UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

MODÉLISATION DE L'EFFET DE LA STRUCTURE SPATIALE À L'INTÉRIEUR DU PEUPLEMENT SUR LA SUCCESSION DE FORÊTS BORÉALES MIXTES

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN ÉCOLOGIE

PAR
ANIMESH GHOSE

NOVEMBRE 2021

UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

MODELLING THE EFFECT OF WITHIN-STAND SPATIAL STRUCTURE ON
MIXED BOREAL FOREST SUCCESSION

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR
THE MASTER IN ECOLOGY

BY
ANIMESH GHOSE

NOVEMBER 2021

ACKNOWLEDGEMENTS

FOREWORD

The thesis is divided into three chapters. First chapter includes the general introduction which puts into context the research problem, the literature review and the objectives. Chapter II is presented in the form of a scientific article with authors "Animesh Ghose, Philippe Marchand, Kobra Maleki and Miguel Montoro Girona". The *Forests* journal of MDPI is kept under consideration for the submission of this article. I had the main responsibility for analyzing the data and writing the article. My director and research committee members helped design the study, assisted in interpretation of the results and critically and constructively revised the content of the article. Third chapter contains the general conclusion and implications in forest management.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

RÉSUMÉ

La configuration spatiale des arbres individuels peut affecter leur croissance et leur survie à une échelle fine et modifier la composition et la structure de la forêt à l'échelle du paysage. Ainsi, la compréhension de la dynamique spatiale des peuplements est cruciale pour la gestion forestière. L'utilisation de SORTIE-ND, un simulateur forestier spatialement explicite et individu-centré, permet de prédire la croissance, la mortalité et le recrutement d'arbres individuels à l'échelle du peuplement en recréant la dynamique des trouées. Notre recherche vise à déterminer les changements dans la structure spatiale des peuplements forestiers à l'aide de SORTIE-ND et à évaluer la précision du modèle en comparant la structure spatiale des peuplements simulés et observés. Les simulations seront effectuées et validées avec deux ensembles de données empiriques provenant de peuplements situés dans la forêt boréale mixte de l'est du Canada. Ces peuplements se sont formés après huit feux de forêt depuis 1760 et représentent une chronoséquence de 249 ans de succession forestière, qui serviront de données d'entrée et de validation pour les modèles. Nous avons calculé une fonction L homogène de la structure spatiale pour chaque peuplement simulé (avec des conditions initiales basées sur des données empiriques de peuplements plus jeunes), et comparé avec la fonction L non homogène des données observées pour vérifier si le modèle SORTIE-ND est capable de produire une structure spatiale similaire à celle observée. Pour les trois espèces les plus communes (*Abies balsamea, Populus tremuloides* et *Picea glauca*) dans les peuplements observés, SORTIE-ND a pu reproduire les patrons spatiaux observés pour les espèces individuelles et les paires d'espèces. Cependant, l'étude ne portait pas sur toutes les espèces des forêts boréales mixtes et des recherches futures sur la performance du modèle pour d'autres espèces devraient être réalisées.

Mot clés : simulation; la modélisation; chronoséquence; perturbation; structure spatiale; échelle fine

CHAPTER 1

GENERAL INTRODUCTION

1.1 Disturbances in the boreal mixedwood forest

MacDonald (1995) defined the boreal mixedwood forest as "an area with climatic, topographic, and edaphic conditions that favour the production of closed canopy stands dominated by trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera* Marsh.) in early successional stages, black spruce (*Picea mariana* [Mill.] B.S.P.) and white spruce (*Picea glauca*) in mid-successional stages, and balsam fir (*Abies balsamea*) in late successional stages."

Major disturbances such as fires, windstorms, ice storms, beavers, snow breakages, insects, and diseases shape the boreal mixedwood forest and the coexistence of the species (Chen & Popadiouk, 2002; Labrecque-Foy et al., 2020). Tree species of the boreal mixedwoods have different survival strategies to reoccupy the disturbed area, including dormant seedbeds, light seeds, serotinous cones, clonal stems and shade tolerance in regeneration dynamics (Chen & Popadiouk, 2002; Greene et al., 1999; Weir & Johnson, 1998).

Under climate change scenarios, natural disturbances are expected to be more frequent and severe (Navarro et al., 2018), increasing the need for research to improve our understanding on fire, insects and windthrow in the boreal forests of North America (Boulanger et al., 2017; Brandt et al., 2013). An increase in temperature due to climate change will change the vegetation dynamics of the boreal biome and can facilitate disturbances like insect outbreaks, fire and drought (Pureswaran et al., 2015; Seidl et

al., 2017). These disturbance agents often help the forest renew itself and create a dynamic mix of different age stands across the landscape (Brandt et al., 2013). However, the frequency of the disturbance, such as fire, has effect on the regeneration failure rate and can adversely affect the stand composition (Splawinski et al., 2019).

1.2 Gap dynamics

Gap dynamics play an important role in forest succession (Krebs, 2019). Canopy openings offer growing condition for shade-intolerant species like trembling aspen, whereas small canopy gaps may increase the abundance of balsam fir (Kneeshaw & Bergeron, 1998; Kneeshaw & Prévost, 2007). The number and size of gaps can be a strong determinant of stand development including sapling density (de Römer et al., 2007). The size of the openings also regulates the abundance and diversity of vegetation within a forest stand (Churchill et al., 2017). It is important to understand the gap dynamics due to the complex composition and structure of the boreal mixedwood forest (Kneeshaw & Prévost, 2007).

1.3 Competition and spatial patterns of trees

Competition is considered as one of the fundamental processes of community ecology, especially in the boreal mixedwood forest (Kneeshaw and Bergeron, 1998; Tilman, 1994). The spatial distribution of trees provides significant information regarding their inter- and intraspecific competition (Gray & He, 2009), as plant communities are structured by the interactions among competing individuals (Harper, 1977). An evenly-distributed pattern of a species in a stand (more spacing and less clustering of individuals) indicates intraspecific competition (Stoll & Bergius, 2005). In general, intra-specific competition is stronger than inter-specific competition and has a greater

impact on the species' growth (Boivin et al., 2010; Coates et al., 2013; Simard et al., 1998)

Moreover, the increasing density of trees accelerates the competition for resources and as a consequence higher density stands experience a higher mortality rate (Gray & He, 2009). In a mixedwood stand, it would be difficult to detect spatial repulsion because of variation in resource requirements for coniferous and deciduous species (Gray & He, 2009).

1.4 Spatial structure of stands and its importance in forest management

The structure of a forest stand includes the size, density, and spatial arrangement of live and dead trees along with other vegetation types, which determines the integrity and stability of a forest (Churchill et al., 2017; Pretzsch, 2009). It plays an important role in the stand dynamics by determining the local environment of each tree and the ecosystem services provided by the forest (Gadow et al., 2012a; Goreaud et al., 1997). Multiple factors (e.g. longevity, shade tolerance and tree size) determine the co-existence of species in a stand, which then determines the stand structure as well (de Römer et al., 2007). On the other hand, natural and anthropogenic disturbances result in a complex and variable spatial structure (Goreaud et al., 1997). Competition with the herbaceous and shrub species may suppress the regeneration of trees and change the dynamics and eventually structure of stands (de Römer et al., 2007; Harvey et al., 2002; Kneeshaw & Bergeron, 1999; Pretzsch, 2009). Besides this, timing of a disturbance is also important, for instance, disturbances occurring during the growing season can be a crucial factor to determine the stand composition (Chen & Popadiouk, 2002; Greene et al., 1999).

That spatial pattern can influence the rate of regeneration as tree spacing can change the amount of diffused light and thus trigger complex vegetation structure within a stand (Canham et al., 2004; Churchill et al., 2017; Lavoie et al., 2019; Sprugel et al.,

2009). As a consequence, the spatial pattern of trees has an influence over the understory development and future stand dynamics (Dovčiak et al., 2001; McKenzie et al., 2000).

As the spatial pattern of trees influences tree establishment, growth, crown development and mortality, a good knowledge of the forest spatial structure is essential for effective forest management (Larson & Churchill, 2012). Besides, the spatial alignment of trees within forest stands interacts with natural disturbances, such as fire and insects, that are considered a fundamental component for the boreal forest productivity (Attiwill, 1994; Carrer et al., 2018; Crump & Scott, 1994; Liu et al., 2019). Information about forest structure can improve our understanding of the functions, past and future development potential of a particular forest ecosystem (Franklin & Wulder, 2002).

1.5 Spatial analysis in forest ecology

Spatial analysis provides a quantitative description of environmental variables across space and time (Illian et al., 2008; Wiegand & Moloney, 2014). The inclusion of spatial structure in ecological analysis and the availability of spatial statistics software and packages are the main factors behind the popularity of spatial analysis (Fortin & Dale, 2005; Legendre & Legendre, 2012). According to Kint et al. (2003), all spatial methods account for the relative position of trees to describe the neighbourhood process that form the stand structure. Spatial statistics for the stand structure can be divided in to two groups: point pattern analysis and surface pattern analysis or geostatistics - The point pattern analysis applies directly to spatial point processes and has therefore often been discussed in the context of forest stands (Chen & Bradshaw, 1999; Illian et al., 2008; Wiegand & Moloney, 2014)(J. Chen & Bradshaw, 1999). The primary focus of point process statistics is to understand the interaction among neighbouring points and underlying processes (Illian et al., 2008).

In the context of a point pattern analysis, complete spatial randomness (CSR) is a theoretical null model where points are independently distributed following constant intensity (Illian et al., 2008; Wiegand & Moloney, 2014). Observed point patterns can be compared with this null hypothesis through the computation of summary statistics. According to Illian et al. (2008), summary statistics quantify the statistical properties of spatial point patterns and provide a brief and concise description of point patterns using numbers, functions or diagrams. Ripley's K function, the pair-correlation function, and the nearest-neighbour distribution function are some of the most common statistics used to summarize spatial point data (Wiegand & Moloney, 2014). These tools allow researchers to determine if the points (e.g. trees) are dispersed, clustered, or randomly distributed throughout the study area and examine how the clustering/dispersion of point features changes at different distances (Dale & Fortin, 2014).

