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NATURELLES DANS LES PEUPELEMENTS D'*ABIES BALSAMEA*-*BETULA* SPP.
DU SUD DU QUÉBEC : EXAMEN DES VARIABLES SPATIO-TEMPORELLES
QUI AFFECTENT LA DIVERSITÉ ET L'ABONDANCE DE LA VÉGÉTATION

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NATURAL DISTURBANCE DYNAMICS IN *ABIES BALSAMEA*-
BETULA SPP. BOREAL MIXEDWOODS OF SOUTHERN QUEBEC:
EXAMINATION OF SPATIO-TEMPORAL FACTORS AFFECTING WOODY
VEGETATION DIVERSITY AND ABUNDANCE

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DEDICATION PAGE

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LIST OF ABBREVIATIONS AND ACRONYMS USED

ANOVA	Analysis of variance
CANOCO	Canonical ordination statistical analysis software
DCA	Detrended Correspondence Analysis
GLM	General Linear Model
MNR/	Ministry of Natural Resources/Ministère de Ressources
MRNQ	Naturelles et de la Faune du Québec
NRC	Natural Resources Canada
NSERC	Natural Sciences and Engineering Research Council of Canada
PAST	Paleontological Statistics software package for education and analysis
RDA	Redundancy Analysis
SEM	Standard error of the mean
SFMN	Sustainable Forest Management Network
SPSS	Statistical Package for the Social Sciences
TVE	Total Variance Explained

LIST OF SYMBOLS USED

α	Alpha (Type I error rate), also refers to alpha diversity
β	Sørensen's similarity index
β	Beta diversity
H'	Shannon's diversity index
J	Evenness
R	Species richness
R^2	Statistical measure quantifying the square of the coefficient of correlation
S	Gamma diversity

RÉSUMÉ GÉNÉRAL

Les perturbations naturelles sont des processus fondamentaux qui produisent des changements dans les écosystèmes forestiers. Les changements spatio-temporels dans l'assemblage des communautés forestières et les réponses individuelles des espèces aux perturbations naturelles dans des peuplements de *Abies balsamea*-*Betula* spp. ont été examinés. Je me suis intéressé à: (a) décrire la diversité et l'abondance des espèces après des perturbations de sévérité modérée, et les principaux facteurs qui affectent les réponses, (b) comparer la diversité et l'abondance des espèces au sein de trois régions distinctes, au niveau physiographique, à travers la zone boréale mixte, (c) examiner la diversité et l'abondance des espèces par rapport aux différents niveaux de mortalité causés par des perturbations naturelles (les trouées de canopée, les perturbations de sévérité modérée, le feu catastrophique), et (d) déterminer la variation des intervalles de retour pour les diverses perturbations représentant les composantes principales du régime de perturbations naturelles à travers la zone de forêt boréale mixte du Québec, Canada (à noter que cette section est dans l'Annexe 1). Les ordinations canoniques, les indices de diversité et les modèles univariés furent les principaux outils analytiques utilisés pour examiner les réponses de la végétation.

Les facteurs écologiques comme la composition du peuplement avant la perturbation et la densité de débris ligneux grossiers ont fortement influencé la diversité et l'abondance de la végétation à la suite de perturbations de sévérité modérée, alors que les types de perturbations n'ont eu que des impacts mineurs sur les patrons.

Différentes séries de facteurs ont déterminé la diversité et l'abondance de la végétation ligneuse après perturbation à travers la zone de forêt boréale mixte, avec l'importance d'un facteur particulier dépendant des caractéristiques spécifiques de l'habitat local. La composition du peuplement avant perturbation et la densité de débris ligneux grossiers furent les seuls facteurs affectant fortement la diversité et l'abondance dans tous les emplacements examinés. La variation dans la diversité alpha (α), gamma (S), et bêta (β) a été observée à travers la région. Shannon's H' était le plus haut le long de la Côte Nord et le plus bas dans la Péninsule Gaspésienne. Les valeurs de evenness (J) indiquent que la variation dans les abondances relatives des espèces d'arbres de la canopée était plus grande le long de la Côte Nord par rapport à la Péninsule Gaspésienne. Les sites trouvés en Temiskaming-Abitibi ont eu des valeurs intermédiaires pour H' et J . Pourtant, malgré des différences physiographiques considérables à travers la région, des patrons de régénération similaires ont été observés partout, avec les peuplements convergeant généralement vers la prédominance de résineux à la suite de perturbations de sévérité modérée.

Les trouées de canopée et les perturbations de sévérité modérée n'ont pas changé le cours de la succession, tandis que les feux catastrophiques ont modifié substantiellement la communauté végétale, les espèces de début de succession intolérantes à l'ombre devenant dominantes. La densité et la diversité des espèces d'arbres et arbustes de sous-étage, mi-tolérantes et intolérantes à l'ombre ont augmenté alors que la mortalité augmentait. Les estimations de richesse d'espèces les plus élevées furent observées suite aux feux catastrophiques, plusieurs des espèces s'établissant exclusivement sous ces conditions. L'abondance relative de la régénération d'arbres de la canopée fut la plus similaire suite à des trouées de canopée et des perturbations de sévérité modérée. Au niveau de la communauté d'arbustes et d'arbres de sous-étage, les abondances relatives des espèces ont été les plus similaires suite à des perturbations de sévérité modérée et des feux catastrophiques. Les réponses de la végétation aux perturbations de sévérité modérée ont donc eu des traits communs avec les deux extrêmes du gradient de mortalité causé par des perturbations naturelles, mais pour des strates de régénération différentes. Ainsi, un changement graduel et linéaire dans les abondances relatives d'espèces ; c.-à-d., de tolérant à intolérant à l'ombre avec des niveaux de mortalité croissants, n'a pas été observé. On a plutôt remarqué des seuils où des changements soudains et importants dans la composition de la communauté sont arrivés, les limites de ces changements étant dépendants de la strate de végétation en question.

Les intervalles de retour estimés pour des trouées de canopée, des perturbations de sévérité modérée et des feux catastrophiques furent respectivement de 30, 39, et entre 170 et 250 ans. Pour la tordeuse des bourgeons d'épinette et le chablis total, ceux-ci furent respectivement de 40 et 17 000 ans. L'agrégation spatiale des divers types de perturbations a été observée, certains secteurs étant plus enclins à l'apparition d'épidémies de tordeuse des bourgeons d'épinette ou au chablis total. L'émergence d'épidémies de tordeuse des bourgeons d'épinette fut dépendante de la densité de sapin baumier présente. Les chablis totaux ont eu tendance à arriver près des secteurs plats et dépressions présents à proximité des lacs dans les emplacements continentaux, alors que les chablis des emplacements côtiers ont plutôt été associés avec les conditions de haut de pente.

Les patrons et processus spatio-temporels de perturbations naturelles dans les forêts boréales mixtes d'*Abies balsamea*-*Betula* spp. sont conformes à un régime de perturbations caractérisé par des événements fréquents et partiels et des événements rares et catastrophiques. Dès lors, la prédominance de conditions associées aux forêts de fin de succession à travers le paysage est favorisée. Le régime actuel de perturbations diffère nettement des modèles historiques des 400 dernières années, caractérisés par la prédominance des feux catastrophiques comme types de perturbations. L'augmentation prévue des intervalles de temps entre feux catastrophiques peut ainsi mener à une diversité de végétation réduite dans le système.

Mots clés: dynamique de perturbations naturelles; trouées de canopée; perturbations de sévérité modérée; tordeuse des bourgeons d'épinette; chablis total; feu catastrophique; diversité et abondance de la végétation ligneuse; intervalles de retour; forêt boréale mixte de *Abies balsamea*-*Betula* spp.

GENERAL ABSTRACT

Natural disturbance is a fundamental process that generates change in forested ecosystems. Spatio-temporal changes in forest community assembly and individual species responses to natural disturbances within *Abies balsamea*-*Betula* spp. boreal mixedwood forests were investigated. I focused on: (a) describing species diversity and abundance after moderate-severity disturbances and the principal factors affecting response, (b) comparing and contrasting species diversity and abundance after moderate-severity disturbances among three, physiographically distinct locations across the boreal mixedwood region, (c) examining species diversity and abundance in relation to different levels of disturbance-caused mortality (canopy gap, moderate-severity disturbance, catastrophic fire), and (d) determining the variation in return intervals for various disturbances representing the main components of the natural disturbance regime across the boreal mixedwood region of Quebec, Canada (note that this section is in Appendix 1). Canonical ordination, diversity indices, and univariate models were the principal analytical tools used to investigate vegetation responses.

Environmental factors such as stand composition prior to disturbance and density of coarse woody debris strongly influenced woody vegetation diversity and abundance after moderate-severity disturbances, whereas the various moderate-severity disturbance types had only minor effects on patterns.

Different suites of factors determined post-disturbance woody vegetation diversity and abundance across the boreal mixedwood region, with the importance of any one factor dependent on specific local habitat characteristics. Stand composition prior to disturbance and density of coarse woody debris were the only factors strongly affecting diversity and abundance throughout the entire study region. Variation in alpha (α), gamma (S), and beta (β) diversity was observed across the region. Shannon's H' was highest along the North Shore and lowest in the Gaspé Peninsula. Evenness (J) values indicate greater variation in canopy tree species relative abundances along the North Shore relative to the Gaspé Peninsula. Sites in Temiskaming-Abitibi had intermediate values for both H' and J . Despite considerable physiographical differences across the region, similar regeneration patterns occurred throughout, as stands generally converged towards conifer dominance after moderate-severity disturbance.

Canopy gap and moderate-severity disturbances did not alter the course of succession whereas catastrophic fire substantially altered the vegetation community, as early successional, shade-intolerant species became dominant. Density and diversity of mid-tolerant and shade-intolerant understory tree and shrub species increased as the amount of mortality increased. Highest species richness estimates were observed after catastrophic fire, with several species establishing exclusively

under these conditions. Relative abundance of the canopy tree regeneration was most similar after canopy gap and moderate-severity disturbances. For the sub-canopy tree and shrub community, relative species abundances were most similar after moderate-severity disturbances and catastrophic fire. Vegetation responses to moderate-severity disturbances thus had commonalities with both extremes of the disturbance-caused mortality gradient, but for different regeneration layers. Thus, a gradual, linear change in relative abundances of species; i.e., from shade-tolerant to shade-intolerant with increasing mortality levels, was not observed. Rather, threshold points where sudden, large changes in community composition occurred, with the limits for change being dependent on the vegetation layer in question.

Return interval estimates for canopy gap, moderate-severity, and catastrophic fire disturbances were 30, 39, and between 170 and 250 years, respectively. Spruce budworm outbreak and windthrow return intervals were approximately 40 and 17 000 years, respectively. Spatial aggregation of specific disturbance types was observed, as certain areas were more prone to budworm outbreak and windthrow. Budworm outbreak was contingent on the density of balsam fir. Windthrow tended to occur near low lying areas near lakes in continental locations because of shallow root systems, whereas windthrow in coastal locations was associated with high slope conditions.

Spatio-temporal patterns and processes of natural disturbances within *Abies balsamea*-*Betula* spp. boreal mixedwood forests are consistent with a disturbance regime characterised by frequent, partial events and rare, catastrophic events. Subsequently, dominance of late-successional forest conditions throughout the landscape is promoted. The current disturbance regime markedly differs from historical patterns over the last 400 years, wherein catastrophic fires were the predominant disturbance type. The projected increase in time intervals between catastrophic fires may thus lead to reduced vegetation diversity within the system.

Key words: natural disturbance dynamics; canopy gap disturbance; moderate-severity disturbance; spruce budworm outbreak; windthrow; interaction disturbance; catastrophic fire; woody vegetation diversity and abundance; return interval; *Abies balsamea*-*Betula* spp. boreal mixedwood forests.

PROLOGUE

My research examines stand, landscape, and regional woody vegetation regeneration patterns in the context of the interrelationships between the natural disturbance regime, abiotic conditions, and biotic processes (Figure P.1). My thesis is composed of five chapters. Chapter I outlines my specific research goals. Chapters II through IV are specific research articles that focus on the following questions: How do disturbance type, site characteristics, and the amount of disturbance-caused mortality affect post-disturbance species diversity and abundance? What are the principal factors or mechanisms regulating vegetation responses? Are vegetation responses even predictable? Lastly, if so, are responses consistent throughout the region? Chapter V provides a synthesis of my results while information on temporal aspects of natural disturbances is included in Appendix A.

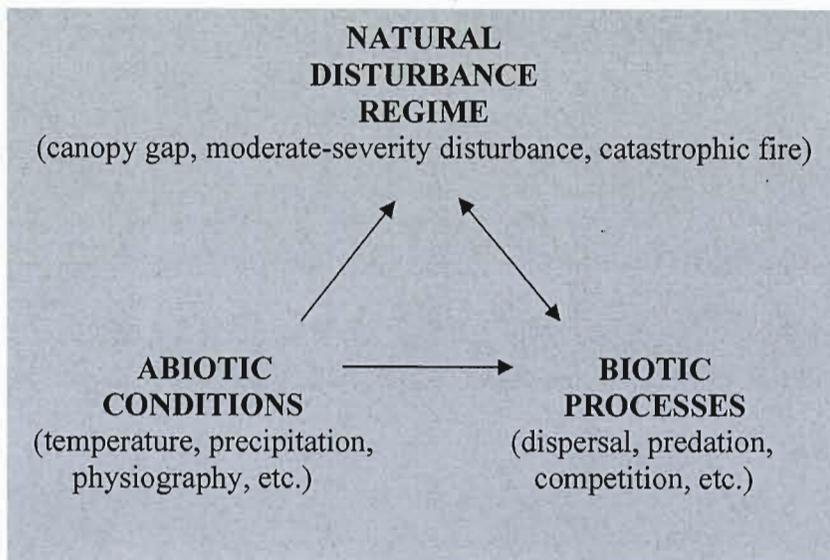


Figure P.1. Principal factors and mechanisms regulating vegetation responses.

