A. C. Scott, N. S. Sodhi, et T. W. Swetnam. 2011. The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223-2236.

Breckle, S. W. 2002. Walter's vegetation of the earth: the ecological systems of the geo-biosphere. Springer-Verlag, Berlin.

Brisson, J., Y. Bergeron, et A. Bouchard. 1988. Les successions secondaires sur sites mésiques dans le haut Saint-Laurent. Canadian journal of botany 66:1192-1203.

Brisson, J., et A. Bouchard. 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Québec, Canada. Écoscience 10:236-246.

Bugmann, H. 2001. A review of forest gap models. Climatic Change 51:259-305.

Bugmann, H., et P. Martin. 1995. How physics and biology matter in forest gap models. Climatic Change 29:251–257.

Bürgi, M., E. W. B. Russell, et G. Motzkin. 2000. Effects of postsettlement human activities on forest composition in the north-eastern United States: a comparative approach. Journal of Biogeography 27:1123-1138.

Burns, R. M., et B. H. Honkala. 1990. Silvics of North America. U.S. Department of Agriculture, Forest Service, Washington, DC, USA.

Burton, P. J., et S. G. Cumming. 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water, Air, and Soil Pollution 82:401-414.

Butler, B. J., J. H. Hewes, B. J. Dickinson, K. Andrejczyk, S. M. Butler, et M. Markowski-Lindsay. 2016. Family Forest Ownerships of the United States, 2013: Findings from the USDA Forest Service's National Woodland Owner Survey. Journal of Forestry 114:638-647.

Canham, C. D., N. Rogers, et T. Buchholz. 2013. Regional variation in forest harvest regimes in the northeastern United States. Ecological Applications 23:515-522.

Chesson, P., et N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. The American Naturalist 150:519-553.

Clark, J. S., D. M. Bell, M. H. Hersh, et L. Nichols. 2011. Climate change vulnerability of forest biodiversity: climate and competition tracking of demographic rates. Global Change Biology 17:1834-1849.

Clark, J. S., M. Lewis, et L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. The American Naturalist 157:537-554.

Clarke, J., et G. F. Finnegan. 1984. Colonial survey records and the vegetation of Essex County, Ontario. Journal of Historical Geography 10:119-138.

Cogbill, C. V., J. Burk, et G. Motzkin. 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. Journal of Biogeography 29:1279-1304.

Connell, J. H. 1961. The influence on interspecific competition and other factors on the distribution of the Barnacle Chthamalus Stellatus. Ecology 42:710-723.

Crumley, C. 1994. Historical Ecology. The International Encyclopedia of Anthropology, H. Callan, Ed.. doi:10.1002/9781118924396.wbiea1887

Crutzen, P. J., et V. Ramanathan. 2000. The ascent of atmospheric sciences. Science 290:299-304.

Crutzen, P. J., et W. Steffen. 2003. How long have we been in the Anthropocene Era? Climatic Change 61:251-257.

Cwynar, L. C. 1977. The recent fire history of Barron Township, Algonquin Park. Canadian journal of botany 55:1524-1538.

Danneyrolles, V., D. Arseneault, et Y. Bergeron. 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.

Danneyrolles, V., S. Dupuis, D. Arseneault, R. Terrail, M. Leroyer, A. de Römer, G. Fortin, Y. Boucher, et J.-C. Ruel. 2017. Eastern white cedar long-term dynamics in eastern Canada: Implications for restoration in the context of ecosystem-based management. Forest Ecology and Management 400:502-510.

Danneyrolles, V., S. Dupuis, G. Fortin, M. Leroyer, A. de Römer, R. Terrail, M. Vellend, Y. Boucher, J. Laflamme, Y. Bergeron, et D. Arseneault. 2019. Stronger influence of anthropogenic disturbance than climate change on century-scale compositional changes in northern forests. Nature Communications 10:1265.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, et S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783-786.

Dearing, J. A., R. W. Battarbee, R. Dikau, I. Larocque, et F. Oldfield. 2006. Human–environment interactions: learning from the past. Regional Environmental Change 6:1-16.

di Castri, F., A. J. Hansen, et M. M. Holland. 1988. A new look at ecotones: emerging international projects on landscape boundaries. Biology International 17:1-163.