1.6 Simulation and SORTIE-ND: A tool to predict forest dynamics

Simulations allow us to experiment with mathematical representations of real-world systems and provide a helpful tool to generate and analyze spatial and temporal patterns (Gadow et al., 2012). Individual-based models of forest dynamics account for neighbourhood variability as two trees with different local environment will grow differently (Goreaud et al., 1997).

Individual-based models have been used for decades to study the successional change of a stand at fine scale or landscape scale (Krebs, 2019). The use of SORTIE-ND, a spatially explicit individual-based forest simulator, allows predictions of the growth, mortality, and recruitment of individual trees at a stand scale by emulating gap dynamics (Pacala et al., 1996). The model considers the regeneration, growth and death of individual trees across the entire stand and can account for both management interventions and natural disturbance regimes to assess the future dynamics of the stand

(Murphy, 2011). A combination of empirical (e.g. seed dispersal, individual tree growth, mortality) and mechanistic process equations determine how the stand changes between time steps (Pacala et al., 1993). The model receives a parameter file with field data as input, local environmental conditions, and initial stand structure (Murphy, 2011). Each behaviour can be assigned with one or more years of time steps and behaviours can be performed in a pre-defined order to structure the forest dynamics in SORTIE-ND (Murphy, 2011). SORTIE-ND develops an output that is derived from complex interactions between light, growth, seed dispersal, and mortality—all ecological factors that have a high variability between stands.

Recently, SORTIE-ND has been widely used to evaluate the fine scale stand dynamics resulting from different silvicultural treatments or natural disturbances. Bose et al. (2015) used the SORTIE-ND model to demonstrate that stand structure and timber production rates are influenced by partial harvesting and by the spatial configuration of the residual trees. In addition, many studies have investigated the impact of different harvesting techniques and gap dynamics over forest succession or regeneration dynamics using SORTIE-ND (Ameztegui et al., 2012; Beaudet et al., 2011; Brown et al., 2018; Yasuda et al., 2013). SORTIE-ND is also used to address the effect of natural disturbances and their aftermath on the stand-level forest dynamics (Case et al., 2017; Dhar & Hawkins, 2011). Maleki et al. (2019) evaluated post-disturbance successional dynamics of the boreal mixedwood with SORTIE-ND.

Several studies combined climate data with the forest harvest data in the SORTIE-ND model to assess future forest dynamics (Ameztegui et al., 2015, 2017; Cristal et al., 2019; Nitschke et al., 2012). However, whereas Maleki et al. (2019) verified that the SORTIE-ND model reproduced the species composition of stands at different successional stages for the Eastern Canadian boreal mixedwood, the model ability to reproduce the spatial structure of the boreal mixedwood stand has to be verified. Therefore, this study aims to validate the spatial structure of a stand predicted by the SORTIE-ND model, by comparing the spatial structure of stands produced by the

simulated succession processes in SORTIE-ND to the observed structure of stands at similar successional stages.

I hypothesize that the simulated stand spatial structure will represent the observed spatial structure of the stands at different successional stages, since SORTIE-ND is a spatially explicit model that simulates the processes like seed dispersal and competition for light that create that spatial structure.

CHAPTER 2

MODELLING THE EFFECT OF WITHIN-STAND SPATIAL STRUCTURE
ON MIXED BOREAL FOREST SUCCESSION

Abstract

The spatial configuration of individual trees can affect their growth and survival at a fine scale and change the forest composition and structure at the landscape scale. Thus, understanding the stand spatial dynamics is crucial for forest management. The use of SORTIE-ND, a spatially explicit individual-based forest simulator, allows predictions of the growth, mortality, and recruitment of individual trees at a stand scale by emulating gap dynamics. Our research aims to determine the changes in the spatial structure of forest stands using SORTIE-ND and evaluate the model accuracy by comparing the spatial structure of simulated and observed stands. The simulations will be done and validated with two sets of empirical data from stands located in the boreal mixedwoods of eastern Canada. These stands were formed after eight wildfires since 1760 and represent a chronosequence of 249 years of forest succession, which will serve as input and validation data for the models. We calculated the homogeneous L function of spatial structure for each simulated stand (with initial conditions based on empirical data from younger stands), and compared it with the inhomogenous L function of observed data to check whether the SORTIE-ND model can produce a spatial structure similar to that of the observed stands. For the three most common species (*Abies balsamea, Populus tremuloides* and *Picea glauca*) in the observed stands, SORTIE-ND was able to reproduce the same spatial pattern for single species and pairs of species. However, the study did not focus on all the tree species of boreal

mixedwood and future research on the model performance for other species need to be evaluated.

Résumé

La configuration spatiale des arbres individuels peut affecter leur croissance et leur survie à une échelle fine et modifier la composition et la structure de la forêt à l'échelle du paysage. Ainsi, la compréhension de la dynamique spatiale des peuplements est cruciale pour la gestion forestière. L'utilisation de SORTIE-ND, un simulateur forestier spatialement explicite et individu-centré, permet de prédire la croissance, la mortalité et le recrutement d'arbres individuels à l'échelle du peuplement en recréant la dynamique des trouées. Notre recherche vise à déterminer les changements dans la structure spatiale des peuplements forestiers à l'aide de SORTIE-ND et à évaluer la précision du modèle en comparant la structure spatiale des peuplements simulés et observés. Les simulations seront effectuées et validées avec deux ensembles de données empiriques provenant de peuplements situés dans la forêt boréale mixte de l'est du Canada. Ces peuplements se sont formés après huit feux de forêt depuis 1760 et représentent une chronoséquence de 249 ans de succession forestière, qui serviront de données d'entrée et de validation pour les modèles. Nous avons calculé une fonction L homogène de la structure spatiale pour chaque peuplement simulé (avec des conditions initiales basées sur des données empiriques de peuplements plus jeunes), et comparé avec la fonction L non homogène des données observées pour vérifier si le modèle SORTIE-ND est capable de produire une structure spatiale similaire à celle observée. Pour les trois espèces les plus communes (*Abies balsamea, Populus tremuloides* et *Picea glauca*) dans les peuplements observés, SORTIE-ND a pu reproduire les patrons spatiaux observés pour les espèces individuelles et les paires d'espèces. Cependant, l'étude ne portait pas sur toutes les espèces des forêts boréales mixtes et des recherches futures sur la performance du modèle pour d'autres espèces devraient être réalisées.

Mot clés : simulation; la modélisation; chronoséquence; perturbation; structure spatiale; échelle fine

2.1 Introduction

The spatial configuration of individual trees can affect their growth and survival at a fine scale and change the forest composition and structure at the landscape scale (Wiegand & Moloney, 2014). That spatial pattern can influence the rate of regeneration as tree spacing can change the amount of diffused light and thus trigger complex vegetation structure within a stand (Canham et al., 2004; Churchill et al., 2017; Lavoie et al., 2019). Spatial patterns of trees influence tree establishment, growth, crown development and mortality; therefore, understanding forest spatial structure is essential for effective forest management (Larson & Churchill, 2012). In boreal forests, the spatial arrangement of trees within forest stands interacts with natural disturbances, such as fire and insects, that are considered a fundamental determinant of forest productivity (Attiwill, 1994; Carrer et al., 2018; Crump & Scott, 1994; Liu et al., 2019).

Gap dynamics plays an important role on the forest succession (Krebs, 2019). Canopy openings offer growing conditions for shade-intolerant species like trembling aspen (*Populus tremuloides*) and small canopy gaps may increase the abundance of balsam fir (*Abies balsamea*) (Kneeshaw & Bergeron, 1998; Kneeshaw & Prévost, 2007). The number and size of gaps can be a strong determinant of stand development including sapling density (de Römer et al., 2007). The size of the openings also regulates the abundance and diversity of vegetation within a forest stand (Churchill et al., 2017). It is important to understand the gap dynamics due to the complex composition and structure of the boreal mixedwood forest (Kneeshaw & Prévost, 2007).

The use of SORTIE-ND, a spatially explicit individual-based forest simulator, allows predictions of the growth, mortality, and recruitment of individual trees at a stand scale

by emulating gap dynamics (Busing & Mailly, 2004; Pacala et al., 1996). The model considers the regeneration, growth and death of individual trees across the entire stand and can account for both management interventions and natural disturbance regimes to assess the future dynamics of the stand (Murphy, 2011). A combination of empirical (e.g. seed dispersal, individual tree growth, mortality) and mechanistic process determine how the stand changes between time steps (Pacala et al., 1993). Recently, SORTIE-ND has been widely used to evaluate the fine scale stand dynamics along with different silvicultural treatments or natural disturbances. For instance, Bose et al. (2015) used the SORTIE-ND model to demonstrate that under partial harvesting treatments, stand structure and timber production rates are influenced by the spatial configuration of the residual trees. In addition, many studies have investigated the impact of different harvesting techniques and gap dynamics over forest succession or regeneration dynamics using SORTIE-ND (Ameztegui et al., 2012; Brown et al., 2018; Yasuda et al., 2013).

This study will allow us to evaluate if the predictions made by SORTIE-ND accurately reflect the spatial distribution of species on a small scale in a mixed boreal forest. This research aims to validate the spatial structure of a stand predicted by the SORTIE-ND model, by comparing the spatial structure of stands produced by the simulated succession processes in SORTIE-ND to the observed structure of stands at similar successional stages. I hypothesize that the simulated stand spatial structure will be consistent with the observed spatial structure of the stand, since SORTIE-ND is a spatially explicit model that simulates the processes like seed dispersal and competition for light that create that spatial structure.