CHAPTER I

GENERAL INTRODUCTION

1.1. The natural disturbance spectrum

Natural disturbance is a fundamental process that produces variation in forest structure and composition. Eastern boreal mixedwood forests are influenced by a variety of natural disturbance agents operating at multiple spatial and temporal scales. Over the last few centuries, however, a significant decrease in fire frequency has occurred (Bergeron et al. 2001), suggesting that partial disturbances now play more prominent roles in stand dynamic patterns than previously observed. While generally accepted that old, eastern boreal mixedwood forests have a multi-cohort structure, and frequently undergo partial disturbances (Frelich and Lorimer 1991, Chen and Popadiuk 2002, Hebert 2003, De Römer et al. 2007), most studies in these forests have placed emphasis on canopy gap dynamics (disturbances smaller than 0.2 ha) (e.g., Kneeshaw and Bergeron 1998, Hebert 2000). Examination of larger, more severe partial disturbances; i.e., moderate severity-disturbances, such as those caused by varying levels of windthrow, insect infestations, ice storms, and drought is relatively uncommon (Seymour et al. 2002). Accordingly, my research focuses attention on moderate-severity disturbances, but places them in the context of the spectrum of natural disturbances (canopy gap, moderate-severity disturbance, catastrophic fire) occurring in eastern boreal mixedwoods.

1.2 Definitions

Before continuing further, a few important definitions are presented here to clarify site descriptions and various concepts used throughout the text:

- a) *Boreal mixedwoods* are defined as “a tree community on a boreal mixedwood site in which no single species comprises 80 % or more of the total basal area”

- (MacDonald 1995); specifically for my research presented here, *Abies balsamea* and *Betula* spp. were always important components of the overstory prior to natural disturbance.
- b) *Biological legacies* refer to both the live and dead material originating from the pre-disturbed stand. Over time, standing dead trees become *coarse woody debris* (downed logs on the forest floor), providing substrate for seed establishment and structural diversity to the stand for several decades after disturbance. Note that *legacy trees* refer to mature canopy trees that survived the disturbance event. These trees act as potential seed sources and can provide partial shade to the regeneration layer. Legacy trees may also be more susceptible to windthrow given their exposed positions in a site and lack of protection from surrounding trees.
 - c) *Canopy gap disturbances* are partial disturbances that kill one to a few canopy trees (Runkle 1992). Canopy gap disturbances result in less than 0.2 ha contiguous canopy mortality. Causes of individual tree mortality include insect outbreaks, windthrow, senescence, and disease.
 - d) *Catastrophic disturbances* are severe disturbances causing extensive mortality to both canopy and regeneration layers; e.g., catastrophic fire. For the purposes of my thesis, contiguous canopy mortality of at least 0.2 ha, with more than 75 % mortality of the canopy trees and the pre-disturbance regeneration layer within the affected area, were the mortality levels required to be considered catastrophic.
 - e) *Intensity* is “the amount of energy released by the physical process of disturbance” (Frelich 2002).
 - f) *Interaction disturbance* refers to a series of disturbances affecting the same area prior to complete canopy recovery from an initial disturbance episode. It is generally unknown whether additive or multiplicative effects of different disturbances are predictable from the independent effects of each disturbance and/or if effects are dependent on the type or timing of the subsequent disturbance (see Paine et al. 1998, Kulakowski et al. 2003, Payette and Delwaide 2003).

- g) *Moderate-severity disturbances* are partial disturbances resulting in at least 0.2 ha contiguous canopy mortality, corresponding roughly to estimates provided by Seymour et al. (2002). An upper limit is not firmly specified, as the spatial extent of moderate-severity disturbances can be quite extensive, some being similar in size or larger than catastrophic disturbances. Differences between these two disturbance classes are primarily determined by effects on the regeneration layer. The regeneration layer is usually unaffected or only partially disturbed after moderate-severity disturbances whereas more than 75 % of the regeneration layer is consumed after catastrophic fire. Moderate-severity disturbances can be the result of a single or multiple disturbance events; i.e., *interaction disturbance* (Harcombe et al. 2004, Lorimer and White 2003). Moderate-severity disturbances are caused by a number of disturbance agents including the spruce budworm (*Choristoneura fumiferana*), other insect pests (e.g., *Dendroctonus* spp., *Malacosoma disstria*), windthrow, flood, fire, and ice storms.
- h) *Multi-cohort* refers to a stand containing at least three distinct age or size classes.
- i) *Natural disturbances* are the primary driver of ecosystem change. They are caused by any number of agents including insect outbreaks, windstorms, ice storms, fire, disease, etc. that result in varying degrees of mortality to the vegetation community.
- j) *Return interval* is the time period between successive disturbances occurring in the same sampled area (see Zhang et al. 1999).
- k) *Severity* refers to the proportion of trees (canopy and regeneration layers) in a given area killed during a disturbance episode (Frelich and Reich 1998).
- l) *Spruce budworm outbreaks* are a result of 20 to 50 year pseudo-periodic cycles of high population levels of the defoliating *Choristoneura fumiferana* larvae, causing synchronous, mass mortality to its principal host, *Abies balsamea*, and to a lesser extent *Picea mariana* and *Picea glauca* (Runkle 1982, Gray et al. 2000). Tree mortality occurs over a number of years, succumbing either to direct effects of defoliation or from a secondary cause as a result of the host's weakened state. Outbreak severity is correlated with the abundance of *Abies balsamea* (Bergeron and Harvey 1997, Kneeshaw and Bergeron 1999) and other stand-level attributes

(Blais 1961, MacLean and MacKinnon 1997, Bergeron and Leduc 1998, Gray et al. 2000).

- m) *Windthrow* is the uprooting or snapping of trees resulting from intense winds. Windthrow can cause mass stand mortality in a relatively short period of time. Windthrow hazard is influenced by local topography, edaphic properties, and stand characteristics (Mitchell 1995, Ruel 2000).

1.3. Disturbance size, severity, and type

Because of differences in structural and micro-environmental conditions after natural disturbances, disturbance size and severity can influence plant species diversity and abundance (Oliver 1981, Lorimer 1989, Peterson 2000). Greater abundance of pioneer species, for example, is often positively correlated with larger, more severe disturbances (Frelich and Reich 1998, Gromtsev 2002), while slower growing, shade-tolerant species are favoured after smaller, canopy gap disturbances (Kneeshaw and Bergeron 1998). Patterns of responses after moderate-severity disturbances remain largely unknown (Seymour et al. 2002). Moreover, various causal agents such as windthrow and the spruce budworm (*Choristoneura fumiferana*) can differentially influence disturbance dynamics, which can interact with other disturbances, the local climate, physiography, and stand structure and composition variables to further influence species diversity and abundance (Drobyshev and Nihlgard 2000, Ruel 2000, Sinton et al. 2000, Wimberly and Spies 2001, Cuevas 2003, Hebert 2003, Kulakowski et al. 2003, Lorimer and White 2003, Nagel and Diaci 2006).

Differences in temporal release of resources can influence the regeneration composition after natural disturbance (Krasny and Whitmore 1992, Kneeshaw and Bergeron 1998, Kneeshaw et al. 2008). Severe windthrow can favour shade-intolerant species, as the combination of sudden canopy openings and high levels of soil disturbance resulting from tree uprooting, creates microsites that facilitate establishment from seed rain, potentially substantially altering the canopy species composition (Oliver 1981, Peterson 2000, Nagel and Diaci 2006). Conversely, tree death by spruce budworm defoliation occurs over a number of years, resulting in a slower release of resources and generally lower levels of incident light available for

the regeneration layer (Kneeshaw and Bergeron 1999) relative to windthrow. So although budworm-caused disturbances may be quite extensive in size, regeneration patterns can be similar to that observed following canopy gap formation, wherein only structural, but not compositional changes occur (Bergeron 2000, Chen and Popadiouk 2002). However, some exceptions exist as conditions where budworm defoliation favours recruitment by shade-intolerant deciduous species have also been observed (MacLean 1984, Bergeron and Dansereau 1993), and can be important for the maintenance of species diversity within boreal mixedwoods (Kneeshaw and Bergeron 1999, Bouchard et al. 2006). Fir waves are another exception. They are a special type of wind disturbance associated with wind direction and rime ice accumulation that cause extensive needle loss and eventual tree death in a pattern that is a function of prevailing winds and the spatial distribution of fir within a stand (Sprugel 1976). Unlike severe windthrow, mortality is a relatively slow and cumulative process, and thus have temporal characteristics more like budworm defoliation.

Windthrow occurrence after budworm outbreak within the same stand; i.e., interaction disturbance, can result in further variability in regeneration diversity and abundance depending on timing of the second disturbance and local stand conditions. Species composition after budworm outbreak in stands in which balsam fir (*Abies balsamea*) and other shade-tolerant species have had sufficient time to re-establish dominance or wherein advance regeneration of these species was present in abundance, will likely not be substantially altered by subsequent windthrow (see Papaik and Canham 2006, Rich et al. 2007); this may not be the case if windthrow occurs soon after the outbreak, or if advance regeneration densities are low. Further, the proportion of uprooted *versus* snapped trees can affect relative species composition. Many shade-intolerant species require exposed mineral soils for germination and establishment (Zasada et al. 1992), and may thus be limited to establishing in and around tip-up mounds (Rich et al. 2007). Variation in the frequency of disturbances also affects long-term species diversity and relative abundance (Oliver 1981, Frelich and Reich 1998, Lassig and Mocalov 2000). If vegetation responses are substantially different after disturbances of varying type,

severity, and frequency, local and regional vegetation distribution patterns should reflect the current disturbance regime.

1.4. Environmental factors

Climate and physiography determine the regional species pool (Dansereau 1954, Neilson et al. 1992, Chen and Popadiouk 2002, Messaoud et al. 2007); however, spatial aggregation of species is often observed at local scales. Differences in local weather and wind patterns (Denton and Barnes 1987, Ruel 2000), stand history (Chen and Popadiouk 2002), edaphic conditions (Abella and Covington 2006), other physiographic features (Cogbill and White 1991, Bouchard et al. 2006), and neighbourhood effects (Frelich and Reich 1995, Kneeshaw and Bergeron 1999, LePage et al. 2000) have been shown to cause variation in species distribution. Some of these factors may also operate at different spatial scales, and can work synergistically with natural disturbances to further influence regeneration diversity and abundance (Ohmann and Spies 1998, Dupont et al. 1991, Baron et al. 2001, Wimberly and Spies 2001).

Research explaining vegetation recovery patterns from a number of physiographically distinct locations found throughout a large, contiguous region is relatively uncommon (but see Ohmann and Spies 1998, Vanderpoorten and Engels 2002). Instead, local patterns are often used to explain broader-scale dynamics (e.g., Schwilk et al. 1997). Note, however, that some of the variation found throughout a region may be overlooked. Differences may occur when local climate, physiography, and other site-specific attributes are not consistent with general, regional habitat conditions (Neilson et al. 1992, Messaoud 2007), potentially leading to misinterpretation or disagreement about expected changes in vegetation communities resulting from natural disturbances, or the role that certain environmental factors play in influencing vegetation responses. Examining patterns at a number of different locations across a region can thus help to resolve any contrasts by accounting for more variation, and can potentially link fine and broad-scale patterns of vegetation recovery to a few important variables that elicit consistent responses. Generalisations of this sort can help to explain system

complexity in a simpler manner, and can help to identify patterns that stimulate further hypotheses (White and Jentsch 2001).

1.5. Species diversity and abundance

A central theme of my thesis is to examine how species diversity and abundance are affected by natural disturbances. But why study biodiversity? Biodiversity is declining. Much is known about the causes of extinctions and for the drastic changes in community organisation, with most being directly or indirectly related to human activity that precipitates habitat loss and degradation (Dietz and Rosa 1994, Ehrlich 1994, van der Wal et al. 2008), but surprisingly very little about the consequences (Worm et al. 2006). Questions pertaining to how species respond to natural disturbances; e.g., which species are most sensitive, which are most resilient, how relative species composition and forest structure change after disturbances of varying magnitudes, etc., remain largely unknown for many ecosystems.

Compositional, structural, and functional attributes of plant species diversity can change after natural disturbance (e.g., McIntyre and Lavorel 1994, Naeem et al. 1994, Wapstra et al. 2003). Better understanding of these changes can provide information on the role biodiversity plays in ecosystem functioning, the levels of functional redundancy within a system, and the thresholds wherein major shifts in species composition occur. Undoubtedly, we need better understanding of the relationships between biodiversity and ecosystem functioning as much of this information remains unclear.

Loss of biodiversity is a key issue in managing our forested landscapes as it is evident that native species influence rates, timing and direction of general ecosystem processes (Whittaker 1960, Bormann and Likens 1979, Naeem et al. 1999, Loreau et al. 2001). Loss of biodiversity may also decrease the ability of forest ecosystems to adjust to environmental changes and reduce the number of options available for rehabilitation or restoration of damaged habitats (Naeem et al. 1994, Bolger 2001, Silver et al. 2002). Maintenance of healthy forest ecosystems is of particular concern when functional redundancy among species is low (Micheli and Halpern 2005), as is the case for boreal systems (Pastor et al. 1996).

Forest vegetation diversity can be assessed a number of different ways: *alpha* diversity (α) is the number of species within a single stand, *beta* diversity (β) reflects the change in species composition along an environmental gradient or series of stands, while *gamma* diversity (S) refers to the total species diversity of a large geographic region (Whittaker 1972, Whittaker 1977, Arrellano and Halffter 2003). Utilising the various diversity measures is important when assessing biodiversity, as values generally change in function of spatial scale (Crawley and Harral 2001, He et al. 2006). Further, different ecological processes and mechanisms influence community structure and composition at different spatial scales (Ricklefs 1987, Herzog and Kessler 2006, Seppä et al. 2009). Quantifying biodiversity at different spatial scales and understanding the processes and mechanisms that can affect these measures will thus provide a more comprehensive and thorough assessment of biodiversity when planning for conservation in managed and natural systems. This will ultimately help in developing better, more viable, and environmentally-conscious resource use practices, with improving restorative efforts, and for simply advancing our knowledge of our surrounding forest ecosystems.