Didion, M., A. D. Kupferschmid, A. Zingg, L. Fahse, et H. Bugmann. 2009. Gaining local accuracy while not losing generality — extending the range of gap model applications. Canadian Journal of Forest Research 39:1092-1107.

Duchesne, L., et R. Ouimet. 2008. Population dynamics of tree species in southern Quebec, Canada: 1970–2005. Forest Ecology and Management 255:3001-3012.

Dupuis, S., D. Arseneault, et L. Sirois. 2011. Change from pre-settlement to present-day forest composition reconstructed from early land survey records in eastern Québec, Canada. Journal of Vegetation Science 22:564-575.

Duveneck, M. J., R. M. Scheller, M. A. White, S. D. Handler, et C. Ravenscroft. 2014. Climate change effects on northern Great Lake (USA) forests: A case for preserving diversity. Ecosphere 5:art23.

Egan, D., et E. Howell. 2001. The historical ecology handbook: a restorationist's guide to reference ecosystems. Island Press, Washington, DC.

Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, et N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19:589-606.

Environment Canada 2019. Canadian Climate Normals and Averages 1981-2010. Available online at: http://climate.weather.gc.ca/climate_normals/index_e.html (accessed January 1, 2019).

Etheridge, D. A., D. A. MacLean, R. G. Wagner, et J. Wilson, S. 2005. Changes in landscape composition and stand structure from 1945–2002 on an industrial forest in New-Brunswick, Canada. Canadian Journal of Forest Research 35:1965-1977.

Fahey, T. J., et W. A. Reiners. 1981. Fire in the forests of Maine and New Hampshire. Bulletin of the Torrey Botanical Club 108:362-373.

Fischlin, A., H. Bugmann, et D. Gyalistras. 1995. Sensitivity of a forest ecosystem model to climate parametrization schemes. Environmental Pollution 87:267-282.

Fisichelli, N., L. Frelich, et P. Reich. 2013. Climate and interrelated tree regeneration drivers in mixed temperate–boreal forests. Landscape Ecology 28:149-159.

Fisichelli, N., L. E. Frelich, et P. B. Reich. 2012. Sapling growth responses to warmer temperatures 'cooled' by browse pressure. Global Change Biology 18:3455-3463.

Fisichelli, N. A., L. E. Frelich, et P. B. Reich. 2014. Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. Ecography 37:152-161.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, et P. K. Snyder. 2005. Global consequences of land use. Science 309:570-574.

Fortin, G. 2018. Transformation de la composition de la forêt de la péninsule gaspésienne au cours du XXème siècle. Université du Québec à Montréal.

Fortin, J.-C., A. Lechasseur, Y. Morin, F. Harvey, J. Lemay, et Y. Tremblay. 1993. Histoire du Bas-Saint-Laurent. Page 861. Institut québécois de recherche sur la culture, Éd. Québec, Québec.

Foster, D. R., S. Clayden, D. A. Orwig, B. Hall, et S. Barry. 2002. Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA. Journal of Biogeography 29:1359-1379.

Foster, D. R., G. Motzkin, et B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. Ecosystems 1:96-119.

Fraver, S., A. S. White, et R. S. Seymour. 2009. Natural disturbance in an old-growth landscape of northern Maine, USA. Journal of Ecology 97:289-298.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, New York.

Frelich, L. E., et C. G. Lorimer. 1991. Natural disturbance regimes in hemlock-hardwood forests of the Upper Great Lakes Region. Ecological Monographs 61:145-164.

Frelich, L. E., et P. B. Reich. 2009a. Wilderness conservation in an era of global warming and invasive species: a case study from Minnesota's Boundary Waters Canoe Area Wilderness. Natural Areas Journal 29:385-393.

Frelich, L. E., et P. B. Reich. 2009b. Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America? Frontiers in Ecology and the Environment 8:371-378.

Frey, J. K. 1992. Response of a mammalian faunal element to climatic changes. Journal of Mammalogy 73:43-50.

Friedman, S. K., et P. B. Reich. 2005. Regional legacies of logging: departure from presettlement forest conditions in northern Minnesota. Ecological Applications 15:726-744.