2.2 Methodology

2.2.1 Study site

The data was collected from the Lake Duparquet Research and Teaching Forest (LDRTF), which is based in north-western Quebec (Canada). The region is part of the balsam fir (*Abies balsamea*) - white birch (*Betula papyrifera*) bioclimatic domain (Saucier et al. 1998). The approximate location of the study site is 79°19' W–79°30' W, 48°86' N–48°32' N and it covers an area of around 8000 ha (Fig. 2.1). The study area harbours a cold continental climate with a mean annual temperature of 1.0 °C and mean annual total precipitation of 985 mm, of which 30 % falls during the growing season. The study area is characterized by a mixed composition of boreal conifers (balsam fir- *Abies balsamea*, white spruce- *Picea glauca* and eastern white cedar- *Thuja occidentalis L.*) and shade-intolerant hardwood species (trembling aspen- *Populus tremuloides* and white birch- *Betula papyrifera*) (Bergeron, 2000). Trembling aspen and white birch dominate the early successional stage, on the other hand, balsam fir and white cedar dominate the late successional stage. Wildfires and insect outbreaks are main natural disturbances of the study area (Bergeron et al., 2001). A major spruce budworm (*Choristoneura fumiferana*) outbreak occurred from 1972 to 1987, before the establishment of the inventory (Bergeron et al., 1995a; Morin & Laprise, 1993).
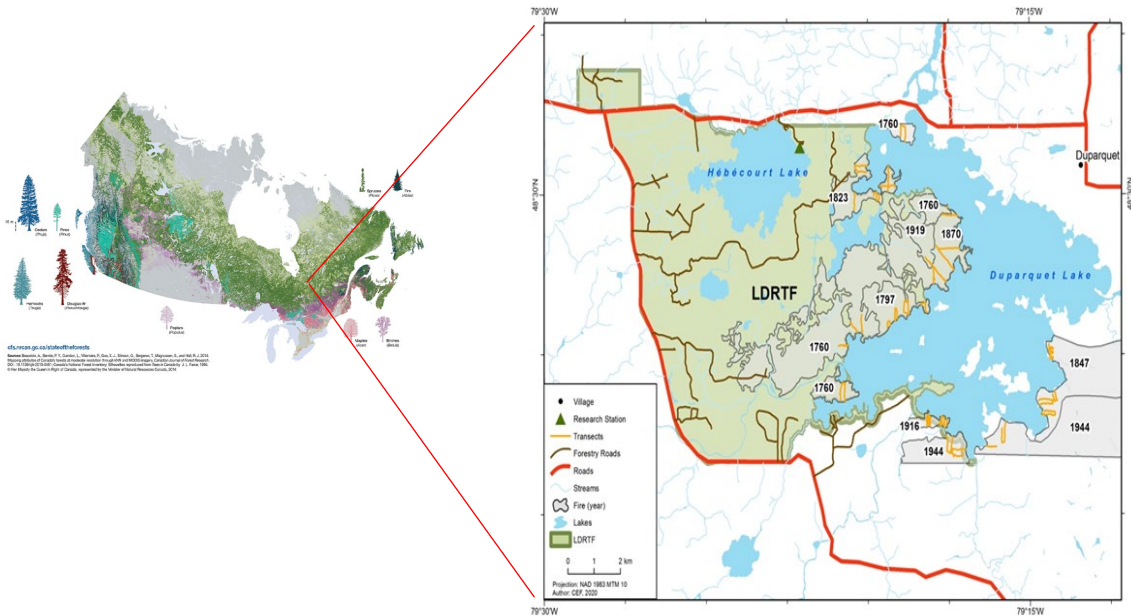
Figure 2.1 Lake Duparquet Research and Teaching Forest station (Maleki et al., 2021)

2.2.2 Sampling protocol

I used data from inventories conducted during 1990-2019 period throughout the LDRTF, particularly two subsets of this data: hectare plot data and transect plot data, entitled as LDRTF-HECTARE and LDRTF-TRANSECT, respectively (Maleki et al., 2021). These plots were established to study the composition and structure of the forest stands using the dendrochronological technique (Bergeron, 2000; Kneeshaw & Bergeron, 1998; Maleki et al., 2021). The 596 transect plots represent different successional stages that regenerated from eight wildfires (1760, 1797, 1823, 1847, 1870, 1916, 1944 and 1964). Plots are located 50 m apart along the transects and each quadratic plot is 256 m^2 (16 m×16 m) in size. In each plot, trees with more than 5 cm diameter at breast height (DBH) were considered for the data set. Their state (alive or dead) and species level identification were documented in the dataset. The quadrats were sampled in 1991 and re-sampled in 2009 and used to develop the SORTIE-ND parameterization file for the LDRTF.

Besides, six one-hectare size permanent plots were established from six fire years (1760, 1823, 1847, 1870, 1916 and 1944), their location selected to be representative of the average stand compositions observed in the transect plots. The compositional changes of all stands were validated by the use of dendrochronological study (Bergeron & Charron, 1994; Bergeron & Dubuc, 1989). All living and dead trees (standing and fallen) with DBH greater than 5 cm were measured and identified to the species level along with their X-Y location within a plot.

2.2.3 SORTIE-ND simulation

I used SORTIE-ND, an individual-based spatially explicit model, to simulate the spatial structure of the stands (Pacala et al., 1996). The model was first launched in 1990s and was improved over time to consider the forest management aspects (Bose et al., 2015). The SORTIE-ND model considers individual trees and their interaction in a spatial and temporal context (Murphy, 2011). Tree attributes, such as size, growth rate, age, morphology, are included (along with their individual location) in the model to characterize an individual tree. The model accounts for biological and environmental processes, such as tree growth, seed dispersal, mortality rate, light intensity to run the simulation (Bose et al., 2015).

Table 2.1 Characteristics of the LDTRF-Transect data in the measurement year, 1991

Fire year	Stand age (years)	Number of transects	Plot counts	Mean basal area (m^2ha^{-1}) of standing live trees				
				Fir	Birch	Spruce	Aspen	Cedar
1823	168	5	66	4.32	3.88	2.46	8.03	0.53
1847	144	4	74	6.84	4.62	5.40	11.88	0.77
1870	121	6	64	3.46	5.86	4.46	12.78	0.02
1916	75	3	52	4.54	7.63	1.99	16.74	0.97
1944	47	4	71	3.81	9.34	0.81	11.57	0.22

A parameter file has been developed and modified over the time for the LDRTF by several studies (Bose et al., 2015; Poulin et al., 2008). This fine tuning allows a significant improvement of the model functions for six of the main tree species present

in the mixed boreal forest of eastern Canada: balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), eastern white cedar (*Thuja occidentalis*), as well as the shrub species mountain maple (*Acer spicatum*) (Bose et al., 2015). The model function includes- tree allometry, light, tree growth, tree mortality, and recruitment etc.

The plot size for simulation runs was set to 100 m x 100 m to match the size of the hectare plot data and the timestep was set to one year. All other parameters were set as in Maleki et al. (2019). An initial tree distribution was created from the species composition data (density of stems by species and DBH class) of each plot in the LDRTF-TRANSECT dataset, with trees positioned at random in the plot for each simulation run. I simulated *T* years with SORTIE-ND using the Maleki et al. (2019) parametrization, where *T* is the difference in age (time since fire) between the initial stand (transect plot) and one of the hectare plots (final stand) to which the simulated stand will be compared (Table 2.2). The fire years chosen for the final stand were 1823, 1847 and 1870 since they represent the mixed stages of succession, with the greatest diversity of species present. The transect plots from 1847, 1870 and 1916 were chosen to produce the initial stands. I did not use the data from the earliest fire year (1760), which are dominated by cedar, or the most recent fire years (1944 and 1964), where coniferous species are almost absent.

2.2.4 Spatial pattern analysis

I used point pattern analysis (Wiegand & Moloney, 2014) to compare the spatial configuration of live adult trees between the stands simulated by SORTIE-ND and the hectare plots at the same successional stage. I focused our comparison on the four most abundant species in the transect plots (~*Abies balsamea, Populus tremuloides, Betula papyrifera, Picea glauca*) (Table 2.1).

Since the spatial pattern was visually inhomogeneous in the observed data (i.e. the density of each species was not constant within the hectares), I applied an inhomogeneous version of the *L* function to determine the relationship between points of the same or different species. The *L* function is a transformation of Ripley's *K(r)* function, which is equal to the mean number of points in a disk of radius *r* drawn around a focal point in the pattern, normalized by the density of points in the pattern (Law et al., 2009; Ripley, 1981). The univariate function is calculated by counting neighbours of the same species, whereas the bivariate (or cross-type) function is calculated by counting neighbours of a different species from the focal point. In both cases, the expected value of the *K(r)* function if points are located independently from each other (no attraction or repulsion) is $K(r) = \pi r^2$. The *L* function is obtained by taking the square root of K/π , so that the expectation under the null model of independence is $L(r) = r$. The square root transformation of Ripley's *K* function also has the effect of stabilizing the variance of the estimator, so that *L* is more appropriate for use in simulation envelopes and hypothesis tests (Baddeley et al., 2015).

The inhomogeneous *L* function is the corresponding transformation of the inhomogeneous *K* function, which was proposed by Baddeley et al. (2005). For the inhomogeneous *K* and *L* functions, the mean number of neighbours in a radius *r* is standardized by the local point density, as determined by a Gaussian smoothing kernel, instead of the overall density of points. The scale of that smoothing kernel separates small-scale patterns that are assumed to be due to interactions between points, and large-scale density fluctuations that may be due to an inhomogeneous environment (Wiegand & Moloney, 2014). I chose a standard deviation of 10 meters for this smoothing kernel for all our analyses, since this is the scale at which I expect neighbour effects to be important in mixed forests (Canham et al. 2004). This value of 10 m also corresponds to maximum distance used for the calculation of the Neighbourhood Crowding Index (NCI) in our SORTIE-ND model.