1.6. Main objectives

My research provides needed information on stand, landscape, and regional woody vegetation regeneration patterns in the context of the interrelationships between the natural disturbance regime, abiotic conditions, and biotic processes. I pay particular attention to moderate-severity disturbances, but examine their effects in relation to the spectrum of natural disturbances (canopy gap, moderate-severity disturbance, catastrophic fire) occurring in eastern boreal mixedwoods. Ultimately my research will be used to help develop a forest management approach that best retains important structural elements and processes found after natural disturbances essential for maintaining biodiversity and natural ecosystem functioning.

1.7. Hypotheses

I addressed three main hypotheses shown and explained below. Note that a hypothesis is not exclusively addressed in any one chapter. Rather, they are generally relevant to all chapters. Nonetheless, the chapters wherein aspects of a main hypothesis are specifically addressed are noted in parentheses.

(a) *Regeneration diversity and abundance patterns are disturbance driven:*

There is a current emphasis on disturbance as the principal factor in determining forest composition and successional pathways (Frelich and Reich 1999, Frelich 2002, Schulte and Mladenoff 2005). I reasoned that if natural disturbances determine vegetation responses, then regeneration after a specific disturbance type and severity will follow similar trajectories (Chapters 2, 3, 4) irrespective of environmental differences among locations (Chapter 3), whereas different types of disturbances that cause similar levels of mortality will result in divergent post-disturbance vegetation communities; specifically, budworm outbreak *vs.* windthrow *vs.* interaction disturbance (Chapter 2). Divergent regeneration patterns can result because of the gradual *versus* sudden availability of light, space, and other resources after these disturbances (Kneeshaw and Bergeron 1998, Bellingham et al. 1996) and the variation in the capabilities of species to exploit these resources. Shade-tolerant species will be favoured after spruce budworm outbreak because of relatively slow canopy mortality whereas shade-intolerant species will rapidly colonise and dominate the regeneration layer after windthrow as canopy trees are snapped or uprooted during the disturbance event (Oliver 1981, Kneeshaw and Bergeron 1999, Shure et al. 2006). Regeneration after interaction disturbances will show intermediate patterns; much of the regeneration established after the initial budworm disturbance will remain unaffected by the subsequent windthrow. But some opportunity for seed establishment by shade-intolerant species will be available because of uprooting of snags and overstory legacy trees from the budworm outbreak that expose mineral soils. Secondly, vegetation responses to disturbances of different magnitudes will result in distinct post-disturbance communities; i.e., light resource availability is also tied to amount of disturbance-caused canopy mortality (e.g., Frelich and Reich 1998, Shure et al. 2006). Thus, an increased proportion of shade-intolerant species diversity and abundance is expected with increasing mortality levels (Chapter 4).

(b) *Regeneration diversity and abundance patterns are controlled by environmental factors:*

Past research has emphasized environmental variability as the principal factor driving vegetation establishment at stand and landscape scales (Dansereau 1954, Whittaker 1960, Osumi *et al.* 2003, Abella and Covington 2006). Variation in temperature, precipitation, physiography, and stand structure and composition both locally (Chapter 2) and across the boreal mixedwood region (Chapter 3) will result in differential species responses and thus variation in species distribution patterns. How species respond will be determined by individual species needs in terms of resource availability and adaptive mechanisms (e.g., responses to light availability, reproductive strategy (*r* vs. *K*), morphological adaptations, life history requirements, competition strategies, etc.) (e.g., Shure *et al.* 2006, Seppä *et al.* 2009, Ilison and Chen 2009) (Chapter 2, 3, 4).

(c) *Regeneration diversity and abundance patterns are a result of both natural disturbance and specific environmental factors:*

The occurrence of a particular natural disturbance type and severity is tied to the availability of specific environmental conditions (e.g., Foster *et al.* 1988). For example, the extent and severity of a spruce budworm outbreak is correlated with the relative abundance of mature *Abies balsamea* (Blais 1983, Morin *et al.* 2008), while windthrow is more likely to occur in older stands having shallow, wet soils, or on exposed slopes that face prevailing winds (Mitchell 1995, Ruel 2000, Nagel and Diaci 2006). Thus, regeneration diversity and abundance is a function of disturbance frequency (see Appendix 1) and the presence of specific environmental conditions that facilitate the onset of specific disturbance types (Chapters 2, 3, 4).

1.8. References

Please see the General Citation List (pp 133-154).

PROLOGUE TO CHAPTER II

I start the body of my thesis with the subject matter that enticed me to come over from the best coast of Canada to southern Québec in the first place: moderate-severity disturbance dynamics. It was amazing really. I left sunny Victoria, BC during a balmy 17 °C mid-February day to meet Dan in Montréal, QC to pursue the matter further. Up to that point in time, I had only ever experienced evil, ridiculously cold temperatures while standing inside a large freezer. Nonetheless, moderate-severity disturbances certainly interested me enough to extend my stay for a number of years (although I didn't start until the following summer ☺). It is the central theme of my thesis, and is an interesting area of research definitely requiring further study. Seymour *et al.* (2002), for example, indicate that natural disturbances of sizes and frequencies between small canopy gap and large catastrophic disturbances have rarely been addressed; and upon completion of my thesis, only a handful of articles have since been published on the matter. Here, I focus on woody vegetation responses to moderate-severity disturbances, in terms of diversity and abundance, and determine the principal factors driving patterns. Please note that the version shown here is slightly modified from the version published in *Ecoscience*. Grammatical revisions have been made and supplementary information is now included in Appendix G - as requested by my examining committee during my dissertation.

CHAPTER II

MODERATE-SEVERITY DISTURBANCE DYNAMICS IN *ABIES BALSAMEA* - *BETULA PAPYRIFERA* FORESTS: THE RELATIVE IMPORTANCE OF DISTURBANCE TYPE AND LOCAL STAND AND SITE CHARACTERISTICS ON WOODY VEGETATION RESPONSE

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2.1.1 Résumé

Une mortalité soudaine ou graduelle après une perturbation peut avoir un effet différent pour les assemblages relatifs d'espèces, mais les caractéristiques locales biotiques et abiotiques de l'habitat peuvent modifier les patrons attendus. Les réponses de la végétation ligneuse à des perturbations de sévérité modérée ont été caractérisées et comparées en lien avec les caractéristiques du peuplement et du site avant et après la perturbation dans les peuplements de *Abies balsamea*-*Betula* spp. du sud-est du Québec, Canada. Les perturbations ont été causées par la mortalité graduelle due à la tordeuse de bourgeons de l'épinette (*Choristeneura fumiferana*), par la mortalité soudaine due à un chablis ou à une combinaison des deux. Une analyse de redondance avec sélection ascendante a été utilisée pour ordonner l'importance du type de perturbation et des variables associées aux caractéristiques locales du peuplement et du site sur les patrons de régénération des espèces. En ordre descendant d'importance, la composition du peuplement avant la perturbation, la densité de débris ligneux grossiers, le pourcentage de la pente, la distance du peuplement de conifères le plus près, la densité des arbres feuillus résiduels, la perturbation causée par la tordeuse de bourgeons de l'épinette, et le drainage du sol étaient importants pour déterminer la composition en espèces après la perturbation. Aucun patron de régénération distinct n'était associé au chablis ou à une interaction entre les types de perturbations. Même si les perturbations de sévérité modérée avaient un effet sur la distribution des espèces, les caractéristiques locales biotiques et abiotiques du peuplement et du site, particulièrement la composition du peuplement avant la perturbation et la densité de débris ligneux grossiers, étaient plus importantes pour déterminer les patrons de distribution des espèces après la perturbation.

Mot-clés: dynamique de perturbation de sévérité modérée, régénération dans des forêts de *Abies balsamea*-*Betula* spp.

Nomenclature: Gleason and Cronquist (1991)

2.1.2 Abstract

Sudden *versus* gradual mortality of canopy trees can differentially affect relative species assemblages after disturbance, although local biotic and abiotic habitat characteristics can modify expected patterns. Woody vegetation responses to moderate-severity disturbances were characterised and compared in relation to pre- and post-disturbance stand and site characteristics within *Abies balsamea*-*Betula* spp. stands of southeastern Quebec, Canada. Disturbances were caused by gradual mortality due to the spruce budworm (*Choristoneura fumiferana*), sudden mortality due to windthrow, or a combination of both. Redundancy Analysis with forward selection was used to rank the importance of disturbance type and local stand and site characteristic influences on species regeneration patterns. In order of decreasing importance, stand composition prior to disturbance, density of coarse woody debris, percent slope, distance to nearest conifer stand, density of deciduous legacy trees, spruce budworm disturbance, and soil drainage were significant determinants of post-disturbance species composition. No distinct regeneration patterns were associated with windthrow or interaction disturbance types. Although moderate-severity disturbances affected species distribution, local biotic and abiotic stand and site characteristics, particularly pre-disturbance stand composition and density of coarse woody debris, were more important in determining post-disturbance species distribution patterns.

Key words: moderate-severity disturbance dynamics, regeneration in *Abies balsamea*-*Betula* spp. forests.

Nomenclature: Gleason and Cronquist (1991)

2.2. Introduction

Abies balsamea-*Betula* spp. forest stands are influenced by a variety of natural disturbance agents operating at multiple spatial and temporal scales. Severe fire has historically been the primary disturbance agent affecting vegetation composition for this system (Bergeron et al. 2001). In the last few centuries, however, a significant decrease in fire frequency has likely occurred in eastern North America (Bergeron and Archambault 1993, Lauzon et al. 2007), suggesting that partial disturbances may now play larger roles in stand dynamic patterns than in the recent past.

While it is understood that the majority of old *Abies balsamea*-*Betula* spp. forests frequently undergo partial disturbances (Chen and Popadiuk 2002), most studies of partial disturbances in this forest type have focused on gap dynamics (e.g., Kneeshaw and Bergeron 1998). Examination of larger partial disturbances, i.e., those of moderate severity, has not been well addressed (Seymour et al. 2002).

Studies of regeneration patterns after natural disturbances have focused on either disturbance type (Osawa 1994, Shimizu 2005) or local environmental variables (Heinselman 1981, Millward and Kraft 2004, Clarke et al. 2005) as principal factors influencing vegetation response. Few researchers have, however, examined their relative importance in a single study. While causal agents such as spruce budworm (*Choristoneura fumiferana*) and windthrow can differentially influence regeneration dynamics (e.g., through gradual *versus* sudden availability of light and growing space, amount of soil disturbance, resulting seedbed quality, area to perimeter ratios), disturbances can also have interactive effects when occurring successively in a stand (Kulakowski et al. 2003). Local habitat characteristics such as stand composition prior to disturbance, seed source and seed bed availability, and abiotic conditions can further interact with disturbance type to affect long-term stand dynamic patterns and processes (Dupont et al. 1991, Huebner and Vankat 2003, Lorimer and White 2003, Osumi et al. 2003). For *Abies balsamea*-*Betula* spp. stands, it remains unclear which of these factors (if any) influence post-disturbance stand composition. Further, the relationship between disturbance and species diversity has received much attention (Pickett et al. 1989, Roberts and Gilliam 1995).

Species diversity is often greatest after intermediate levels of disturbance severity or frequency (Connell 1978). Yet information on how moderate-severity disturbances affect species diversity within *Abies balsamea*-*Betula* spp. forests is lacking.

The purpose of our study is to examine compositional changes in forest vegetation following contrasting moderate-severity disturbances, focusing on tree and shrub species responses. Specifically, we determine the relative influence of disturbance type and a suite of local stand and site characteristics on subsequent regeneration patterns, and discuss possible mechanisms for the observed responses. Secondly, we compare tree and shrub species diversity in relation to disturbance type and stand composition prior to disturbance.

2.3. Study area

Abies balsamea-*Betula* spp. stands located in the Chaleur Bay region of the Gaspé Peninsula, Quebec, Canada (between 48°10' to 48°35'N and 65°45' to 66°15' W) were sampled. This forest type is characteristic of the boreal mixedwood forest zone of Quebec, a vegetation zone marking the transition to the boreal forests to the north and north-temperate deciduous forests to the south. The study sites are part of the Temiscouata-Restigouche section (L.6) of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). Fire cycles for the region are relatively long, with catastrophic fires occurring every 170 to 250 years (Lauzon et al. 2007). *Abies balsamea*, *Betula papyrifera* and *Betula alleghaniensis* dominate the canopy layer. *Picea glauca*, *Picea mariana*, and *Acer rubrum* can also be abundant in some sites while *Thuja occidentalis*, *Pinus strobus* and *Acer saccharum* are occasionally present.

Climate is humid-continental, with long cold winters and short summers (Landry et al. 2002). Mean minimum daily temperature of the coldest month is -16 °C (January) while mean daily maximum of the warmest month is 23 °C (July). Precipitation is high, averaging 984 mm annually, with approximately 79 % falling as rain (Environment Canada 2004). Topography is rolling to montane with several rivers and very few lakes interspersed. Much of the forested area lies between 80 and 600 m elevation (mean 286 m). Soils are derived from thin glacial tills, glaciolacustrine, fluvio-lacustrine, or alteration deposits (defined as deposits that are physically or chemically modified as a result of heat, pressure, or other post-

depositional conditions) (Robitaille and Saucier 1998). The soil moisture regime for our study area is classified as xeric-mesic to mesic, while soil drainage ranges from imperfect to rapid.