Fuller, J. L., D. R. Foster, J. S. McLachlan, et N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1:76-95.

Gennaretti, F., D. Huard, M. Naulier, M. Savard, C. Bégin, D. Arseneault, et J. Guiot. 2017. Bayesian multiproxy temperature reconstruction with black spruce ring widths and stable isotopes from the northern Quebec taiga. Climate Dynamics 49:4107-4119.

Gerwing, J. J. 2002. Degradation of forests through logging and fire in the eastern Brazilian Amazon. Forest Ecology and Management 157:131-141.

Gimmi, U., et H. Bugmann. 2013. Preface: integrating historical ecology and ecological modeling. Landscape Ecology 28:785-787.

Gimmi, U., T. Wohlgemuth, A. Rigling, C. W. Hoffmann, et M. Bürgi. 2010. Land-use and climate change effects in forest compositional trajectories in a dry Central-Alpine valley. Annals of Forest Science 67:701-701.

Goldblum, D., et L. S. Rigg. 2005. Tree growth response to climate change at the deciduous–boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research 35:2709-2718.

Goldblum, D., et L. S. Rigg. 2010. The deciduous forest – boreal forest ecotone. Geography Compass 4:701-717.

Guay, J. É. 1942. Inventaire des ressources naturelles du comté municipal de Rimouski, section forestière. Ministère de l' Industrie et du Commerce et Ministère des Terres et Forêts, de la Chasse et de la Pêche du Québec, Québec.

Gullison, J. J., et C. P. A. Bourque. 2001. Spatial prediction of tree and shrub succession in a small watershed in Northern Cape Breton Island, Nova Scotia, Canada. Ecological Modelling 137:181-199.

Guyette, R. P., R.-M. Muzika, et D. C. Dey. 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5:472-486.

Hall, B., G. Motzkin, D. R. Foster, M. Syfer, et J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography 29:1319-1335.

Harvey, B. D., A. Leduc, S. Gauthier, et Y. Bergeron. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. Forest Ecology and Management 155:369-385.

He, H. S., Z. Hao, D. R. Larsen, L. Dai, Y. Hu, et Y. Chang. 2002. A simulation study of landscape scale forest succession in northeastern China. Ecological Modelling 156:153-166.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. Van der Linden, X. Dai, K. Maskell, et C. A. Johnson. 2001. Climat Change: The scientific basis, contribution of working group I to the third assessment report of the intergovernmental panel on climate change. Cambridge University Press.

Houghton, R. A. 1994. The worldwide extend of land-use change. Bioscience 44:305-313.

IPCC. 2013. Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Iverson, L. R., et A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465-485.

Jackson, S. M., F. Pinto, J. R. Malcolm, et E. R. Wilson. 2000a. A comparison of pre-European settlement (1857) and current (1981-1995) forest composition in central Ontario. Canadian Journal of Forest Research 30:605-612.

Jackson, S. T., R. S. Webb, K. H. Anderson, J. T. Overpeck, T. Webb Iii, J. W. Williams, et B. C. S. Hansen. 2000b. Vegetation and environment in Eastern North America during the Last Glacial Maximum. Quaternary Science Reviews 19:489-508.

Kellomäki, S., H. Peltola, T. Nuutinen, K. T. Korhonen, et H. Strandman. 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Philosophical Transactions of the Royal Society B: Biological Sciences 363:2339-2349.

Krankina, O. N., R. A. Houghton, M. E. Harmon, E. Hogg, D. Butman, M. Yatskov, M. Huso, R. F. Treyfeld, V. N. Razuvaev, et G. Spycher. 2005. Effects of climate, disturbance, et species on forest biomass across Russia. Canadian Journal of Forest Research 35:2281-2293.

Kullman, L., et L. KjÄLlgren. 2006. Holocene pine tree-line evolution in the Swedish Scandes: Recent tree-line rise and climate change in a long-term perspective. Boreas 35:159-168.

Landhäusser, S. M., D. Deshaies, et V. J. Lieffers. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. Journal of Biogeography 37:68-76.

Landres, P. B., P. Morgan, et F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9.