To test our hypothesis that the spatial structure of stands simulated from the SORTIE-ND model is consistent with that of observed stands, I compared the single-species and two-species L functions for the main species in each observed stand to a simulation envelope formed by the L functions calculated from all simulated stands of a comparable age (1 simulation based on each transect plot in a given fire year). As the precision of the L function depends on the number of points in the pattern, it is important to have both a sufficient number of trees and the same number of trees in the different patterns to be compared. Therefore, I considered species with a minimum of 100 adult trees in the hectare data. I also retained only the simulation results with at least as many individuals as the hectare to which they would be compared for a given species or pair of species, and trees at random from the simulation output to match the number of individuals in the hectare was 'removed'. I confirmed via simulation results (not shown) that this random subsampling does not create a bias in the calculation of the homogeneous L function, though it does create a bias in the inhomogeneous case. Since I know the simulated stands were homogeneous (any resulting spatial pattern would be due to intrinsic spatial dynamics of the species rather than external gradients), I calculated the simulation envelope using the homogeneous L function and compared it with the inhomogeneous L function estimated from the observed stand.

I repeated the steps above for different combinations of initial and final stand ages (Table 2.2). All point pattern analyses were performed with the 'spatstat' package in R software version 4.0.2 (Baddeley & Turner, 2005).

Table 2.2 Matrix of simulation timesteps for different combination of initial and final stand age

	Observation for model verification	Hectare Fire Years	1823	1847	1870
Observation for model initialization		Stand age at measure year (2011)	188	164	141
Transect Fire years	Stand age at measure year (1991)				
1847	144		T=44		
1870	121		T=67	T=43	
1916	75		T=113	T=89	T=66

2.3 Results

The observed hectare data illustrates different density levels of the species for different fire years. *Populus tremuloides* was more abundant for the 1870 and 1823 fire years, whereas *Abies balsamea* was the most abundant species for the 1847 fire year (Table 2.3, Fig. 2.2).

Table 2.3 Number of trees per hectare plot with their intensity

Hectare/Species	ABA	BPA	PGL	PTR
1870	72	115	226	243
1847	298	43	127	162
1823	194	22	61	208

** ABA= *Abies balsamea*; BPA= *Betula papyrifera*; PGL= *Picea glauca*; PTR= *Populus tremuloides*

For the spatial analysis, I did not consider species with less than 100 adult trees per hectare plot: *Abies balsamea* for the 1870 hectare, *Picea glauca* for the 1823 hectare

and *Betula papyrifera* for the 1823 and 1847 hectares. The density plots illustrate the distribution of each species across each plot (Fig. 2.2).

Figures 2.3 to 2.5 compare the observed and simulated spatial patterns (as described by the *L* function) for each pair of an initial (transect) and final (hectare) stand. In those graphs, the black dashed line indicates a neutral pattern (complete spatial randomness), so that values of the *L* function above or below that line represent clustering (excess of neighbours) or repulsion (deficit of neighbours) at a given distance. Furthermore, I consider that the observed and simulated patterns are consistent when the observed *L* function lies within the range of the simulation results (shaded area).

The species balsam fir (*Abies balsamea*) showed repulsion (a deficit of same-species neighbours) at short distance for the 1823 and 1847 observed data and a mix of aggregated and neutral pattern at larger distances (Fig. 2.3, 2.4 & 2.5). Compared to this pattern, the SORTIE-ND simulations produced a similar pattern at short distance. There was a slight difference between the simulated (1870 and 1916 transects) and observed pattern for the 1847 hectare (Fig. 2.4). However, the simulated result from the 1847, 1870 and 1916 transects produced a similar pattern compared with the 1823 hectare (Fig. 2.3 & Fig. 2.5).
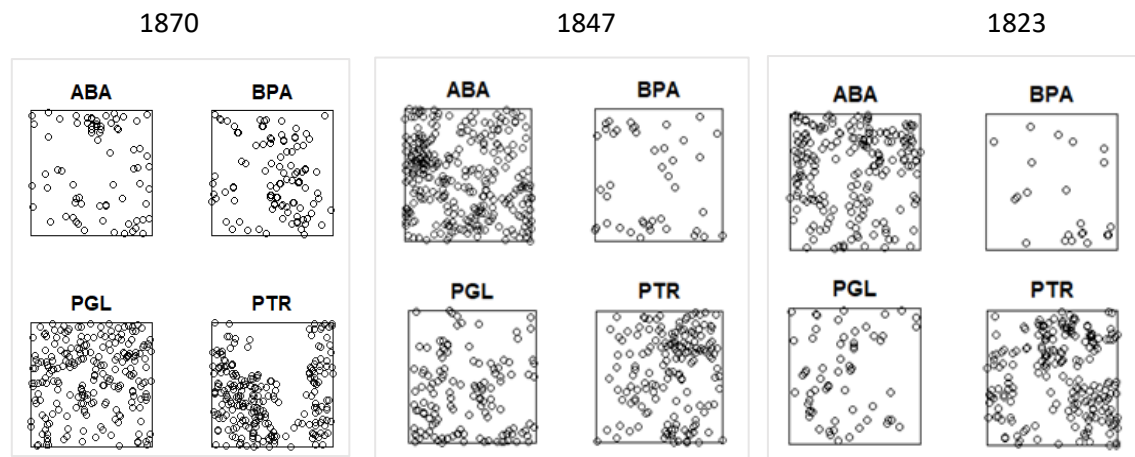
1870   1847   1823

Figure 2.2 Spatial pattern of each species in 1 ha size plot from the 1870, 1847 and 1823 fire years
** ABA= Abies balsamea; BPA= Betula papyrifera; PGL= Picea glauca; PTR= Populus tremuloides

Trembling aspen (*Populus tremuloides*) showed a neutral pattern for the 1823 hectare whereas repulsion was observed in the 5 – 10 m range for the 1847 hectare (Fig. 2.3 & 2.5). The SORTIE-ND simulations from the 1870 and 1847 transects produced a similar pattern up to 10 meters when I compared with the 1823 observed data (Fig. 2.3). The simulated pattern from the 1870 transect produced a neutral pattern which is quite different from the 1847 observed pattern (Fig. 2.5). Too few simulations from the 1916 transects had as many individuals as the hectares, so I could not use this initial year; therefore, no comparison was possible with the 1870 hectare.

The bivariate *L* function illustrates the spatial pattern of balsam fir and trembling aspen (Fig. 2.3 & 2.5). The observed pattern for 1823 produced a slight clustered pattern, however, the SORTIE-ND simulations produced a similar pattern.

White spruce (*Picea glauca*) showed a different pattern for the 1847 and 1870 observed data (Fig. 2.4 & Fig. 2.5). A neutral pattern exists for both years, however, for distances

between 5 and 7 meters, I observed a slightly aggregated pattern. The model produced a similar spatial pattern except for certain distances.

White spruce and balsam fir showed an aggregated pattern for the observed year 1847, though I found a dispersed pattern at short distance (Fig. 2.4). However, SORTIE-ND was unable to reproduce the same pattern.

Paper birch showed a clustered pattern for the 1870 hectare and a random pattern for the simulated pattern derived from the 1916 transect plots (Fig. 2.5).

Figure 2.3 Comparison between the inhomogeneous L function for the observed fire year 1823 and the homogenous L function for the simulated fire years 1847 and 1870. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIE-ND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).

Observed pattern: 1847 hectare
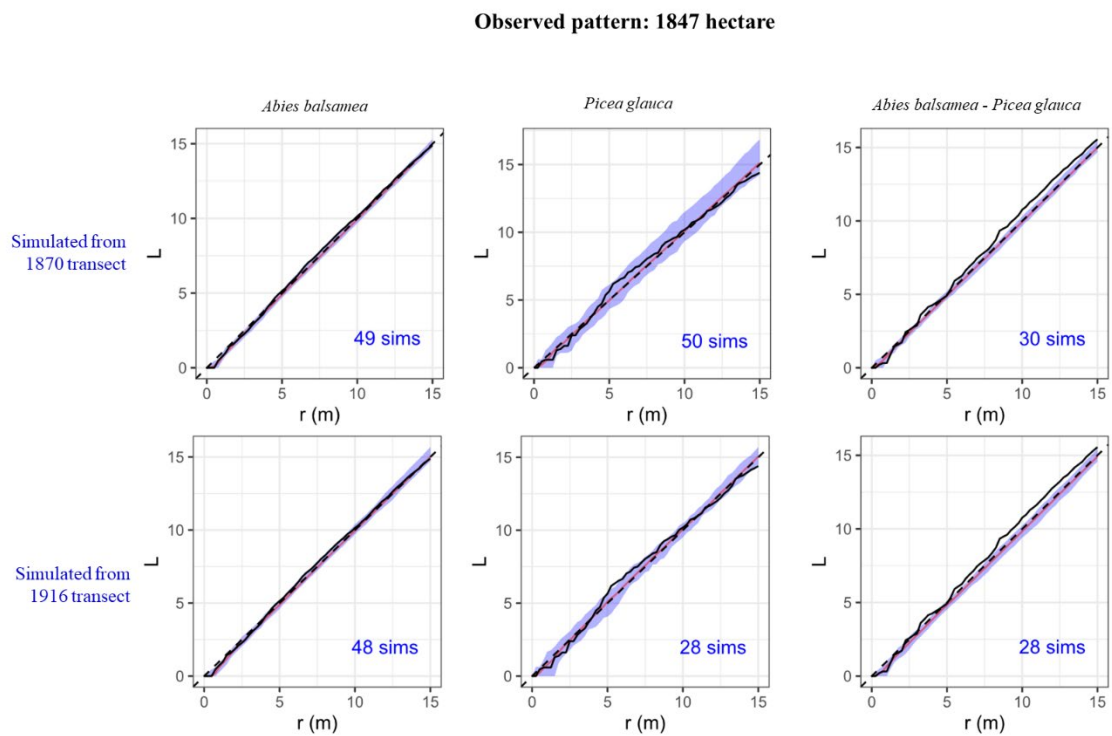
Figure 2.4 Comparison between the inhomogeneous L function for the observed fire year 1847 and the homogenous L function for the simulated fire years 1870 and 1916. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIE-ND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).