2.4. Methods

We define moderate-severity disturbances as those creating a minimum canopy opening of 0.2 ha. Smaller canopy disturbances were considered to be undergoing gap dynamics (Kneeshaw and Bergeron 1998). An upper spatial limit is not firmly specified, as moderate-severity disturbances can be quite extensive, differing primarily in relation to severity with catastrophic fire. Moderate-severity disturbances principally affect the canopy layer whereas the majority of both canopy and regeneration layers are destroyed after catastrophic fire. All moderate-severity disturbances we sampled had at least 75 % mortality of canopy trees within the disturbed area. This was initially assessed from forest inventory maps and verified in the field with counts of snags, coarse woody debris, and surviving legacy trees. In all sites, some coniferous and/or deciduous canopy trees survived the disturbance episode. Further, at least part of each disturbed site was adjacent to mature and intact *Abies balsamea*-*Betula* spp. stands that could also act as a seed source. Moderate-severity disturbances causing between 50 and 74 % canopy mortality are also common in the region. We restricted sampling to more severe moderate-severity disturbances as it is difficult to differentiate canopy gap dynamics from more severe partial disturbances within this range of canopy mortality. Prévost and Pothier (2003), for example, note that light level transmission does not significantly change in aspen-conifer mixedwood stands until >50 % canopy mortality has occurred, while Pham et al. (2004) report gap dynamics to occur with as much as 60 % canopy opening.

Spruce budworm and windthrow disturbances, separately and through their interaction, cause the majority of moderate-severity disturbances within *Abies balsamea*-*Betula* spp. forests of southeastern Quebec. Relative species composition of the forest canopy can be quite variable within this forest type. We restricted sampling of the three disturbance types to stands having two of the more common relative species compositions: stands were either conifer-dominated (≥ 75 % density

of conifers in canopy) or mixed coniferous-deciduous (50-74 % density of conifers in canopy) prior to disturbance. In all cases, *Abies balsamea* represented at least 60 % of the density of all conifer trees prior to disturbance.

We examined regeneration patterns after the most recent province-wide spruce budworm epidemic, which occurred between 1965 and 1992 (Gray et al. 2000). Defoliation was moderate to severe (≥ 35 to 100 %) (Archambault et al. 2006), causing extensive mortality to *Abies balsamea*, its principal host, in many *Abies balsamea*-*Betula* spp. stands in the region (Blais 1983). For comparison of stands disturbed by spruce budworm with those having undergone windthrow or interaction disturbances, we chose stands that were of similar mean age, height, and tree density prior to disturbance, had similar soil moisture and soil drainage regimes, experienced similar levels of canopy mortality resulting from a moderate-severity disturbance, and had a similar number of years elapsed since the initial moderate-severity disturbance episode (Table 2.1). Disturbance type was initially assessed from forest inventory maps provided by the Quebec Ministry of Natural Resources (QMNR), then verified in the field. Death of the majority of severely affected trees occurred 21 ± 1.2 (mean \pm SE) years ago for sites experiencing spruce budworm disturbance and 20 ± 1.0 years ago for those disturbed by windthrow. For sites experiencing interaction disturbance, subsequent windthrow occurred 9 ± 0.5 years after the initial spruce budworm disturbance. Thus, we believe comparisons of regeneration patterns among disturbance types to be justifiable as results were not confounded by large differences in pre-disturbance stand conditions, disturbance severity or in post-disturbance stand age.

Three to six, 20 x 20 m quadrats were established within each stand for each type of moderate-severity disturbance examined. In every quadrat, density of tree and shrub regeneration was quantified according to size class [(1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 m), (3) 4 to 8 cm dbh] using a nested plot design: class 1 seedlings in a 5 x 10 m area, class 2 seedlings in a 10 x 10 area, and those in class 3 using the entire 20 x 20 m quadrat. Snags (standing dead trees >10 cm dbh) and coarse woody debris (fallen trees >10 cm dbh) were identified to species and their densities were determined using the entire quadrat area. Coarse woody debris was

classed as uprooted or snapped. Five individuals of the largest regenerating shade-intolerant species [e.g., *Betula papyrifera*, *Sorbus* spp., or *Prunus pensylvanica*] were cut at ground level to obtain estimates of year of establishment, and thus time since disturbance. When these species were not available, timing of release of *Abies balsamea* advance regeneration was determined using the same methods.

Density of legacy trees, defined as mature canopy trees that survived the moderate-severity disturbance, within a 35 m radius of the quadrat centre was determined, as was distance of the quadrat to the nearest remnant mature conifer-dominated and mixed coniferous-deciduous stand (proximity to seed sources). Slope (grouped into the following classes: (1) 0 to 10°, (2) >10 to 20°, (3) >20 to 30°, (4) >30 to 40°, (5) >40°) and elevation were calculated using a clinometer and GPS unit, respectively. Aerial photos, a GIS database, and eco-forestry maps were used to determine canopy composition prior to disturbance, soil moisture, soil drainage class (grouped as follows: (1) excessive, (2) rapid, (3) good, (4) moderate, (5) imperfect, (6) poor, (7) very poor), and surface deposits. No sign of human impacts to the forest canopy was evident prior to disturbance, nor did any forest interventions occur (e.g., thinning, salvage logging) until after sampling was completed.

2.5. Analyses

We determined the relative contributions of spruce budworm, windthrow, and interaction disturbance types and local stand and site characteristics to natural regeneration patterns, in terms of species density, by inputting all of these factors as environmental variables in analysis. *Stand composition prior to disturbance variables* were: conifer-dominated or mixed coniferous-deciduous canopy and stand density. *Seed source and seed bed variables* were: distance to nearest conifer-dominated or mixed coniferous-deciduous stand, density of coniferous or deciduous legacy trees, density of snags, density of coarse woody debris, and proportion of coarse woody debris uprooted *versus* snapped. *Abiotic habitat characteristic variables* were: soil drainage and percent slope. Canonical ordination techniques were used to examine the relationship between woody vegetation density (dependent variable) and these environmental variables. Detrended correspondence analysis (DCA) using CANOCO 4.02 software (ter Braak and Smilauer 1998) showed density

data to have only a weak unimodal distribution along the gradients extracted by DCA (lengths of gradients were 2.5, 2.4, 2.2, and 1.9 SD for axes 1 to 4, respectively). Therefore, Redundancy analysis (RDA), a constrained linear canonical ordination technique, was used (van den Wollenberg 1977). The forward selection option was implemented to both rank the importance of environmental variables in predicting species distribution patterns, and to exclude redundant environmental variables from the model. The procedure was as follows: the environmental variable best fitting the species data was selected first, followed by the inclusion of the next best fitting variable, and so forth, until additional variables no longer significantly contributed to explaining the remaining observed variation. The significance of the explanatory effect of an environmental variable was determined using the Monte Carlo permutation test (500 permutations, $\alpha = 0.05$) prior to the addition of the next best fitting variable. Rare species were down-weighted in DCA and all data were \log_{10} transformed for both DCA and RDA prior to analyses. All other default options were applied.

Species richness (S), defined as the total number of tree and shrub species, Shannon's diversity index:

$$H' = - \sum p_i \ln p_i \quad [1]$$

where p_i = proportion of the total sample belonging to species i (in this case the relative density of a species), and evenness (J):

$$J = H' / \ln S \quad [2]$$

where J is an index of how relative abundances are distributed among species (Pielou 1966), were determined for each site, and compared in relation to disturbance type and stand composition prior to disturbance using GLM procedures (factorial ANOVA) (SPSS 10.0 1999). The Student-Newman-Keuls multiple range test ($\alpha = 0.05$) was used for post-hoc comparisons. Data transformation was unnecessary as

S , H' , and J data met the parametric assumptions of normality and homogeneity of variances among treatment groups (Zar 1996).

2.6. Results

2.6.1. General species distribution patterns in relation to disturbance type and stand composition prior to disturbance

No clear regeneration patterns emerged as a result of disturbance type. Both divergent responses to the same disturbance type and similar responses to different disturbance types occurred (Figure 2.1). After spruce budworm disturbance, for example, conifers remained dominant within stands that were conifer-dominated prior to disturbance. Conversely, in previously mixed coniferous-deciduous stands, an 8 to 27 % decrease in the conifer component was observed depending on size class. Relative density of deciduous species increased in all other combinations of disturbance type and pre-disturbance stand composition. *Abies balsamea* was the most abundant conifer species present after disturbance (Table AG1 – Appendix G). Accounting for at least 88 % of the conifer component in each stand, it was present in all regeneration size classes, irrespective of disturbance type or pre-disturbance stand composition. *Betula papyrifera* was the most abundant deciduous tree species followed by *Betula alleghaniensis*. Relative densities of *Betula* spp. were substantially reduced in size class 1 compared to classes 2 and 3 in almost all disturbance and stand type combinations. Densities of *Picea glauca* and *Pinus strobus* were relatively low throughout. Although present in nearby stands of severe fire or clearcut origin, early succession colonisers such as *Populus* spp. were not found after moderate-severity disturbances (Table AG2 – Appendix G).

With the exception of after windthrow disturbance in previously conifer-dominated stands, wherein *Betula papyrifera* was abundant, the overall shift to dominance by deciduous species was primarily due to increased relative abundances of sub-canopy tree species and shade-intolerant shrubs (Figure 2.1). *Acer spicatum* represented 47 % of this post-disturbance component. When present in abundance, *Acer spicatum* aggregated to produce dense, mono-specific clusters that precluded establishment of other species (G. Reyes, personal observation). This was

particularly the case after windthrow in mixed coniferous-deciduous stands, where it represented between 71 and 96 % of the sub-canopy tree and shrub component. *Amelanchier* spp. and *Corylus cornuta* also produced mono-specific clusters but were less important, composing 11 and 9 % of the overall density, respectively. *Sorbus* spp. represented 18 % of the sub-canopy tree and shrub component, but had a more dispersed distribution. Other sub-canopy tree and shrub species that were present, but at generally low densities included: *Acer rubrum*, *Acer pensylvanicum*, *Cornus stolonifera*, *Lonicera canadensis*, *Nemopanthus mucronatus*, *Prunus pensylvanica*, *Prunus virginiana*, *Ribes* spp., *Rubus* spp., *Sambucus* spp., *Taxus canadensis*, *Vaccinium* spp., *Viburnum cassinoides*, *Viburnum edule*, and *Viburnum trilobum*.

2.6.2. Relative importance of the various disturbance types and local stand and site characteristic variables

In order of decreasing importance, stand composition prior to disturbance, density of coarse woody debris, percent slope, distance to the nearest mature coniferous stand, drainage, spruce budworm disturbance, and density of deciduous legacy trees were the environmental variables significantly affecting patterns of species abundance (see Table AG3 for F values - Appendix G). Neither windthrow nor interaction disturbance types significantly affected species distribution patterns ($P > 0.05$). Local habitat characteristics not affecting species distribution patterns were distance to nearest mature mixed coniferous-deciduous stand, density of coniferous legacy trees, density of snags, proportion of coarse woody debris uprooted versus snapped, and stand density prior to disturbance ($P > 0.05$). The first four Eigenvalues in RDA explained 14, 5, 4, and 2 % of the total variance in species composition, respectively (25 % of total variance). Stand composition prior to disturbance, density of coarse woody debris, spruce budworm disturbance, drainage, and density of deciduous legacy trees were the environmental variables significantly related to axes 1 and 2 while distance to nearest conifer stand, slope, and drainage were significantly related to axis 3 and 4 in ordination space ($P < 0.05$) (Table 2.3).

Stand composition prior to disturbance and density of coarse woody debris most strongly affected regeneration patterns along axis 1 (Figure 2.2a). *Abies balsamea*, *Picea glauca* and *Picea mariana* were more abundant in previously conifer-dominated stands and in areas with an abundance of coarse woody debris. *Abies balsamea* also was present in abundance after spruce budworm disturbance when occurring in previously conifer-dominated stands, concurring with our results from Figure 1 showing that stand type had an overriding influence on *Abies balsamea* density. *Pinus strobus* and *Thuja occidentalis* were more prevalent in areas with steeper slopes (Figure 2.2b). *Acer pensylvanicum*, *Acer spicatum*, *Corylus cornuta*, and *Sambucus* spp. were more abundant in stands that were of mixed coniferous-deciduous origin and readily established in the absence of coarse woody debris. Other shrub species such as *Prunus* spp. and *Rubus* spp. successfully established in areas with poorer drainage, and along with *Amelanchier* spp. and *Nemopanthus mucronata*, were more abundant in previously conifer-dominated stands with high coarse woody debris densities.

Acer pensylvanicum, *Acer rubrum*, *Acer saccharum*, and *Betula alleghaniensis* were more strongly associated with a higher density of deciduous legacy trees, good to rapid drainage, and increasing distance from conifer-dominated stands than to pre-disturbance stand composition. *Abies balsamea* and *Betula papyrifera* were the most abundant legacy trees (Table 2.2). *Picea glauca* legacy trees were also relatively abundant, but regeneration densities were low throughout all sampled stands. The majority of *Abies balsamea* seedlings established prior to disturbance in most sites, suggesting post-disturbance seedling establishment to be relatively unimportant in terms of *Abies balsamea* retaining its importance in the future canopy. *Betula papyrifera* generally established after disturbance, yet only the largest seedlings were more abundant with higher densities of legacy trees. Smaller size classes did not show this affinity; this is perhaps due to larger individuals quickly establishing canopy positions near legacy trees, thus suppressing further conspecific establishment. Some appropriate germination sites were still available with greater distances from seed sources, as evidenced by other size classes

of *Betula papyrifera* establishing within conifer-dominated stands and in areas with high levels of coarse woody debris.