Landsberg, J. 2003. Modelling forest ecosystems: state of the art, challenges, and future directions. Canadian Journal of Forest Research 33:385-397.

Larocque, G. R. 2016. Ecological forest management handbook. CRC Press.

Larocque, G. R., L. Archambault, et C. Delisle. 2006. Modelling forest succession in two southeastern Canadian mixedwood ecosystem types using the ZELIG model. Ecological Modelling 199:350-362.

Larocque, G. R., L. Archambault, et C. Delisle. 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. Ecological Modelling 222:2570-2583.

Leahy, M. J., et K. S. Pregitzer. 2003. A comparison of presettlement and present-day forest in northeastern lower Michigan. American Midland Naturalist 149:71-89.

Lévesque, F. 1997. Conséquences de la dynamique de la mosaïque forestière sur l'intégrité écologique du Parc National Forillon. Université Laval, Québec.

Lindenmayer, D. B., et J. F. Franklin. 2002. Conserving forest biodiversity. Island Press, Washington, DC.

Lindner, M., R. Sievanen, et H. Pretzsch. 1997. Improving the simulation of stand structure in a forest gap model. Forest Ecology and Management 95:183-195.

Little, E. L. 1971. Atlas of United States trees - Conifers and important hardwoods. U. S. Department of Agriculture Miscellaneous Publication

Loehle, C., et D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90:1-31.

Lorimer, C. G. 1977. The presettlement forest and natural disturbance cycle of Northeastern Maine. Ecology 58:139-148.

Lorimer, C. G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61:1169-1184.

Lorimer, C. G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin 29:425-439.

Lorimer, C. G., et A. S. White. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management 185:41-64.

Makela, A., R. Sievanen, M. Lindner, et P. Lasch. 2000. Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. Tree Physiology 20:347-355.

Malhi, Y., J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, et C. A. Nobre. 2008. Climate change, deforestation, and the fate of the Amazon. Science 319:169-172.

Mann, M. E., R. S. Bradley, et M. K. Hughes. 1999. Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. Geophysical Research Letters 26:759-762.

Miller, C., et D. L. Urban. 1999. Forest pattern, fire, and climatic change in the Sierra Nevada. Ecosystems 2:76-87.

Mladenoff, D. J., M. A. White, J. Pastor, et T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3:294-306.

Mohren, G. M. J., et H. E. Bukhart. 1994. Contrasts between biologically-based process models and management-oriented growth and yield models. Forest Ecology and Management 69:1-5.

MRNFQ. 2008. La forêt, pour construire le Québec de demain.in G. d. Québec, editor., Québec.

Nowacki, G. J., et M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the Eastern United States? Global Change Biology 21:314-334.

Nowacki, G. J., et P. A. Trianosky. 1993. Literature on old-growth forests of eastern North America. Natural Areas Journal 13:87-107.

Oosting, H. J., et J. F. Reed. 1944. Ecological composition of pulpwood forests in northwestern Maine. American Midland Naturalist 31:182-210.

Orwig, D. A., et M. D. Abrams. 1994. Land-use history (1720-1992), composition, and dynamics of oak-pine forests within the Piedmont and Coastal Plain of northern Virginia. Canadian Journal of Forest Research 24:1216-1225.

Orwig, D. A., et M. D. Abrams. 1999. Impacts of early selective logging on the dendroecology of an old-growth, bottomland hemlock-white pine-northern hardwood forest on the Allegheny Plateau. Journal of the Torrey Botanical Society 126:234-244.

Pabst, R. J., M. N. Goslin, S. L. Garman, et T. A. Spies. 2008. Calibrating and testing a gap model for simulating forest management in the Oregon Coast Range. Forest Ecology and Management 256:958-972.

Pacala, S. W., C. D. Canham, et J. A. Silander Jr. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Canadian Journal of Forest Research 23:1980-1988.

Palik, B. J., et K. S. Pregitzer. 1992. A comparison of presettlement and present-day forests on two Bigtooth aspen-dominated landscape in northern lower Michigan. American Midland Naturalist 127:327-338.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. Townsend Peterson, et R. Sagarin. 2005. Empirical perspectives on species borders: from traditional biogeography to global change. Oikos 108:58-75.