Observed pattern: 1847 hectare

Populus tremuloides — *Abies balsamea - Populus tremuloides* — *Populus tremuloides - Picea glauca*

Simulated from 1870 transect

47 sims — 22 sims — 27 sims

Observed pattern: 1823 hectare   **Observed pattern: 1870 hectare**

Abies balsamea — *Betula papyrifera* — *Picea glauca*

Simulated from 1916 transect
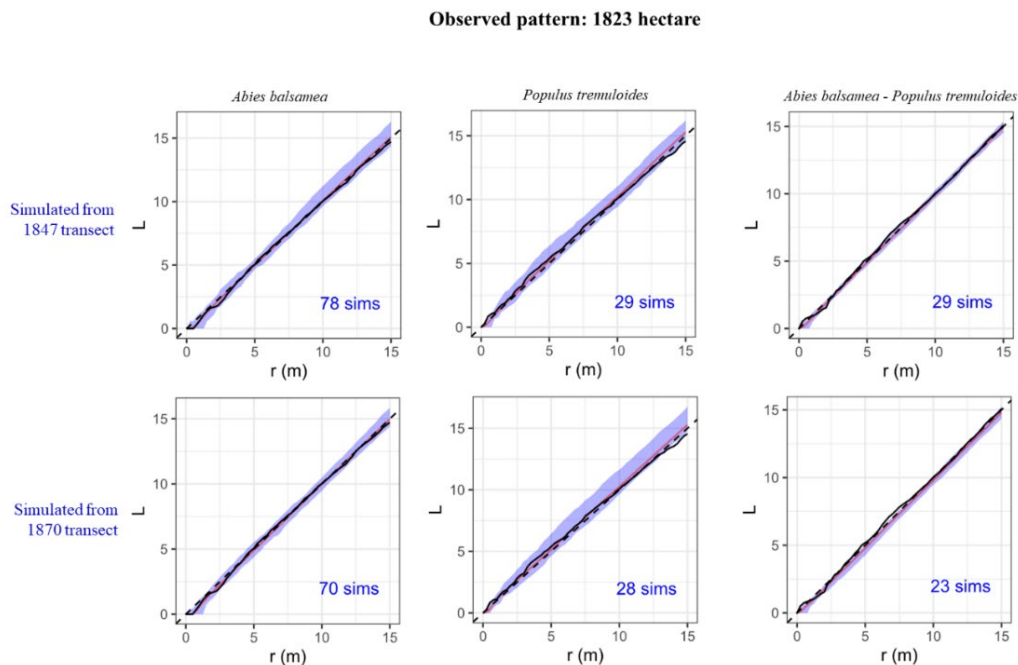
49 sims — 11 sims — 16 sims

Figure 2.5 Comparison between the inhomogeneous L function for the observed fire years 1823, 1847, 1870 and the homogenous L function for the simulated fire years 1870 and 1916. The black solid line is the observed pattern in the hectare plot; the red line is the mean of the simulations from SORTIE-ND and the blue shaded area is the range of values across all simulation runs. The black dashed line represents a neutral pattern (complete spatial randomness).
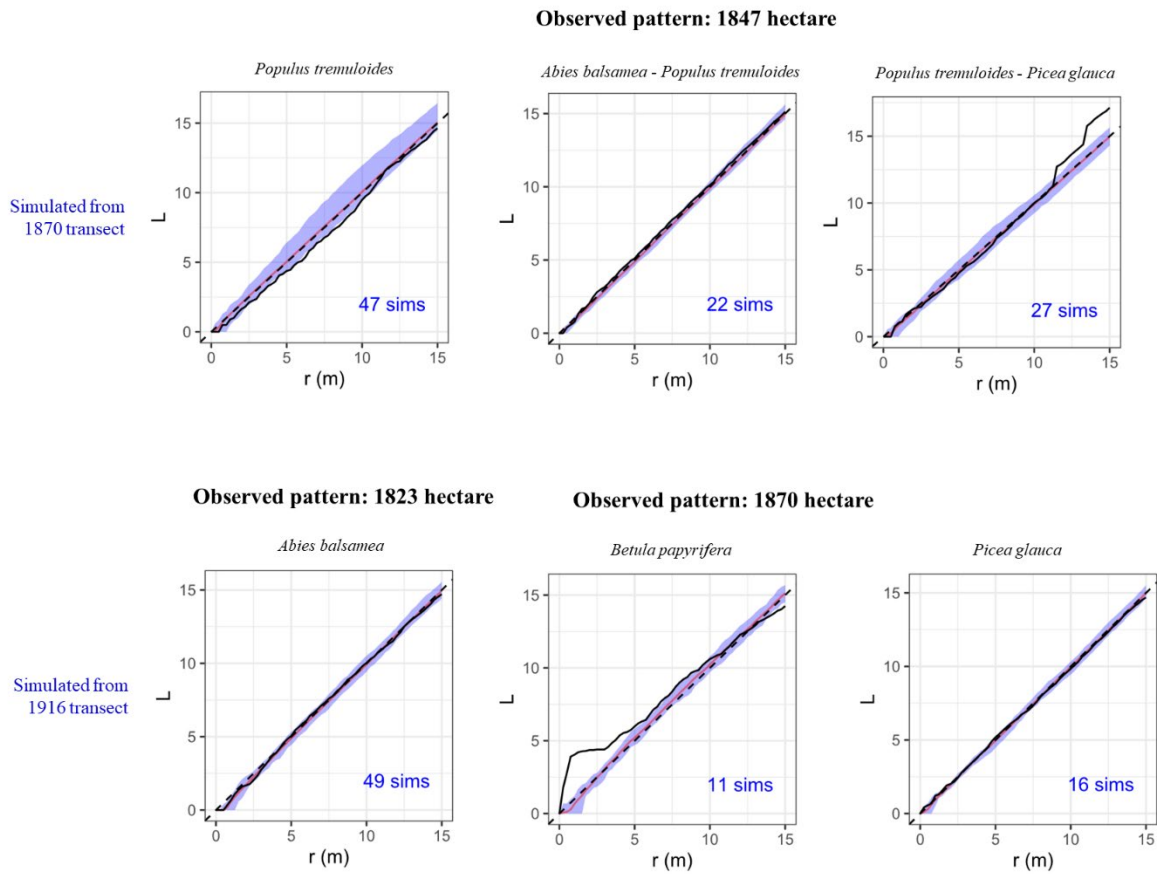
2.4 Discussion

The SORTIE-ND simulations were able to reproduce the same spatial pattern as the observed plots for balsam fir and trembling aspen. Our results showed evidence of intraspecific competition for balsam fir (*Abies balsamea*) as I did not find a clustering pattern for this species and either random or repulsion patterns were detected for the observed data. The model also reproduced the observed spatial pattern for trembling aspen (*Populus tremuloides)*. I found a small deviation between the simulated and the observed pattern for balsam fir and trembling aspen, however, the deviation did not exceed the simulation envelope. The simulated pattern for paper birch (*Betula papyrifera)* did not emulate the observed one. Also, the simulated pattern of white spruce (*Picea glauca)* deviated slightly from the observed pattern. The paired spatial pattern between balsam fir and trembling aspen was consistent between the simulations and observations. However, the model was unable to reproduce the paired spatial pattern for balsam fir and white spruce as well as the spatial pattern between trembling aspen and white spruce.

2.4.1 Balsam fir

This shade tolerant species (Frank, 1990), which often germinates and establishes itself under the canopy cover, showed intraspecific competition at short distance. Intraspecific competition has impact on the species growth and crown morphology (Duchesneau et al., 2001). Competition is observed within dense fir thickets. As balsam fir mostly reproduce through large seeds (Asselin et al., 2001; Kneeshaw & Bergeron, 1999; Pureswaran et al., 2015), I can assume that strong intraspecific competition between seedlings would be the reason for the dispersed pattern (repulsion) at a short scale. The mortality rate of a species can be triggered by the species composition (Bergeron et al., 1995), which eventually affect the spatial configuration at fine scale

by creating gaps. Kneeshaw and Bergeron (1995) reported the importance of gaps for the recruitment of the species. Thus, gap dynamics play a crucial role on the distribution and recruitment of this species. Our results showed the SORTIE-ND model was able to predict the spatial pattern at fine scale from a random distribution. This is quite interesting and has a management implication as balsam fir is one of the abundant species for most of the boreal mixedwood ecoregion in Quebec, Canada. Also, this species is prone to spruce budworm outbreak infestation and by predicting the spatial pattern of this species we can control the damage.

2.4.2 Trembling aspen

Our observed pattern for the 1823 hectare was close to the theoretical L function for certain distances, indicating the presence of a pattern either clustering or even dispersion. However, the spatial pattern for the 1847 hectare data slightly deviated between 6 m and 10 m and showed a dispersed spatial pattern (Fig. 2.5). The greater dispersion for the younger stand (1847) compared with the older one (1823) is consistent, however, with a decrease in the relative importance of intraspecific competition over successional stages (Gray & He, 2009). Part of the reason why the dispersion pattern in the 1847 hectare is not reproduced correctly in the simulations may be due to the vegetative propagation of aspen, where suckers emerge far from their mother tree. As the SORTIE-ND model does not incorporate the detailed behavior of vegetative propagation, it could be underestimating the distance between suckers and the source tree in this case.