2.6.3. Species richness and diversity estimates

Species richness (S) was similar among sites regardless of disturbance type ($F_{2,21} = 1.5, P > 0.05$), stand composition prior to disturbance ($F_{1,21} = 1.9, P > 0.05$), or for any factorial combination of main effects ($F_{2,21} = 1.2, P > 0.05$), averaging 11.0 ± 0.5 species per quadrat. Species diversity (H') was lower in spruce budworm disturbed sites ($H' = 0.8 \pm 0.1$) versus those experiencing windthrow ($H' = 1.1 \pm 0.1$) or interaction ($H' = 1.2 \pm 0.1$) disturbances ($F_{2,21} = 4.0, P < 0.05$). Species diversity was similar after windthrow and interaction disturbances. No significant differences in H' were observed in relation to stand composition prior to disturbance ($H' = 1.0 \pm 0.1; F_{1,21} = 3.7, P > 0.05$) or for any factorial combinations of these main effects ($F_{2,21} = 0.9, P > 0.05$). Species evenness (J) was similar among all disturbance types ($F_{2,21} = 0.8, P > 0.05$), between stand compositions prior to disturbance ($F_{1,21} = 0.6, P > 0.05$), and for all factorial combinations of these main effects ($F_{2,21} = 0.6, P > 0.05$). Species diversity was generally low in these *Abies balsamea*-*Betula* spp. stands overall, as most individuals belonged to only a few abundant species present at each site ($S = 11.0 \pm 0.5$ species per quadrat, $H' = 1.0 \pm 0.1, J = 0.4 \pm 0.03$). In previously conifer-dominated stands *Abies balsamea*, *Betula papyrifera*, and *Acer spicatum* were a large component of species diversity while various combinations of *Abies balsamea*, *Acer spicatum*, *Betula papyrifera*, and *Betula alleghaniensis* were the main components of species diversity after disturbance in previously mixed coniferous-deciduous stands.

2.7. Discussion

Local biotic and abiotic habitat characteristics have been shown to affect vegetation responses in similar forest systems. Turner et al. (1997) and Frelich and Reich (1999), for example, found stand composition prior to disturbance to be important in determining post-disturbance stand composition in conifer forests of northwestern Wyoming and northern Minnesota regions of the United States, respectively. Frelich and Reich (1999) further suggest that legacy trees and the presence of advance regeneration can significantly affect patterns of response while

Albani et al. (2005) found a positive correlation with hardwood occurrence and distance from *Picea* stands in boreal mixedwoods of northern British Columbia, Canada. Greater light availability has been associated with the prevalence of shrub competitors such as *Acer spicatum* and *Corylus cornuta* (Batzler and Popp 1985, Kneeshaw and Bergeron 1999) while differences in drainage (Osawa 1994) and slope position (Archambault et al. 1997, Laflèche et al. 2000) can be important in determining spatial distribution of canopy trees.

The importance of pre-disturbance stand composition and other stand-level attributes was exemplified by regeneration patterns observed after spruce budworm disturbance. While re-establishment of conifer dominance was evident after spruce budworm disturbance in previously conifer-dominated stands, this relationship did not hold true in mixed coniferous-deciduous stands. Conifers did not maintain relative species density in the 50 to 74 % range after moderate-severity disturbance. Rather, deciduous shrub and tree species dominated the regeneration, with the relative success of the various species dependent on the specific microhabitat requirements of each species being met. The deciduous component increased after moderate-severity disturbance in almost all of the study sites. Laflèche et al. (2000) and Belle-Isle and Kneeshaw (2007), found similar results after clearcut harvests that protected advance regeneration and soils in other *Abies balsamea*-*Betula* spp. forests of eastern Quebec. While *Abies balsamea* regenerated in these sites, competing species such as *Acer spicatum* and *Prunus pensylvanica* rapidly established and potentially suppressed *Abies balsamea* re-establishment and growth.

Density of coarse woody debris also strongly affected species distribution patterns, with effects dependent on a species' specific microhabitat requirements. Variation in the effects of coarse woody debris on regeneration success has also been observed elsewhere (Debeljak 2006, Motta et al. 2006). Shade intolerant shrub species such as *Acer spicatum*, *Corylus cornuta*, and *Prunus* spp. readily established in areas with a low coarse woody debris density. Areas with a high density of coarse woody debris limited available growing space for new seedling establishment, but also reduced exposure and desiccation for pre-established regeneration. High debris density conditions particularly benefited *Abies balsamea*, as the majority of *Abies*

balsamea seedlings were from advance regeneration. However, *Betula papyrifera* was also able to establish from seed under high coarse woody debris conditions, albeit at low densities. Closer observations in these sites revealed that *Betula papyrifera* germination tended to occur near standing dead conspecifics and in exposed soils resulting from tree uprooting. Coarse woody debris can also be exploited as an elevated substrate that avoids the dense competing vegetation established directly on the ground (Harmon and Franklin 1989). In our sites, however, downed logs were generally not sufficiently decomposed to allow for new seedling establishment. Further, most of the regeneration established on the ground was already >2 m tall. It remains unclear whether or not many more new seedlings will be able to exploit this medium over time or if surrounding vegetation will have completely overgrown decomposing logs, mitigating the initial advantage of the reduced competition that decomposing logs provide.

We can distinguish five main vegetation responses according to our measured environmental variables: (1) re-establishment of conifer dominance after spruce budworm disturbance, particularly by *Abies balsamea*, occurred only in previously conifer-dominated stands, (2) high densities of coarse woody debris were associated with conifer success, but also with that of *Betula papyrifera*, (3) low densities of coarse woody debris in previously mixed coniferous-deciduous stands was associated with the creation of mono-specific clusters of *Acer spicatum* and *Corylus cornuta*, (4) the combination of a higher density of deciduous legacy trees and good to rapid drainage were beneficial to the establishment of *Acer pensylvanicum*, *Acer rubrum*, *Acer saccharum*, and *Betula alleghaniensis*, and (5) areas with moderate to imperfect drainage in previously conifer-dominated stands were associated with higher densities of *Prunus* spp. and *Rubus* spp. Although species richness was similar among all sites investigated, regardless of moderate-severity disturbance type or relative stand composition prior to disturbance, changes in relative species abundances did occur after disturbance. Despite a general increase in deciduous species abundances, conifer species should retain their importance within this forest system irrespective of disturbance type, owing to their presence in almost all regeneration size classes in all sites investigated, and resilience under extreme shade

conditions. In the absence of subsequent moderate-severity or catastrophic disturbance, stands will likely develop towards a conifer-dominated old growth condition.

2.8. Conclusions

Understanding how local habitat characteristics affect vegetation responses to disturbance is important, as the various combinations of biotic and abiotic habitat characteristics can leave distinct legacies on the landscape. Information is currently lacking on the importance of moderate-severity disturbances in maintaining relative species mixtures across the landscape over time. If moderate-severity disturbances are indeed an integral component of forest dynamics within boreal mixedwoods, coupled with the fact that canopy gaps can cover up to 35 % of a particular mixedwood stand (Kneeshaw and Bergeron 1998), and given the rarity of stand-initiating disturbances within this forest type (Hebert 2003), the large-scale, even-aged management approach currently being applied to much of the region may be inappropriate for maintaining long-term ecosystem health. As the forest industry works towards integrating ecological principles into forestry practices, better knowledge of the importance of natural disturbance regimes is essential. We believe our results are a step forward in this regard.

2.9. Acknowledgements

We would like to thank Jean-François Gagnon, Julie Messier, Isabelle Nault, Maude Beauregard, Andre De Römer, Mathieu Bouchard, Jonatan Belle-Isle, David Saucier, and Steve Bujold for assisting with fieldwork. Comments from two anonymous reviewers and Craig Lorimer were invaluable to the preparation of this manuscript. Additionally, this study would not have been possible without financial and/or technical support from TEMBEC, the Natural Sciences and Engineering Research Council of Canada, the Canadian Forestry Service, and the Sustainable Forest Management Network.

2.10. Literature Cited

Please see the General Citation List (pp 133-154).

Table 2.1. Summary of site attributes grouped according to disturbance type (spruce budworm, windthrow, interaction) and stand composition prior to disturbance (conifer-dominated: ≥ 75 % conifers in canopy, mixed coniferous-deciduous: 50-74 % conifers in canopy). Values in parentheses indicate number of stands having the particular attribute.

Attribute	Spruce budworm		Windthrow		Interaction	
	coniferous	mixed coniferous-deciduous	coniferous	mixed coniferous-deciduous	coniferous	mixed coniferous-deciduous
Stand density ¹	B(3), C(3)	B(4), C(2)	C(4)	B(2), C(1)	B(1), C(3)	B(3), C(3)
Height ²	2(1), 3(5)	2(1), 3(5)	3(4)	2(2), 3(1)	2, 3(3)	2(2), 3(4)
Elevation (m): mean \pm SE	442.9 \pm 29.3	442.5 \pm 39.4	415.1 \pm 32.3	423.0 \pm 23.1	451.0 \pm 45.5	375.5 \pm 22.1
Slope ³	1(5), 2(1)	1(2), 2(1), 3(3)	3(2), 4(1), 5(1)	4(2), 5(1)	1(1), 2(1), 3(2)	1(2), 2(2), 3(2)
Drainage ⁴	2(3), 2(3), 4(1)	2(4), 3(2)	2(4)	2(3)	2(2), 3(2)	2(4), 3(2)
Soil moisture ⁵	2(3), 3(3)	2(4), 3(2)	2(4)	2(3)	2(2), 3(2)	2(5), 3(1)
Surface deposits ⁶	8A(3), 8C(1), 8AR(1), 1A(1)	8A(4), 8A(1), 1AR(1)	8C(4)	8C(3)	8A(3), 8AR(1)	1A(1), 1AR(1), 8A(2), 8C(2)
Number of disturbed stands examined (n)	6	6	4	3	4	6

¹B: 60-80 %, C: 40-60 % stocked;

²2: 17-22 m, 3: 12-17 m tall;

³1: 0 to 100, 2: >10 to 200, 3: >20 to 300, 4: >30 to 400, 5: >400;

⁴2: good, 3: moderate; 4: imperfect;

⁵2: xeric-mesic, 3: mesic;

⁶1A: undifferentiated till >1 m thick, 1AR: undifferentiated till >1 m thick with rocky substratum, 8A: alteration deposits >1 m thick, 8AR: alteration deposits >1 m thick with rocky substratum, 8C: colluvial deposits.

Table 2.2. Density of legacy trees.

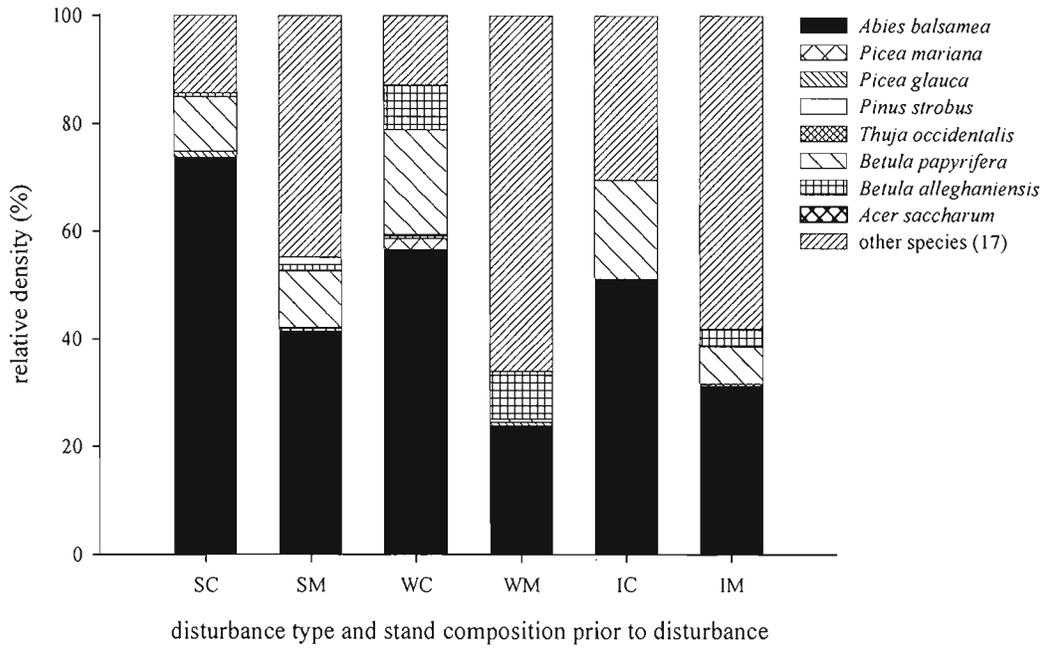
Species	Density of legacy trees (trees ha ⁻¹)
<i>Abies balsamea</i>	4.2
<i>Picea glauca</i>	1.7
<i>Picea mariana</i>	0.7
<i>Thuja occidentalis</i>	0.1
<i>Pinus strobes</i>	0.03
<i>Betula papyrifera</i>	3.6
<i>Betula alleghaniensis</i>	1.0
<i>Acer rubrum</i>	0.6
<i>Acer saccharum</i>	0.1

Table 2.3. Canonical correlation coefficients between significant environmental variables and the first four ordination axes in Redundancy Analysis ($P < 0.05$, ns indicates non-significance).