Parmesan, C., et G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Pastor, J., et D. J. Mladenoff. 1992. The southern boreal-northern hardwood forest border. Pages 216-240 in R. L. H. H. Shugart, and G. B. Bonan, editors, editor. A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.

Payette, S., L. Filion, et A. Delwaide. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns: the Tantaré ecological reserve, Quebec. Canadian Journal of Forest Research 20:1228-1241.

Peng, C., J. Liu, Q. Dang, M. J. Apps, et H. Jiang. 2002. TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. Ecological Modelling 153:109-130.

Peng, C., X. Wen, G. Shao, et K. Reynolds. 2006. Forest simulation models: Computer Applications in Sustainable Forest Management. Pages 101-125. Springer Netherlands.

Phillips, O. L., L. E. O. C. Aragão, S. L. Lewis, J. B. Fisher, J. Lloyd, G. López-González, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Bánki, L. Blanc, D. Bonal, P. Brando, J. Chave, Á. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jiménez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patiño, M. C. Peñuela, A. Prieto, F. Ramírez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. t. Steege, J. Stropp, R. Vásquez, P. Zelazowski, E. A. Dávila, S. Andelman, A. Andrade, K.-J. Chao, T. Erwin, A. Di Fiore, E. H. C., H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramírez-Angulo, A. Rudas, R. Salamão, N. Silva, J. Terborgh, et A. Torres-Lezama. 2009. Drought sensitivity of the Amazon rainforest. Science 323:1344-1347.

Pinto, F. P., S. R. Romaniuk, et M. F. Ferguson. 2008. Changes to preindustrial forest tree composition in central and northeastern Ontario, Canada. Canadian Journal of Forest Research 38:1842-1854.

Plieninger, T., H. Draux, N. Fagerholm, C. Bieling, M. Bürgi, T. Kizos, T. Kuemmerle, J. Primdahl, et P. H. Verburg. 2016. The driving forces of landscape change in Europe: A systematic review of the evidence. Land Use Policy 57:204-214.

Price Brothers & Company Limited, S. W. D. 1944. Working - plan report for Rimouski establishment. Archives Nationales du Québec - Chicoutimi.

Proulx, L. 1985. Les chantiers forestiers de la Rimouski (1930 - 1940), Techniques traditionnelles et culture matérielle. Université du Québec à Rimouski (UQAR).

Reich, P. B., et J. Oleksyn. 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. Ecology Letters 11:588-597.

Risch, A. C., C. Heiri, et H. Bugmann. 2005. Simulating structural forest patterns with a forest gap model: a model evaluation. Ecological Modelling 181:161-172.

Robitaille, A., et J.-P. Saucier. 1998. Paysage régionaux du Québec méridional, Direction de la gestion des stock forestiers et Direction des relations publiques, Ministère des Ressources naturelles du Québec. Publication du Québec, Québec.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57-60.

Rowe, J. S. 1972. Forest regions of Canada. Information Canada, Canadian Forest Service publication number 1300, Ottawa.

Schauffler, M., et G. L. J. Jacobson. 2002. Persistence of coastal spruce refugia during the Holocene in northern New England, USA, detected by stand-scale pollen stratigraphies. Journal of Ecology 90:235-250.

Scheller, R. M., et D. J. Mladenoff. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Global Change Biology 11:307-321.

Schenk, H. J. 1996. Modeling the effects of temperature on growth and persistence of tree species: A critical review of tree population models. Ecological Modelling 92:1-32.

Scull, P. R., et J. L. Richardson. 2007. A method to use ranked timber observations to perform forest composition reconstruction from land survey data. American Midland Naturalist 158:446-460.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, et C. P. O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change 7:395.

Shugart, H. H., et T. M. Smith. 1996. A review of forest patch models and their application to global change research. Climatic Change 34:131-153.

Siccama, T. G. 1971. Presettlement and present forest vegetation in northern Vermont with special reference to Chittenden county. American Midland Naturalist 85:153-172.

Simard, H., et A. Bouchard. 1996. The precolonial 19th century forest of the Upper St Lawrence Region of Quebec: A record of its exploitation and transformation through notary deeds of wood sales. Canadian Journal of Forest Research 26:1670-1676.