2.4.3 White spruce

The spatial pattern for a species at different successional stage would be unique as the relative importance of intraspecific competition is reduced at later successional stages

(Gray & He, 2009). This is consistent with the observation of a clustered pattern for the 1847 hectare data, which indicates low competitive interactions within the individual of same species, whereas the younger stand (1870 hectare) shows a random pattern.

Our simulations did not reproduce the same pattern of clustering at medium ranges (5 – 10 m) as the observations for the 1847 hectare data. We note that compared with balsam fir, white spruce seedling recruitment is more sensitive to substrate (Simard et al., 1998), and we do not have information on the spatial distribution of substrates in the plots. If the favorable substrates are present in clusters in the hectare plots, that could be one reason for the discrepancy between observations and simulations for that species.

2.4.4 Paper birch

Paper birch has a similar recruitment pattern as trembling aspen (Bergeron, 2000). The species regenerates within the gap areas that are created due to the mortality of other species like balsam fir and trembling aspen (Kneeshaw & Bergeron, 1998), thus the spatial pattern of paper birch can be influenced by the mortality pattern of fir and aspen species. In our study, the species showed a clustered pattern from distances of 0 to 5 m and a neutral pattern at greater distances. The SORTIE-ND model was not able to reproduce the pattern observed for the empirical data. The small number of simulated plots along with the absence of stump sprouting in the model may lead to inability to predict the spatial pattern. Also, the empirical data does not include information that would allow us to verify if the small clusters of paper birch are indeed stump sprouts.

2.4.5 Balsam fir- Trembling aspen

The bivariate L(r) analysis found a random spatial pattern between balsam fir and trembling aspen for the empirical and simulated spatial pattern. However, a slight amount of clustering was detected in our study, which is negligible. As Gray and He (2009) mentioned on their work, the combination of coniferous and deciduous trees reduces the competition for the light resource and it would be hard to find interspecific competition when two species have different resource requirements. Also, balsam fir experiences a weak competitive effect from trembling aspen (Boivin et al. 2010; Coates et al. 2009), which could be a reason for not finding any distinctive pattern within this pair.

2.4.6 Balsam fir- White Spruce

Balsam fir has wide range of adaptation ability over white spruce and that make it a successful compatible species with white spruce (Asselin et al., 2001). White spruce (*Picea glauca*) seedling density remains low compared to balsam fir (*Abies balsamea*) in a stand (Bergeron & Charron, 1994), which could help to reduce competitive effects in the stand.

Moisture is considered as an important factor for the growth of balsam fir and white spruce compared to light (Frank, 1990). The SORTIE-ND model was developed on the basis of gap dynamics (Murphy, 2011; Pacala et al., 1996) where soil moisture level was neglected during the parametrization. Unaccounted variation in soil moisture levels could be one of the explanations that our model could not reproduce the same clustered pattern of the observed data.

2.4.7 Trembling aspen- white spruce

Several studies mentioned evidence of a positive association between trembling aspen and white spruce in the boreal mixedwood forest (Filipescu & Comeau, 2007; Man & Lieffers, 1999). Our result did not provide any conclusive remarks here as the graph illustrated an existence of neutral pattern. This happens due to have a weak competition between two types of species (Holmgren et al. 2007). The different growing rate of these two species (Man & Lieffers, 1999) also helps them co-exist by reducing competition. Also, trembling aspen recruits through suckers and white spruce depends on their seeds for recruitment, this allow them to co-exist by reducing the interspecific competition for the resources. The bivariate analysis was unable to distinguish a pattern between clustering and repulsion. However, the SORTIE-ND model was able to reproduce the similar spatial pattern as it is found in the empirical data.

There are a few exceptional cases where the model was not able to reproduce the empirical pattern. Several explanations can be provided for these cases, however, a rigorous study to improve the model's ability to predict spatial pattern would help resolve this problem. I did not account episodic mortality in our model. Future research can include episodic mortality (e.g., due to insect outbreaks) to see its effect on the spatial pattern at a fine scale and whether the model can accurately predict that spatial pattern. Also, the species' sensitivity to a disturbance other than episodic mortality has not been explored in detail for the model parametrization (Aakala et al., 2007; Senecal et al., 2004).

Maleki et al. (2019) suggested to include growth and mortality data for white cedar (*Thuja occidentalis)* to improve the model accuracy, however that species was not prevalent enough in the transects we used to initiate our simulations. It was only abundant in the late successional stages, but simulations are initiated with data from the earlier stages.

Moreover, Coates et al. (1994) found that dense herb communities would be a barrier for regeneration, and it may structure the spatial pattern of the population. Also, snowfall or herbivores can affect the dispersion of boreal species (Galipeau et al., 1997). By including herb or shrub density, snowfall and the presence of herbivore in the SORTIE-ND model, we may be able to improve the accuracy of predictions of spatial patterns, and can devise forest management plan according to those patterns.

2.5 Conclusion

The spatial pattern of a forest provides information on the intra and interspecific competition of tree species. The efficient utilization of silvicultural practice relies on the knowledge of the trees' spatial pattern. The lack of long term data would restrict our understanding about successional cycles, however, understanding spatial patterns can help us to infer competitive interactions within and between species to reveal the ecological complexity. Our results partially support our initial hypothesis, as the SORTIE-ND model reconstructed the observed spatial structure with a few exceptions. The inclusion of growth and mortality data for other boreal species may help to address the effect of these species as well. Besides, factors like the presence of herbivory can influence the species composition and spatial configuration of trees in a stand. I believe further research on the SORTIE-ND parametrization will help managers and researchers produce more accurate spatial pattern predictions considering the future climate change and natural disturbances. The improved model would allow precise predictions of stand structure following different disturbances or harvest treatments. The traditional forest management in boreal mixedoods requires more up-to-date information regarding the spatial pattern to optimize the forest productivity and biodiversity by minimizing costs. Our study will help forest managers to predict the spatial pattern of a forest stand more precisely. That will allow them to understand the competition pattern and thus, selection of species for plantation over space.

CHAPTER 3

GENERAL CONCLUSION

The spatial pattern in a forest is regulated by self-thinning processes and may progress from a clustered to a random or regular pattern. Different silvicultural practice such as clear cuts or partial cuts affect the spatial pattern. The random mortality hypothesis predicts that the equal death probability of trees would lead an unchanged spatial pattern in the second-order characteristics (Sterner et al. 1986). Along with competition, factors like environmental heterogeneity and disturbances (e.g. insects, windthrows) that affect trees and their neighbours (creating gaps of different sizes) can contribute to produce a specific spatial pattern.

This study emphasized that the individual-based spatially explicit simulation model could be used to predict the spatial pattern of forest stands at a fine scale. I analyzed our results under the theory of neighbourhood competition. The competition takes place based on the availability of resources. Individuals from same genus compete for resources. At that point, trees tend to form clusters, whereas species competing for resources tend to avoid each other. When I consider a single species, dispersal near the parent tree creates clusters but intraspecific competition limits how many trees can be near each other. For pairs of species, patterns are based on the relative strength of interspecific competition vs. facilitation (e.g. litter from deciduous trees can be a positive or negative factor for the neighbouring species). The competition between coniferous and deciduous trees shapes the characteristics of a forest stand. The light requirements and resource consumption trigger interspecific competition which leads to a dispersed pattern. On the other hand, a clustered pattern is a result of facilitation, which happens when individual trees do not compete with each other.

The SORTIE-ND model simulates the spatial pattern by predicting light environments as well as other environmental requirements for each tree. However, the model did not predict that pattern accurately for *Betula papyrifera*. Also, we did not include few other parameters, such as topographical variation, soil types or insect outbreaks, in our model. Thus it would be a research interest to check the model performance after incorporating such parameters. Besides, the changing environment due to climate change and incorporating future changes in the model would be a fascinating work that could enhance the model reliability. Thus, I recommend to extend this study to other species and check the model fit. This iconic model works with individual trees and offers a great extension to study forest stands at fine scale. Our study extensively focused on the ability of predicting spatial patterns, as the model is developed based on the gap dynamics and neighbourhood competition index. I believe the model can be used to predict the spatial pattern, which will provide information on the status of species interactions and will help managers to plan silvicultural operations.

The improvement of the model parameter file for the boreal mixedwood could help in improving the model accuracy level. In our study I found that the SORTIE-ND model could not produce the exact same spatial pattern for a few simulations. The improvement of model parameterization may help to fix this issue.

Also, changing scenarios, such as climate change, insect outbreaks, etc. in the model need to be addressed and I need to check whether model can perform accurately to reproduce the spatial pattern.