Environmental Variable	Axis	Axis	Axis	Axis
	1	2	3	4
Conifer-dominated stand prior to disturbance	0.56	ns	ns	ns
Coarse woody debris density	0.52	-0.35	ns	ns
Percent slope	ns	ns	0.35	-0.48
Distance to nearest mature conifer-dominated stand	ns	ns	0.45	0.45
Drainage	0.31	0.43	ns	0.05
Spruce budworm disturbance	0.31	ns	ns	Ns
Deciduous legacy tree density	-0.11	-0.42	ns	Ns

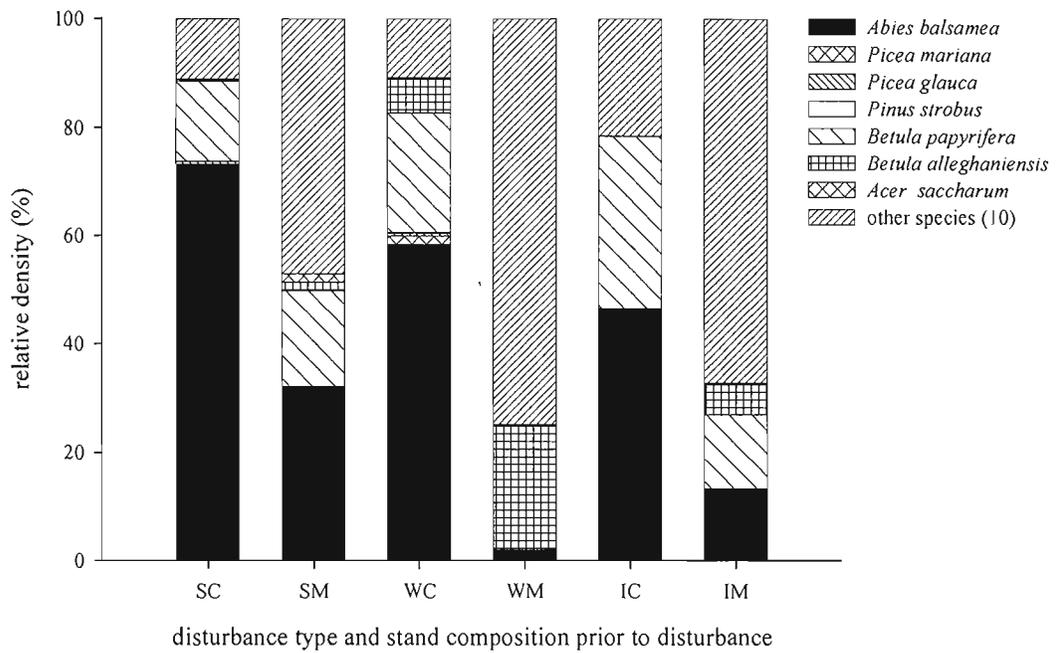
Regeneration: Class 1 (1 - 2 m tall)

a



Regeneration: Class 2 (>2 m tall & <4 cm dbh)

b



Regeneration: Class 3 (4 - 8 cm dbh)

c

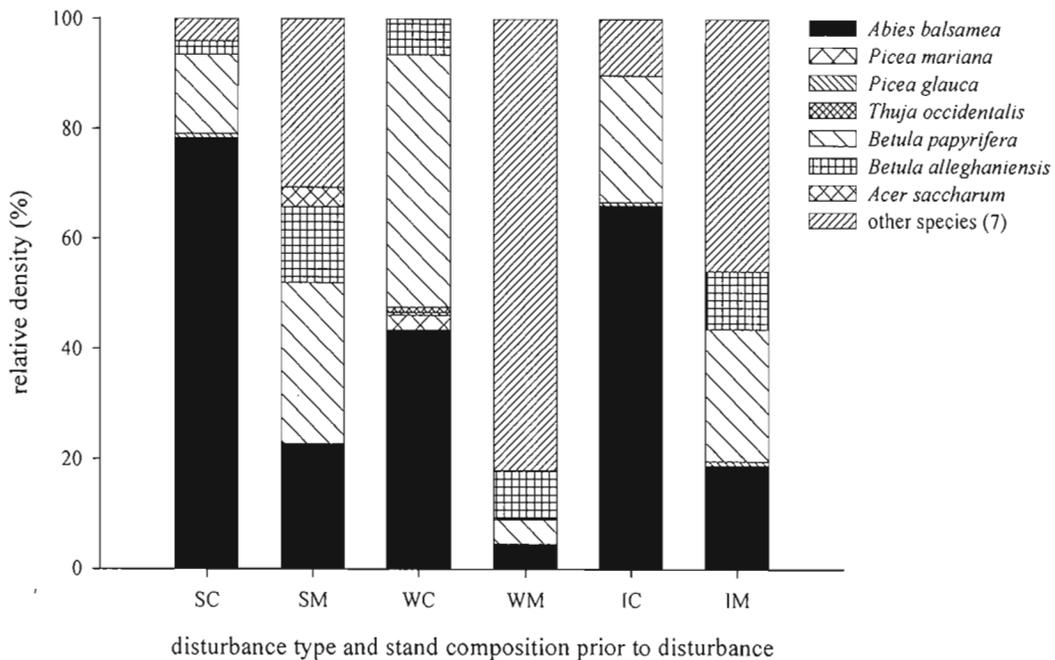


Figure 2.1 a-c. Relative density of the regeneration for important tree species in boreal mixedwoods grouped according to size class, disturbance type [spruce budworm (S), windthrow (W), and interaction (I) disturbances] and stand composition prior to disturbance [conifer-dominated (C) or mixed coniferous-deciduous canopy (M)]. Other sub-canopy arboreal and shrub species were grouped together, with the total number of species found included in brackets. Codes indicate the following (1st letter = disturbance type, 2nd letter = stand composition prior to disturbance).

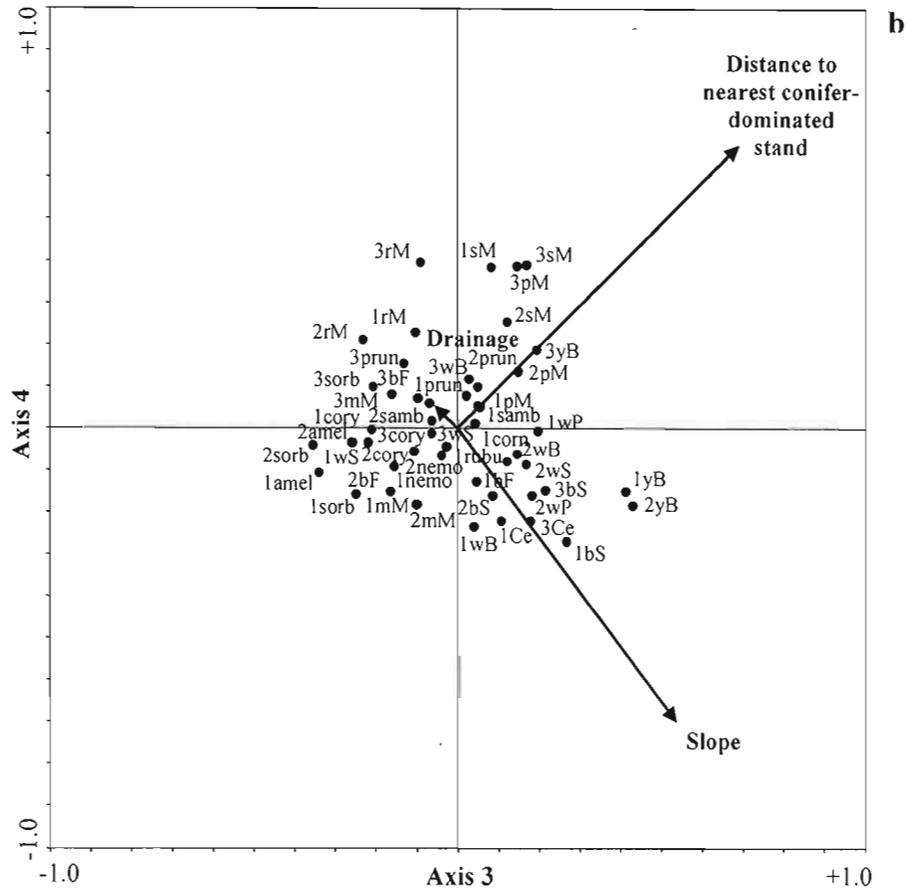


Figure 2.2 a-b. Redundancy Analysis ordination biplots showing vegetation distribution in relation to environmental variables significantly influencing regeneration patterns after forward selection ($P < 0.05$). Axes 1 through 4 explained 49.6, 17.9, 14.3, and 7.8 % of the variance in the species-environment relationships, respectively. Length and position of vectors and points from the origin in relation to axes 1 and 2 indicate strength of relationships among variables in ordination space, where greater distances from the origin in conjunction with closer positions to either axis 1 or 2 indicate stronger associations. Numbers preceding species codes indicate the following regeneration size classes: (1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 m), (3) 4 to 8 cm dbh. Species and environmental variable codes are as follows: bF = *Abies balsamea*, bS = *Picea mariana*, Ce = *Thuja occidentalis*, mM = *Acer spicatum*, pM = *Acer pensylvanicum*, rM = *Acer rubrum*, sM = *Acer saccharum*,

wB = *Betula papyrifera*, wS = *Picea glauca*, wP = *Pinus strobus*, yB = *Betula alleghaniensis*, amel = *Amelanchier* spp., corn = *Cornus stolonifera*, cory = *Corylus cornuta*, prun = *Prunus* spp., nemo = *Nemopanthus mucronata*, rubu = *Rubus* spp., samb = *Sambucus* spp., sorb = *Sorbus* spp., and SBW = spruce budworm disturbance.

**variable passively added after ordination and thus does not affect species-environment relationships

PROLOGUE TO CHAPTER III

In the last chapter we observed that responses to moderate-severity disturbances are contingent on a number of environmental factors, more so than the specific disturbance type itself. I now wish to determine if these results are consistent across Quebec, Canada's boreal mixedwood region; i.e., are site-specific, local factors driving post-disturbance patterns or is there a common set of factors that predominate throughout? Secondly, are environmental factors always the primary determinants of species diversity and abundance or are there some instances where a particular disturbance type more strongly affects vegetation distribution patterns? Read on!

CHAPTER III

**FACTORS CAUSING REGIONAL VARIATION
IN WOODY VEGETATION DIVERSITY AND ABUNDANCE
AFTER NATURAL DISTURBANCES**

Gerardo Reyes, Daniel Kneeshaw, and Louis De Grandpré

Article submitted to *Ecography* (Nov 2009)

3.1. Abstract

Differences in factors controlling vegetation responses to natural disturbances across a contiguous forest region can occur because of variation in local habitat conditions. We compared the relative influence of three types of natural disturbances (spruce budworm (*Choristeneura fumiferana*) outbreak, windthrow, interaction disturbance) and environmental factors (climate, physiography, and stand structure and composition variables) on woody vegetation regeneration among three, physiographically distinct locations within the eastern boreal mixedwood region. Our main objectives were to: (1) determine the principal factors shaping post-disturbance woody species stand composition; (2) determine if the importance of factors controlling woody vegetation responses is consistent throughout the region; and (3) compare species diversity and abundance after natural disturbances across the eastern boreal mixedwood region. Seventy-six *Abies balsamea*-*Betula* spp. stands affected by natural disturbance were compared and analysed using canonical ordination methods, diversity indices, and ANOVA. Disturbance type was not the primary driver of post-disturbance vegetation composition across the region. Regional species distribution patterns were strongly correlated with stand composition prior to disturbance and coarse woody debris density. Coarse woody debris density was the only factor always associated with vegetation distribution and abundance at each location and level of examination. Despite considerable physiographical differences across the region, similar regeneration patterns occurred throughout, as conifer species dominated the regeneration in most stands after disturbance. Variation in alpha (α), gamma (S), and beta (β) diversity were observed across the region. Shannon's H' was highest along the North Shore and lowest in the Gaspé Peninsula. Evenness (J) values indicate greater variability in canopy tree species relative abundances along the North Shore relative to the Gaspé Peninsula. Sites in Temiskaming-Abitibi had intermediate values for both H' and J . Our findings indicate that while stand composition prior to disturbance and coarse woody debris density can generally explain relative species composition across the region for the main canopy species, different suites of factors were important for creating variation in species diversity and abundance at the local level.

Key words: natural regeneration; moderate-severity disturbances; environmental factors; species diversity; eastern boreal mixedwood region.

3.2. Introduction

Natural disturbances are an integral component of forest ecosystems that modify forest structure and composition. While natural disturbance may be the primary driver of ecosystem change, various biotic and physical environmental factors can influence community response. Climate (Denton and Barnes 1987, Wimberly and Spies 2001), physiography (Cogbill and White 1991, Millward and Kraft 2004, Bouchard et al. 2006, Hayes et al. 2007), pre-disturbance stand characteristics (Dupont et al. 1991, Osumi et al. 2003, Johnstone and Chapin III 2006), biotic processes (Lautenschlager 1991, Le Page et al. 2000), and structural and biological legacies (Nagel et al. 2006, Iijima et al. 2007, Reyes and Kneeshaw 2008), have all been shown to affect successional trajectories after disturbance. However, there is no consensus as to which factors are most important in driving general woody vegetation community patterns or under which conditions the effects of particular factors are more prevalent. Moreover, various factors can operate at local or regional scales, show variation in importance among locations across a region, and can work synergistically to affect regeneration distribution and abundance (Ohmann and Spies 1998, Wimberly and Spies 2001, Hillebrand, H., and T. Blenckner. 2002, Huebner and Vankat 2003).

Research utilising data from different locations across a contiguous forest region can provide insight that may not be evident from only a single location (Messier et al. 2005). Disparity in responses to disturbance may occur when effects of local weather, topography, edaphic properties, and other site-specific attributes are not consistent with more general, regional characteristics of the forest system (Neilson et al. 1992, Messaoud 2007). This can lead to conflicting conclusions about expected changes in vegetation communities resulting from natural disturbances, or the role that certain environmental factors play in influencing vegetation responses. Examining vegetation responses to natural disturbances at various locations across a contiguous region within the same forest system can thus help to resolve potential

contrasts, and potentially link fine and broad-scale vegetation recovery patterns to a suite of principal factors that elicit consistent responses.

The purpose of our study was to examine the combined effects of natural disturbance and environmental factors on woody vegetation diversity and abundance. We attempt to resolve and explain potential regional differences in factors affecting vegetation diversity and abundance by examining a large, contiguous area of study. We specifically addressed the following questions: do natural disturbances have the dominant influence or do environmental variables associated with climate and the physical and biotic characteristics of the landscape determine woody vegetation diversity and abundance after disturbance? Alternatively, do natural disturbances work synergistically with environmental factors? Lastly, do different factors control woody species diversity and abundance for specific locations or can a common suite of factors explain vegetation responses across a contiguous forest system?

3.3. Study area

The *Abies balsamea*-*Betula* spp. boreal mixedwood zone spans east to west across southern Quebec from 46 to 50° N and 64 to 80° W (Fig. 3.1). It encompasses 23.8 million ha and represents 18.6 % of the forested land of the province (MRNQ 2003). The physiography of the region is highly variable. The western portion is continental, and is relatively flat to rolling. Topography becomes increasingly hilly to montane towards the east, as the eastern portion of the region includes the northeastern limit of the Appalachian mountain chain that runs southwest into the United States. The eastern portion is also bounded by the Gulf of St. Lawrence, and thus contrasts with the western portion of the region by having a maritime influence. Elevations of forested areas range from 80 to 400 m in the west, and from sea level to 900 m in the east. Surface deposits are mostly glacial till or of lacustrine origin (Robitaille and Saucier 1998). The soil moisture regime is classified as xeric-mesic to mesic, while soil drainage ranges from imperfect to rapid.