Smith, T. M., et D. L. Urban. 1988. Scale and Resolution of Forest Structural Pattern. Vegetatio 74:143-150.

Song, C., et C. E. Woodcock. 2003. A regional forest ecosystem carbon budget model: impacts of forest age structure and landuse history. Ecological Modelling 164:33-47.

Steenberg, J. N., P. Duinker, et P. Bush. 2013. Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. Annals of Forest Science 70:61-73.

Steffen, W., J. Grinevald, P. Crutzen, et J. McNeill. 2011. The Anthropocene: conceptual and historical perspectives. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 369:842-867.

Steffen, W., R. A. Sanderson, P. D. Tyson, J. Jäger, P. A. Matson, B. Moore, F. Oldfield, K. Richardson, H. J. Schellnhuber, B. L. Turner, et R. J. Wasson. 2004. Global Change and the Earth System - A planet under pressure. Springer-Verlag Berlin Heidelberg.

Swetnam, T. W., C. D. Allen, et J. L. Betancourt. 1999. Applied historical ecology: Using the past to manage for the future. Ecological Applications 9:1189-1206.

Terrail, R. 2013. Influence de la colonisation sur les transformations du paysage forestier depuis l'époque préindustrielle dans l'Est du Québec (Canada). Doctoral thesis. Université du Québec a Rimouski (UQAR).

Terrail R, J. Morin-Rival, G. de Lafontaine, M.J. Fortin and D. Arseneault. 2020. Effects of 20th-century settlement fires on landscape structure and forest composition in Eastern Québec, Canada. Journal of Vegetation Science, https://doi.org/10.1111/jvs.12832

Thompson, J. R., D. N. Carpenter, C. V. Cogbill, et D. R. Foster. 2013. Four centuries of change in Northeastern United States forests. PLoS ONE 8:e72540.

Uhl, C., et J. B. Kauffman. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the Eastern Amazon. Ecology 71:437-449.

Urban, D. L. 1990. A versatile model to simulate forest pattern: A user’s guide to ZELIG version 1.0. University of Virginia, Charlottesville, Virginia.

Urban, D. L. 2000. Using model analysis to design monitoring programs for landscape management and impact assessment. Ecological Applications 10:1820-1832.

Urban, D. L., G. B. Bonan, T. M. Smith, et H. H. Shugart. 1991. Spatial applications of gap models. Forest Ecology and Management 42:95-110.

Urban, D. L., et H. H. Shugart. 1992. Individual-based models of forest succession. Pages 249-292 in R. K. P. D. C. Glenn- Lewin, and T. T. Veblen, editors, editor. Plant succession: theory and prediction. Chapman and Hall, London, UK.

Vayreda, J., J. Martinez-Vilalta, M. Gracia, J. G. Canadell, et J. Retana. 2016. Anthropogenic-driven rapid shifts in tree distribution lead to increased dominance of broadleaf species. Global Change Biology 22:3984-3995.

Vitousek, P. M. 1994. Beyond global warming: Ecology and global change. Ecology 75:1861-1876.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, et F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Wein, R. W., et J. M. Moore. 1977. Fire history and rotations in the New Brunswick Acadian Forest. Canadian Journal of Forest Research 7:285-294.

Wein, R. W., et J. M. Moore. 1979. Fire history and recent fire rotation periods in the Nova Scotia Acadian Forest. Canadian Journal of Forest Research 9:166-178.

White, M. A., et D. J. Mladenoff. 1994. Old-growth forest landscape transition from pre-European settlement to present. Landscape Ecology 9:191-205.

Whitney, G. G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America, 1500 to the present. Cambridge University Press, Cambridge.

Whitney, G. G., et J. P. DeCant. 2003. Physical and historical determinants of the pre- and post-settlement forests of northwestern Pennsylvania. Canadian Journal of Forest Research 33:1683-1697.

Woodward, F. I. 1987. Climate and Plant Distribution. Cambridge University Press.

Yaussy, D. A. 2000. Comparison of an empirical forest growth and yield simulator and a forest gap simulator using actual 30-year growth from two even-aged forests in Kentucky. Forest Ecology and Management 126:385-398.