BIBLIOGRAPHY

Aakala, T., Kuuluvainen, T., De Grandpré, L., & Gauthier, S. (2007). Trees dying standing in the northeastern boreal old-growth forests of Quebec: Spatial patterns, rates, and temporal variation. *Canadian Journal of Forest Research*, *37*(1), 50–61. https://doi.org/10.1139/X06-201

Ameztegui, A., Cabon, A., De Cáceres, M., & Coll, L. (2017). Managing stand density to enhance the adaptability of Scots pine stands to climate change: A modelling approach. *Ecological Modelling*, *356*, 141–150. https://doi.org/10.1016/j.ecolmodel.2017.04.006

Ameztegui, A., Coll, L., Benavides, R., Valladares, F., & Paquette, A. (2012). Understory light predictions in mixed conifer mountain forests: Role of aspect-induced variation in crown geometry and openness. *Forest Ecology and Management*, *276*, 52–61. https://doi.org/10.1016/j.foreco.2012.03.021

Ameztegui, A., Coll, L., & Messier, C. (2015). Modelling the effect of climate-induced changes in recruitment and juvenile growth on mixed-forest dynamics: The case of montane-subalpine Pyrenean ecotones. *Ecological Modelling*, *313*, 84–93. https://doi.org/10.1016/j.ecolmodel.2015.06.029

Asselin, H., Fortin, M. J., & Bergeron, Y. (2001). Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *Forest Ecology and Management*, *140*(1), 29–37. https://doi.org/10.1016/S0378-1127(00)00273-5

Attiwill, P. M. (1994). The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecology and Management*, *63*(2–3), 247–300. https://doi.org/10.1016/0378-1127(94)90114-7

Baddeley, A., Rubak, E., & Turner, R. (2015). Spatial Point Patterns: Methodology and Applications with R. In *Spatial Point Patterns*. CRC Press. https://doi.org/10.1201/b19708

Baddeley, A., & Turner, R. (2005). spatstat: An R Package for Analyzing Spatial Point Patterns. *Journal of Statistical Software*, *12*(6), 282–290. https://doi.org/10.1111/j.1540-4781.1939.tb01339.x

Beaudet, M., Harvey, B. D., Messier, C., Coates, K. D., Poulin, J., Kneeshaw, D. D., Brais, S., & Bergeron, Y. (2011). Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: A modelling approach. *Forest Ecology and Management*, *261*(1), 84–94. https://doi.org/10.1016/j.foreco.2010.09.033

Bergeron, Y. (2000). Species and Stand Dynamics in the Mixed Woods of Quebec's Southern Boreal Forest. *Ecology*, *81*(6), 1500–1516.

Bergeron, Y., & Charron, D. (1994). Postfire stand dynamics in a southern boreal forest (Québec): A dendroecological approach. *Écoscience*, *1*(2), 173–184.

Bergeron, Y., & Dubuc, M. (1989). Succession in the southern part of the Canadian boreal forest. *Vegetatio*, *79*(1–2), 51–63. https://doi.org/10.1007/BF00044848

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., & Lesieur, D. (2001). Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Canadian Journal of Forest Research*, *31*(3), 384–391. https://doi.org/10.1139/cjfr-31-3-384

Bergeron, Y., Leduc, A., Morin, H., & Joyal, C. (1995a). Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*, *25*, 1375–1384.

Bergeron, Y., Leduc, A., Morin, H., & Joyal, C. (1995b). Balsam fir mortality

following the last spruuce budworm outbreak in northwestern Quebec. *Canadian Journal of Forest Research*, *25*, 1375–1384.

Boivin, F., Paquette, A., Papaik, M. J., Thiffault, N., & Messier, C. (2010). Do position and species identity of neighbours matter in 8-15-year-old post harvest mesic stands in the boreal mixedwood? *Forest Ecology and Management*, *260*(7), 1124–1131. https://doi.org/10.1016/j.foreco.2010.06.037

Bose, A. K., Harvey, B. D., Coates, K. D., Brais, S., & Bergeron, Y. (2015a). Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. *Ecological Modelling*, *300*, 123–136. https://doi.org/10.1016/j.ecolmodel.2015.01.002

Bose, A. K., Harvey, B. D., Coates, K. D., Brais, S., & Bergeron, Y. (2015b). Modelling stand development after partial harvesting in boreal mixedwoods of eastern Canada. *Ecological Modelling*, *300*, 123–136. https://doi.org/10.1016/j.ecolmodel.2015.01.002

Boulanger, Y., Taylor, A. R., Price, D. T., Cyr, D., McGarrigle, E., Rammer, W., Sainte-Marie, G., Beaudoin, A., Guindon, L., & Mansuy, N. (2017). Climate change impacts on forest landscapes along the Canadian southern boreal forest transition zone. *Landscape Ecology*, *32*(7), 1415–1431. https://doi.org/10.1007/s10980-016-0421-7

Brandt, J. P., Flannigan, M. D., Maynard, D. G., Thompson, I. D., & Volney, W. J. A. (2013). An introduction to Canada's boreal zone: Ecosystem processes, health, sustainability, and environmental issues1. *Environmental Reviews*, *21*(4), 207–226. https://doi.org/10.1139/er-2013-0040

Brown, M. L., Canham, C. D., Murphy, L., & Donovan, T. M. (2018). Timber harvest as the predominant disturbance regime in northeastern U.S. forests: effects of harvest intensification. *Ecosphere*, *9*(3), e02062.

https://doi.org/10.1002/ecs2.2062

Busing, R. T., & Mailly, D. (2004). Advances in Spatial, Individual-Based Modelling of Forest Dynamics. *Journal of Vegetation Science*, *15*(6), 831–842.

Canham, C. D., LePage, P. T., & Coates, K. D. (2004). A neighborhood analysis of canopy tree competition: Effects of shading versus crowding. *Canadian Journal of Forest Research*, *34*(4), 778–787. https://doi.org/10.1139/x03-232

Carrer, M., Castagneri, D., Popa, I., Pividori, M., & Lingua, E. (2018). Tree spatial patterns and stand attributes in temperate forests: The importance of plot size, sampling design, and null model. *Forest Ecology and Management*, *407*(August 2017), 125–134. https://doi.org/10.1016/j.foreco.2017.10.041

Case, B. S., Buckley, H. L., Barker-Plotkin, A. A., Orwig, D. A., & Ellison, A. M. (2017). When a foundation crumbles: Forecasting forest dynamics following the decline of the foundation species Tsuga canadensis. *Ecosphere*, *8*(7). https://doi.org/10.1002/ecs2.1893

Chen, H. Y. H., & Popadiouk, R. V. (2002). Dynamics of North American boreal mixedwoods. *Environmental Review*, *10*, 137–166. https://doi.org/10.1139/A02-007

Chen, J., & Bradshaw, G. A. (1999). Forest structure in space: A case study of an old growth spruce-fir forest in Changbaishan Natural Reserve, PR China. *Forest Ecology and Management*, *120*(1–3), 219–233. https://doi.org/10.1016/S0378-1127(98)00543-X

Churchill, D. J., Carnwath, G. C., Larson, A. J., & Jeronimo, S. A. (2017). *Historical Forest Structure , Composition , and Spatial Pattern in Dry Conifer Forests of the Western Blue Mountains , Oregon* (Issue November).

Coates, K. D., Lilles, E. B., & Astrup, R. (2013). Competitive interactions across a

soil fertility gradient in a multispecies forest. *Journal of Ecology*, *101*(3), 806–818. https://doi.org/10.1111/1365-2745.12072

Cristal, I., Ameztegui, A., González-Olabarria, J. R., & Garcia-Gonzalo, J. (2019). A Decision support tool for assessing the impact of climate change on multiple ecosystem services. *Forests*, *10*(5), 1–20. https://doi.org/10.3390/f10050440

Crump, M. L., & Scott, N. J. (1994). Visual Encounter Surveys. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, & M. S. Foster (Eds.), *Measuring and Monitoring Biological Diversity - Standard Methods for Amphibians* (1st ed., pp. 84–92). Smithsonian Institution.

Dale, M. R. T., & Fortin, M.-J. (2014). Spatial Analysis:A Guide for Ecologists. In *Encyclopedia of Environmental Change* (2nd ed.). Cambridge University Press. https://doi.org/10.4135/9781446247501.n3655

de Römer, A. H., Kneeshaw, D. D., & Bergeron, Y. (2007). Small gap dynamics in the southern boreal forest of eastern Canada: Do canopy gaps influence stand development? *Journal of Vegetation Science*, *18*(6), 815. https://doi.org/10.1658/1100-9233(2007)18[815:sgdits]2.0.co;2

Dhar, A., & Hawkins, C. D. B. (2011). Regeneration and growth following mountain pine beetle attack : A synthesis of knowledge. *BC Journal of Ecosystems and Management*, *12*(2), 1–16.

Dovčiak, M., Frelich, L. E., & Reich, P. B. (2001). Discordance in spatial patterns of white pine (Pinus strobus) size-classes in a patchy near-boreal forest. *Journal of Ecology*, *89*(2), 280–291. https://doi.org/10.1046/j.1365-2745.2001.00545.x

Duchesneau, R., Lesage, I., Messier, C., & Morin, H. (2001). Effects of light and intraspecific competition on growth and crown morphology of two size classes of understory balsam fir saplings. *Forest Ecology and Management*, *140*(2–3), 215–225. https://doi.org/10.1016/S0378-1127(00)00281-4

Filipescu, C. N., & Comeau, P. G. (2007). Aspen competition affects light and white spruce growth across several boreal sites in western Canada. *Canadian Journal of Forest Research*, *37*(9), 1701–1713. https://doi.org/10.1139/X07-011

Fortin, M.-J., & Dale, M. (2005). *Spatial Analysis: A Guide for Ecologists* (1st ed.). Cambridge University Press.