Numerous disturbances such as fire, insect pests, and windthrow occur at varying frequency and severity in eastern boreal mixedwoods. The current return interval length for catastrophic fires across the region ranges from 170 to 645 years

(Bergeron and Archambault 1993, Grenier et al. 2005, Bergeron et al. 2006, Lauzon et al. 2007), suggesting that less severe, but more frequent disturbances now assert greater influence on post-disturbance boreal mixedwood dynamics than in the recent past. Moderate-severity disturbances (defined as disturbances causing more than 0.2 ha of contiguous canopy mortality, and differing from catastrophic fire in that the regeneration layer remains relatively intact after disturbance), in particular, can considerably affect regeneration patterns, as they cause substantial mortality to large expanses of forest canopy (Reyes and Kneeshaw 2008) and can recur at relatively frequent intervals; e.g., spruce budworm (*Choristoneura fumiferana*) outbreak (Blais 1983, Bergeron 2000).

Understanding of regeneration dynamics after moderate-severity disturbances remains poor. Only recently have species distribution patterns after different moderate-severity disturbances been addressed (Frelich and Reich 1998, Seymour et al. 2002, Hanson and Lorimer 2007, Reyes and Kneeshaw 2008), with most research showing that multiple post-disturbance successional pathways are possible (Frelich and Reich 1999, Bergeron 2000, Chen and Popadiouk 2002, Reyes and Kneeshaw 2008). Given the current relevance of this disturbance type to models of forest dynamics, and the need for improved understanding of regeneration pathways after moderate-severity disturbances, we focused our attention on patterns of recovery after moderate-severity disturbances. We examined three types of moderate-severity disturbances: spruce budworm outbreak, windthrow, and their interaction (where a stand affected by spruce budworm outbreak experiences windthrow prior to complete canopy recovery).

We sampled within three physiographically distinct locations across the boreal mixedwood region of Quebec, Canada (Figure 3. 1). The continental, western sites are located in the Temiskaming and Abitibi municipalities (47°30' to 48°20'N and 77°30' to 79°10' W). Two eastern coastal locations, differing mainly by latitude and elevation, were examined: the North Shore area is situated along the north shore of the St. Lawrence River, within the Haute Côte Nord and Manicouagan municipalities, and between 48°30' to 50°00' N and 68°00' to 69°50' W. Stands in this area are near the northern limit of the boreal mixedwood region. The southern

coastal sites are situated across the southern part of the Gaspé Peninsula, along the Chaleur Bay area of the Atlantic coast (between 48°10' to 48°35'N and 65°45' to 66°15' W).

Various climate, physiographic, and forest structure and composition characteristics differed among geographic locations (Table 3.1). Our focus was on stands that were mature prior to disturbance (≥ 80 years old - verified within each site by counting annual rings of remnant trees or old stumps). *Abies balsamea*, *Betula papyrifera*, and *Betula alleghaniensis* dominated the forest canopy prior to disturbance, and represented at least 60 % of the coniferous and deciduous components within each stand, respectively. *Picea glauca*, *Picea mariana*, *Acer rubrum*, *Populus balsamifera*, and *Populus tremuloides* were also abundant in some sites while *Thuja occidentalis*, *Pinus resinosa*, *Pinus strobus*, *Pinus banksiana*, *Larix laricina*, *Acer saccharum*, *Fraxinus americana*, and *Fraxinus nigra* were occasionally present.

3.4. Sampling methods

Disturbance type, climate, and physiographical data were derived from digitised aerial photos, eco-forestry maps, or sourced from various provincial and federal government agencies (MNRQ 2003, Environment Canada 2004), with the exception of slope and elevation, which were determined on site using a clinometer and GPS unit, respectively. A total of 76 sites affected by moderate-severity disturbance were examined: 24, 22, and 30 sites for Temiskaming-Abitibi, the North Shore, and Gaspé Peninsula, respectively. Up to six 20 x 20 m quadrats were sampled within each disturbed site. All quadrats were at least 40 m from the nearest intact forest and 30 m from the nearest logging road to avoid edge effects.

Density of tree and shrub regeneration was quantified within each quadrat for three size classes: (1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 cm), and (3) between 4 and 8 cm dbh using a nested plot design. Class 1 regeneration were sampled in a 2 x 10 m area, class 2 in a 5 x 10 m area, and class 3 within the entire quadrat. Density of snags (standing dead trees >10 cm dbh) and coarse woody debris (downed trees >10 cm dbh) were determined and classified using a modified decay classification scale developed by Imbeau and Desrochers (2002). Coarse woody

debris was also categorised as uprooted or snapped when possible. Crown cover (m²) of legacy trees (mature overstory trees that survived the moderate-severity disturbance) within each quadrat, and density of deciduous and coniferous legacy trees within a 35 m radius of the quadrat centre were also determined.

3.5. Analyses

We analysed woody vegetation responses to natural disturbance in relation to climate, physiography, and stand structure and composition variables. Comparisons of these environmental variables among locations were made using analysis of variance (ANOVA) (SPSS 10.0 1999) followed by the Student-Newman-Keuls multiple range test when significant differences were observed ($\alpha = 0.05$) (Table 3.1).

3.5.1. Direct gradient analysis

We used a series of redundancy analyses (RDA) (van den Wollenberg 1977) to examine the relationships between environmental variables (i.e., the various disturbance types, climate, physiographic, and stand structure and composition variables) and woody vegetation species distribution patterns across the region and for each of the three study locations. For each analysis, the forward selection option was selected to both rank the importance of each variable and to exclude redundant and non-significant variables from the model. The significance of the explanatory effect of an environmental variable was determined using a Monte Carlo permutation test (200 permutations, $p < 0.05$) prior to the addition of the next best fitting variable. The three study locations were inputted as covariables when examining regional level relationships. CANOCO 4.0 software (ter Braak and Smilauer 1998) was used to run analyses. Variables were centred and standardized as a number of environmental variables were measured using different units.

3.5.2. Species diversity

Five measures of species diversity were calculated for the entire study region and for each geographic location. Calculations were made for the entire woody vegetation community and for each of the woody vegetation layers separately (canopy tree regeneration, sub-canopy tree & shrub regeneration). Regional level species diversity estimates were the following: alpha diversity (α) represented mean site level richness, gamma diversity (S) represented the total richness across the

study region, and beta diversity (β) represented differences in richness among sites across the region of study; i.e., the differences in species composition among spatial units (Novotny and Weiblen 2005). Beta diversity (Whittaker 1960) was computed as:

$$\beta = (S / \alpha) - 1 \quad [1]$$

For each of the three study locations, α was measured as the mean species richness per quadrat within a site, S was measured as the total richness within a study location, and β , the differences in species richness among sites within a location. Shannon's diversity index (Shannon and Weaver 1949):

$$H' = - \sum p_i \ln p_i \quad [2]$$

where p_i = proportion of the total sample belonging to species i (in this case the relative density of a species), and evenness (J):

$$J = H' / \ln \alpha \quad [3]$$

where J is an index of how relative abundances are distributed among species (Pielou 1966), were determined for the regeneration layer for each site. Analysis of variance followed by the Student-Newman-Keuls multiple range tests were used to compare the various diversity estimates among geographical locations and vegetation layers ($p < 0.05$).

Species richness is partly a function of spatial scale (Palmer and White 1994, Kallimanis et al. 2008). We acknowledge that differences in richness may be an artefact of sampling effort among locations. The total disturbed area examined for sites in Temiskaming-Abitibi, the North Shore, and the Gaspé Peninsula were 405.2, 505.6, and 1238.3 ha, respectively. We sampled the three locations using 35, 57, and 95 quadrats, respectively, to make sampling effort more equitable among locations. However, bias in species richness may also occur due to the unequal number of

quadrats. Sample rarefaction (Krebs 1989) was used to compute a species accumulation curve in function of number of quadrats examined for each location. PAST version 1.94b (Hammer et al. 2001) was used to run analysis. Results show that differences in species richness due to differences in the number of quadrats examined in each location was negligible (Figure 3.2). Given these results, we felt that making comparisons of diversity estimates among the three locations using our sampling protocol was a valid undertaking.

3.6. Results

3.6.1. Factors influencing woody vegetation diversity and abundance

3.6.1.1. Regional patterns

While the different moderate-severity disturbances caused substantial structural changes to the woody vegetation community, disturbance type was not the principal driver of post-disturbance vegetation distribution across the region. A combination of various environmental factors more strongly influenced woody vegetation regeneration diversity and abundance (Table 3.2). Stand composition prior to disturbance and coarse woody debris density were most important in determining species distribution patterns across the region.

Cyclical regeneration patterns occurred in stands that were conifer-dominated prior to disturbance as *Abies balsamea* and *Picea mariana*, both shade-tolerant conifer species, dominated the regeneration layer (Figure 3.3 a, Table 3.3). Stands that were mixed-coniferous prior to disturbance maintained their deciduous canopy tree components, while deciduous sub-canopy tree and shrub competitors such as *Acer spicatum* and *Corylus cornuta* were more abundant there. Shade-tolerant conifer tree species were also strongly associated with high densities of coarse woody debris. However, *Betula papyrifera*, a shade-intolerant deciduous species, was able to maintain its relative abundance in stands that were conifer-dominated prior to disturbance, and was able to establish in areas with high coarse woody debris densities. Closer examination showed that most of the *Betula papyrifera* regeneration was restricted to microsites with exposed mineral soils resulting from tree uprooting (G. Reyes, personal observation). Shade-tolerant and

mid-tolerant deciduous species such as *Acer pensylvanicum* and *Betula alleghaniensis* were more often present in mixed-coniferous sites in the *Abies balsamea*-*Betula alleghaniensis* Ecozone, particularly in sites situated in lower elevations. Mid-tolerant *Acer rubrum*, *Sorbus* spp., and *Amelanchier* spp. were more abundant in high elevation sites as well as in sites where coarse woody debris was more decomposed and less abundant.

3.6.1.2 Local patterns

The relative importance of specific disturbance types, climate, physiography, and stand structure and composition variables on woody vegetation diversity and abundance varied among the three locations (Table 3.4). In decreasing order of importance, woody vegetation responses in Temiskaming-Abitibi were primarily driven by windthrow, annual rainfall, and coarse woody debris density. Responses for sites along the North Shore were most strongly associated with latitude, elevation, annual rainfall, coarse woody debris density, and windthrow, while responses in the Gaspé Peninsula were associated mostly by stand composition prior to disturbance, coarse woody debris density, decay class, spruce budworm outbreak, and elevation.

The different disturbance types had only small influences on regeneration diversity and abundance in the coastal locations, whereas windthrow produced distinctive woody vegetation responses in the continental sites of Temiskaming-Abitibi (Table 3.4). With the exception of *Betula papyrifera*, shade-intolerant and mid-tolerant deciduous species in all strata were more abundant after windthrow in the Temiskaming-Abitibi sites, particularly in areas with low coarse woody debris densities (Figure 3.3 b).

Variables associated with forest structure and composition had large influences on woody vegetation regeneration diversity and abundance. Coarse woody debris density, in particular, accounted for a large proportion of the variation at all locations across the boreal mixedwood region, with the shade-tolerant *Abies balsamea* and *Picea mariana* dominating high density areas (Figure 3.3 b-d).

Significant effects of variation in local climate on woody vegetation responses were only evident in the Temiskaming-Abitibi and North Shore locations. In Temiskaming-Abitibi, sites with higher mean annual rainfall were associated with greater *Betula alleghaniensis*, *Prunus pensylvanica*, *Diervilla lonicera*, and *Acer rubrum* densities (Figure 3.3 b), while along the North Shore, sites with higher mean annual rainfall were associated with greater densities of *Abies balsamea*, *Picea glauca*, *Picea mariana*, *Nemopanthus mucronata*, *Acer rubrum*, and *Amelanchier* spp. (Figure 3.3 c).

Physiographic variables were responsible for a large proportion of the observed variation along the North Shore. Sites at higher latitudes were dominated by *Abies balsamea*, *Picea mariana*, and *Betula papyrifera* while *Acer spicatum* was most abundant at lower latitudes. *Abies balsamea* and *Picea mariana* were also more abundant at high elevations, as were, to a lesser degree *Picea glauca*, *Acer rubrum* and *Amelanchier* spp., as relationships with some size classes of these species were weaker. In the Gaspé Peninsula, sites at low elevation were dominated by *Betula alleghaniensis*, *Acer saccharum*, and *Acer pensylvanicum* (Figure 3.3 d).

While stand composition prior to disturbance, elevation, and spruce budworm outbreak influenced regeneration patterns both across the region and at certain locations, coarse woody debris density was the only variable significantly affecting species distribution patterns at both levels of study and at all locations. In terms of species responses, all height classes of each species generally responded in the same manner, indicated by the clustering of intra-specific species points in the biplots (Figure 3.3 a-d). Relative abundances of *Abies balsamea*, *Betula papyrifera*, and *Betula alleghaniensis*, the dominant coniferous and deciduous species in the system, were maintained or had increases in the coniferous component relative to pre-disturbance conditions (Figure 3.4 a-b).