Franklin, S. E., & Wulder, M. A. (2002). Remote sensing methods in medium spatial resolution satellite data land cover classification of large areas. *Progress in Physical Geography*, *26*(2), 173–205. https://doi.org/10.1191/0309133302pp332ra

Gadow, K. v., Zhang, C. Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G. Y., Kiviste, A., & Zhao, X. H. (2012a). Forest Structure and Diversity. In T. Pukkala & K. von Gadow (Eds.), *Continuous Cover Forestry* (2nd ed., Vol. 23, p. 296). Springer Netherlands. https://doi.org/10.1007/978-94-007-2202-6

Gadow, K. v., Zhang, C. Y., Wehenkel, C., Pommerening, A., Corral-Rivas, J., Korol, M., Myklush, S., Hui, G. Y., Kiviste, A., & Zhao, X. H. (2012b). Forest Structure and Diversity. In T. Pukkala & K. von Gadow (Eds.), *Continuous Cover Forestry* (2nd ed., Vol. 23, p. 296). Springer Netherlands. https://doi.org/10.1007/978-94-007-2202-6

Galipeau, C., Kneeshaw, D., & Bergeron, Y. (1997). White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. *Canadian Journal of Forest Research*, *27*(2), 139–147. https://doi.org/10.1139/x96-148

Goreaud, F., Courbaud, B., & Collinet, F. (1997). Spatial structure analysis applied to modelling of forest dynamics: a few examples. *Proceedings of the IUFRO Workshop, Empirical and Process Based Models for Forest Tree and Stand*

Growth Simulation, *21*(January 1997), 27.
http://wwwlisc.clermont.cemagref.fr/Labo/MembresEtPagesIntermediaires/page
sperso/Anciens_membres/goreaud/Documents/1999_Goreaud_etal_ActesOeiras
_Preprint.pdf

Gray, L., & He, F. (2009). Spatial point-pattern analysis for detecting density-
dependent competition in a boreal chronosequence of Alberta. *Forest Ecology
and Management*, *259*(1), 98–106. https://doi.org/10.1016/j.foreco.2009.09.048

Greene, D. F., Zasada, J. C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., &
Simard, M. J. (1999). A review of the regeneration dynamics of North American
boreal forest tree species. *Canadian Journal of Forest Research*, *29*(6), 824–
839. https://doi.org/10.1139/x98-112

Harper, J. L. (1977). *Population Biology of Plants* (1st ed.). Academic Press.

Harvey, B. D., Leduc, A., Gauthier, S., & 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.
https://doi.org/10.1016/S0378-1127(01)00573-4

Illian, J., Penttinen, A., Stoyan, H., & Stoyan, D. (2008). *Statistical Analysis and
Modelling of Spatial Point Patterns* (1st ed.). John Wiley & Sons Ltd.
https://doi.org/10.1111/j.1751-5823.2008.00062_23.x

Kneeshaw, D. D., & Bergeron, Y. (1998). Canopy Gap Characteristics and Tree
Replacement in the Southeastern Boreal Forest. *Ecology*, *79*(3), 783–794.

Kneeshaw, D. D., & Bergeron, Y. (1999). Spatial and temporal patterns of seedling
and sapling recruitment within canopy gaps caused by spruce budworm.
Ecoscience, *6*(2), 214–222. https://doi.org/10.1080/11956860.1999.11682522

Kneeshaw, D. D., & Prévost, M. (2007). Natural canopy gap disturbances and their

role in maintaining mixed-species forests of central Quebec, Canada. *Canadian Journal of Forest Research*, *37*(9), 1534–1544. https://doi.org/10.1139/X07-112

Krebs, C. (2019). Ecological World View. In *Ecological World View*. https://doi.org/10.1071/9780643098398

Labrecque-Foy, J. P., Morin, H., & Girona, M. M. (2020). Dynamics of territorial occupation by North American beavers in Canadian boreal forests: A novel dendroecological approach. *Forests*, *11*(2), 1–12. https://doi.org/10.3390/f11020221

Larson, A. J., & Churchill, D. (2012). Forest Ecology and Management Tree spatial patterns in fire-frequent forests of western North America , including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *Forest Ecology and Management*, *267*, 74–92. https://doi.org/10.1016/j.foreco.2011.11.038

Lavoie, J., Girona, M. M., & Morin, H. (2019). Vulnerability of conifer regeneration to spruce budworm outbreaks in the Eastern Canadian boreal forest. *Forests*, *10*(10), 1–14. https://doi.org/10.3390/f10100850

Law, R., Illian, J., Burslem, D. F. R. P., Gratzer, G., Gunatilleke, C. V. S., & Gunatilleke, I. A. U. N. (2009). Ecoogical information from satial patterns of plants: Insights from point process theory. *Journal of Ecology*, *97*(4), 616–628. https://doi.org/10.1111/j.1365-2745.2009.01510.x

Legendre, P., & Legendre, L. (2012). Numerical Ecology. In *Elsevier* (3rd ed., Vol. 24). Elsevier.

Liu, Z., Peng, C., Grandpre, L., Work, T., Huang, C., & Kneeshaw, D. (2019). Simulation and Analysis of the Effect of a Spruce Budworm Outbreak on Carbon Dynamics in Boreal Forests of Quebec. *Ecosystems*, *22*, 1838–1851. https://doi.org/10.1007/s10021-019-00377-7

Maleki, K., Gueye, M. A., Lafleur, B., Leduc, A., & Bergeron, Y. (2019). Modelling Post-Disturbance Successional Dynamics of the Canadian Boreal Mixedwoods. *Forests*, *11*(3), 1–28.

Maleki, K., Marchand, P., Charron, D., Lafleur, B., & Bergeron, Y. (2021). A 249-year chronosequence of forest plots from eight successive fires in the Eastern Canada boreal mixedwoods. *Ecology*. https://doi.org/10.1002/ecy.3306

Man, R., & Lieffers, V. J. (1999). Are mixtures of aspen and white spruce more productive than single species stands? *Forestry Chronicle*, *75*(3), 505–513. https://doi.org/10.5558/tfc75505-3

McKenzie, D., Halpern, C. B., & Nelson, C. R. (2000). Overstory influences on herb and shrub communities in mature forests of western Washington, U.S.A. *Canadian Journal of Forest Research*, *30*(10), 1655–1666. https://doi.org/10.1139/x00-091

Morin, H., & Laprise, D. (1993). Chronology of spruce budworm outbreaks near Lake Duparquet, Abitibi region, Quebec. *Canadian Journal of Forest Research*, *23*, 1497–1506.

Murphy, L. E. (2011). *SORTIE-ND User Manual, Version 6.11*. Institute of Ecosystem Studies. http://www.sortie-nd.org/software/index.html

Navarro, L., Morin, H., Bergeron, Y., & Girona, M. M. (2018). Changes in spatiotemporal patterns of 20th century spruce budworm outbreaks in eastern Canadian boreal forests. *Frontiers in Plant Science*, *9*(December), 1–15. https://doi.org/10.3389/fpls.2018.01905

Nitschke, C. R., Amoroso, M., Coates, K. D., & Astrup, R. (2012). The influence of climate change, site type, and disturbance on stand dynamics in northwest British Columbia, Canada. *Ecosphere*, *3*(1), art11. https://doi.org/10.1890/es11-00282.1

Pacala, S. W., Canham, C. D., Saponara, J., Jr, J. A. S., Kobe, R. K., & Ribbens, E. (1996). Forest Models Defined by Field Measurements : Estimation , Error Analysis and Dynamics. *Ecological Monographs*, *66*(1), 1–43.

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

Poulin, J., Messier, C., Papaik, M., Beaudet, M., & Coates, K. D. (2008). Rapport de paramétrisation du modèle de simulation de la dynamique forestière SORTIE-ND pour la forêt boréale et sub-boréale de l'ouest du Québec: SORTIE-ND/Boréal. *Centre d'étude de La Forêt*, 59. http://sortie-nd.org/

Pretzsch, H. (2009). Forest Dynamics, Growth and Yield. In *Forest Dynamics, Growth and Yield*. https://doi.org/10.1007/978-3-540-88307-4

Pureswaran, D. S., Grandpré, L. De, Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., & Kneeshaw, D. D. (2015). Climate-induced changes in host tree-insect phenology may drive ecological state-shift in boreal forest. *Ecology*, *96*, 1840–1891.

Ripley, B. D. (1981). *Spatial Statistics* (1st ed.). John Wiley & Sons, Inc. https://doi.org/10.1002/0471725218.fmatter

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., & Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, *7*(6), 395–402. https://doi.org/10.1038/nclimate3303

Senecal, D., Kneeshaw, D., & Messier, C. (2004). Temporal, spatial, and structural patterns of adult trembling aspen and white spruce mortality in Quebec's boreal forest. *Canadian Journal of Forest Research*, *34*(2), 396–404.

https://doi.org/10.1139/x03-263

Simard, A. M., Bergeron, Y., & Sirois, L. (1998). Conifer Seedling Recruitment in a Southeastern Canadian Boreal Forest : The Importance of Substrate. *Journal of Vegetation Science*, *9*(4), 575–582.

Splawinski, T. B., Cyr, D., Gauthier, S., Jetté, J. P., & Bergeron, Y. (2019). Analyzing risk of regeneration failure in the managed boreal forest of northwestern quebec. *Canadian Journal of Forest Research*, *49*(6), 680–691. https://doi.org/10.1139/cjfr-2018-0278

Sprugel, D. G., Rascher, K. G., Gersonde, R., Dovčiak, M., Lutz, J. A., & Halpern, C. B. (2009). Spatially explicit modeling of overstory manipulations in young forests: Effects on stand structure and light. *Ecological Modelling*, *220*(24), 3565–3575. https://doi.org/10.1016/j.ecolmodel.2009.07.029

Stoll, P., & Bergius, E. (2005). Pattern and process: Competition causes regular spacing of individuals within plant populations. *Journal of Ecology*, *93*(2), 395–403. https://doi.org/10.1111/j.0022-0477.2005.00989.x

Weir, J. M. H., & Johnson, E. A. (1998). Effects of escaped settlement fires and logging on forest composition in the mixedwood boreal forest. *Canadian Journal of Forest Research*, *28*(3), 459–467. https://doi.org/10.1139/x98-001

Wiegand, T., & Moloney, K. A. (2014). *Handbook of Spatial Point- Pattern Analysis in Ecology*. CRC Press.

Yasuda, A., Yoshida, T., Miya, H., & Harvey, B. D. (2013). An alternative management regime of selection cutting for sustaining stand structure of mixed forests of northern Japan: A simulation study. *Journal of Forest Research*, *18*(5), 398–406. https://doi.org/10.1007/s10310-012-0362-1