3.6.2. Species diversity

A total of 33 woody species were observed in the system (12 canopy trees, 21 sub-canopy tree and shrubs) (Table 3.3). No species were considered rare or endangered. Alpha (α) diversity for canopy tree species was similar among locations ($p > 0.05$) (Table 3.5). Alpha diversity for all woody vegetation regeneration and for

sub-canopy tree and shrub regeneration was higher in the North Shore than in the Gaspé Peninsula ($p < 0.05$). Alpha diversity in Temiskaming-Abitibi was intermediate between the other two locations, and did not significantly differ from either coastal location ($p > 0.05$). Gamma (S) diversity for all woody vegetation was highest in Temiskaming-Abitibi, as 28 different species were observed there. Beta (β) diversity for all vegetation layers was generally higher in the Gaspé Peninsula. Shannon's diversity index (H') was similar among locations for all woody vegetation combined and for when testing the canopy tree layer separately ($p > 0.05$). Sub-canopy tree and shrub H' was greater in the North Shore relative to the Gaspé Peninsula. Greater variability in canopy tree species relative abundances were observed in the North Shore relative to the Gaspé Peninsula, as indicated by the evenness (J) estimates. Temiskaming-Abitibi sites had intermediate J values. Alpha, S , β , and H' were greater for the sub-canopy tree and shrub layer than for the canopy tree regeneration within and among all geographical locations and for across the region.

3.7. Discussion

3.7.1. Factors influencing woody vegetation diversity and abundance

The relative influence of disturbance type, climate, physiographic, and stand structure and composition variables on regeneration diversity and abundance was contingent on the level of study and the specific location examined. To some degree, each group of environmental variables was important in determining woody vegetation responses and the successional trajectory of the ecosystem. However, stand structure and composition variables, particularly stand composition prior to disturbance and density of coarse woody debris accounted for most of the observed variation at the regional level, while different suites of variables were important at each location. The only factor common to both levels of study and among locations was coarse woody debris density.

Conifer-dominated stands generally had abundant *Abies balsamea* advance regeneration in the understory prior to disturbance (Reyes and Kneeshaw 2008). Because moderate-severity disturbances had little impact on the regeneration layer, stand composition after natural disturbance was dominated by *Abies balsamea*,

irrespective of disturbance type. The presence of advance regeneration reduced the ability of shade-intolerant deciduous species to establish after natural disturbance by limiting available growing space, light, and other resources (Morin et al. 2008), resulting in cyclical regeneration patterns (Baskerville 1975).

Mixed-coniferous stands either maintained their relative coniferous-deciduous species ratios or increased in the deciduous component. However, much of this increase was related to greater densities of deciduous sub-canopy tree and shrub species. The influx of sub-canopy tree and shrub species can temporarily alter species composition ratios relative to pre-disturbance conditions and/or delay canopy development for a number of years, but will have little effect on canopy species composition once the tree canopy grows beyond a few metres in height. In fact, when considering only the canopy tree regeneration, mixed-coniferous stands generally maintained their pre-disturbance relative coniferous-deciduous species ratios or displayed increases in the conifer component. Retaining a deciduous component in areas with high levels of coarse woody debris was also observed, but was mostly restricted to microsites with exposed mineral soils resulting from tree uprooting. Thus, it appears that canopy tree coniferous-deciduous ratios will be maintained or may develop towards a more conifer-dominated old-growth condition over time in the absence of a subsequent moderate-severity or larger-scale disturbance. Post-disturbance vegetation community composition contingent on pre-disturbance stand composition has also been observed elsewhere (Webb 1989, Rich et al. 2007, Reyes and Kneeshaw 2008).

We observed a strong relationship with coarse woody debris density and species distribution. This may simply be an artifact of an abundance of coarse woody debris being a residual effect of disturbance; i.e., the relationship may be correlative rather than be causative in nature. However, coarse woody debris is recognised for its importance in ecosystem function and productivity (Janisch and Harmon 2002, Brunner and Kimmins 2003), its role in maintaining biological diversity (Angelstam et al. 2003), in providing suitable substrate for seedling establishment (Nakagawa et al. 2001), providing shade for established seedlings (Gray and Spies 1997), and acting as a structural deterrent to ungulate browsing (Ripple and Larsen 2001). Its

irregular spatial distribution and variation in decay rates throughout the landscape was important for the creation of environmental heterogeneity that was associated with variation in woody vegetation responses. In this system, where abundant, coarse woody debris provided shade to established seedlings and deterred germination and establishment from seed.

Generally weak relationships with disturbance type (with the exception of windthrow in Temiskaming-Abitibi) were surprising, as different types of disturbances have been shown to cause divergent successional trajectories in similar forest systems (Denslow 1980, Abrams et al. 1985, Frelich and Reich 1999). These earlier studies have shown disturbance to drive succession towards different trajectories depending on disturbance type or severity. It may be that the range of disturbances examined was not large enough to observe marked differences in species responses, as we focused on moderate-severity disturbances.

Despite a considerable degree of heterogeneity across the study region, many of the climate and physiographic factors had little impact on vegetation responses to natural disturbance. However, variation in elevation did have some influence on vegetation diversity and abundance along the North Shore and the Gaspé Peninsula. Some separation between deciduous and conifer species according to elevation was observed in these coastal montane sites, with sites at lower elevations often having higher densities of deciduous species.

3.7.2. Species richness and diversity

Greater species richness and a larger degree of variation in environmental conditions were observed at a regional scale relative to local conditions, concurring with the hypothesis that species richness is a function of habitat area (MacArthur and Wilson 1967, Crawley and Harral 2001). Greater environmental heterogeneity allows for more species that have different germination requirements, growth rates, competitive abilities, mycorrhizal associations, and other specific habitat requirements to establish. Furthermore, across the region, species composition and abundance changed from one location to the next.

Our study shows that the choice of spatial scale and location is important when evaluating species diversity, as variation in the different diversity estimates were observed. Variation in the importance of factors causing divergent responses of the woody vegetation across the boreal mixedwood region reinforces the concept that species distribution is not only controlled by natural disturbance, but that local environmental characteristics and constraints on plant biology can dictate re-establishment success. Forest species have diverse habitat requirements, and have different means or strategies for obtaining resources, for preventing or avoiding herbivory, and for meeting other life history requirements. Many species have specific adaptations or interspecific associations that also facilitate niche partitioning. Thus, maintaining species diversity is dependent upon retaining a diverse array of habitat features.

3.8. Conclusions

Our study provides insight on an assortment of disturbance and environmental factors affecting woody vegetation responses across a contiguous portion of the eastern boreal mixedwood region. Although natural disturbances caused substantial structural changes to forest stands, the various moderate-severity disturbance types were not the principal factors causing variation in woody species diversity and abundance. Stand composition prior to disturbance, specifically the density of *Abies balsamea* advance regeneration associated with these stand types, and coarse woody debris density had general effects across the region, while different combinations of disturbance type, climate, physiographic, and other stand structure and composition variables were responsible for imparting variation in species distribution at a local level. Furthermore, several woody species (and all size classes of each species) examined in this study consistently responded to these factors in the same manner throughout the mixedwood region, suggesting that they can be effective predictors of post-disturbance community composition.

3.9. Acknowledgements

Many thanks to all my field assistants. Your various personalities, quirks, and habits that were amplified during long, buggy, hot and/or rainy days in the field made data collection quite memorable and fun! Additionally, this study would not have been possible without financial and/or technical support from TEMREX, NSERC-CFS and the SFMN.

3.10. References

Please see the General Citation List (pp 133-154).

Table 3.1. Comparison of climate, physiographic, and forest structure and composition variables at each location and for across the region using factorial ANOVA. Unlike letters along row indicate values are significantly different among locations ($p < 0.05$).

Variable	Local sites			Boreal mixedwood region
	Temiskaming – Abitibi	North Shore	Gaspé Peninsula	
Climate				
Annual rain (mm)	691.3 a	691.0 a	724.3 b	708.0
Annual snow (mm)	274.3 a	303.4 b	238.6 c	265.0
Annual precipitation (mm)	965.6 ab	988.9 b	963.1 a	971.4
Annual temperature (°C)	2.1 a	2.2 a	3.6 b	2.9
Mean monthly temperature - summer (°C)	16.3 a	15.3 a	16.6 a	16.1
Mean monthly temperature - winter (°C)	-10.4 a	-8.8 b	-7.3 c	-8.3
Mean windspeed (km h ⁻¹)	12.9 a	15.6 b	18.7 c	16.7
Maximum windspeed (km h ⁻¹)	52.8 a	75.6 b	76.0 b	71.5
Maximum gust speed (km h ⁻¹) [†]	98.4	105.2	no data	---

Physiography

Elevation (m)	311.2 a	274.2 a	421.4 b	355.9
Slope ¹ (%)	1.0 a	1.2 a	2.1 b	1.6
Latitude (degrees)	47.3 a	49.0 b	48.5 b	48.4
Longitude (degrees)	78.4 a	68.8 b	66.1 c	69.3
Soil drainage ²	3.5 a	3.1 a	2.3 b	2.8

**Forest structure
and composition**

Mean disturbance area (ha)	11.6 ab	8.9 a	13.2 b	11.6
Snag density (ha ⁻¹)	138.2 a	294.1 b	499.3 c	371.2
Course woody debris density (ha ⁻¹)	1176.4 a	1729.1 b	2159.9 c	1849.4
Percentage of trees uprooted	28.0 a	31.9 a	37.2 a	33.8
Decay class average ³	11.2 a	11.2 a	10.4 b	10.8
Tree regeneration density (ha ⁻¹)	12 907.9 a	36 825.6 b	15 284.5 a	21 405.6
Shrub regeneration density (ha ⁻¹)	11 982.9 a	33 969.6 b	7 454.0 a	16 384.0
Total regeneration density (ha ⁻¹)	24 890.7 a	70 895.2 b	22 738.6 a	37 789.6
Coniferous legacy tree density (ha ⁻¹)	1.3 a	8.9 b	0.1 c	3.0
Deciduous legacy tree density (ha ⁻¹)	0.1 a	2.7 b	0.2 a	1.0

Crown cover of coniferous legacy trees (%)	3.5 a	3.5 a	4.2 a	3.8
Crown cover of deciduous legacy trees (%)	1.6 a	1.7 a	6.8 b	4.3
Stand density prior to disturbance (ha ⁻¹)	926.6 a	1 474.0 b	1 718.7 b	1 496.1

†insufficient data to include in analyses.

¹1: 0 to 10°, 2: >10 to 20°, 3: >20 to 30°, 4: >30 to 40°, 5: >40°;

²2: good, 3: moderate; 4: imperfect;

³ see Imbeau and Desrochers (2002).

Table 3.2. Canonical correlation coefficients between significant environmental variables and the first four ordination axes for Redundancy Analysis examining species-environment relationships at the regional level (Critical value for t-statistic = 1.96, $P < 0.05$, ns indicates non-significance).

Environmental Variable	Axis 1	Axis 2	Axis 3	Axis 4
Decay class ¹	-0.20	0.31	0.20	ns
Elevation (m)	0.15	0.30	-0.19	-0.18
Annual Temperature (°C)	-0.18	ns	-0.38	ns
Spruce budworm outbreak	0.20	ns	ns	0.25
Ecozone (BF-WB) ²	0.23	ns	-0.22	ns
Coarse woody debris density (ha ⁻¹)	0.45	ns	ns	ns
Deciduous legacy tree crown cover (%)	ns	0.16	ns	0.36
Conifer-dominated stand prior to disturbance	0.52	ns	ns	ns
Drainage ³	0.20	ns	ns	ns

¹from Imbeau and Desrochers (2002);

²*Abies balsamea*-*Betula papyrifera* Ecozone;

³2: good, 3: moderate; 4: imperfect.

Table 3.3. Mean regeneration density (ha⁻¹) for a selection of woody species establishing within the boreal mixedwood region of Quebec, Canada. Shade tolerance: ● high, ○ mid, ○ low.

Species	Temiskaming- Abitibi	North Shore	Gaspé Peninsula	Region
canopy trees				
<i>Abies balsamea</i>	● 2576.1	7427.8	2714.7	4125.4
<i>Picea mariana</i>	● 194.3	459.8	22.5	188.0
<i>Thuja occidentalis</i>	● 22.9	1.0	0.8	5.0
<i>Acer saccharum</i>	● 21.4	-	-	12.2
<i>Picea glauca</i>	○ 73.7	211.7	25.1	91.1
<i>Betula alleghaniensis</i>	○ 7.3	-	183.1	94.4
<i>Pinus strobes</i>	○ -	-	2.1	1.1
<i>Fraxinus americanus</i>	○ 1.4	-	-	0.3
<i>Fraxinus nigra</i>	● 8.6	-	-	1.6
<i>Larix laricina</i>	○ 1.4	-	-	0.3
<i>Betula papyrifera</i>	○ 268.9	1103.4	856.7	821.9
<i>Populus tremuloides</i>	○ 50.3	2.8	16.2	10.3
sub-canopy trees & shrubs				
<i>Acer pensylvanicum</i>	● -	-	38.0	19.3
<i>Corylus cornuta</i>	● 1004.5	-	169.0	273.8
<i>Taxus canadensis</i>	● -	1170.6	-	356.8
<i>Acer rubrum</i>	● 44.3	90.4	98.3	85.8
<i>Acer spicatum</i>	● 491.8	3011.0	884.0	1458.9
<i>Alnus spp.</i>	● 437.9	525.1	-	242.0
<i>Amelanchier spp.</i>	● 21.4	686.5	204.2	317.0
<i>Cornus stolonifera</i>	● 15.7	104.4	2.1	35.8
<i>Diervella lonicera</i>	● 1.4	58.3	-	18.0
<i>Kalmia angustifolium</i>	○ -	318.9	-	97.2

<i>Ledum groenlandicum</i>	○	5.7	26.3	-	8.7
<i>Lonicera</i> spp.	○	1.4	-	-	0.3
<i>Myrica gale</i>	●	-	31.6	-	9.6
<i>Nemopanthus mucronata</i>	●	90	30.3	3.7	27.9
<i>Sambucus</i> spp.	●	1.4	-	18.9	9.9
<i>Sorbus</i> spp.	●	197.1	641.7	348.3	409.4
<i>Viburnum cassinoides</i>	●	40.0	-	-	7.5
<i>Viburnum edule</i>	●	236.4	486.8	-	192.6
<i>Prunus</i> spp.	○	66.6	72.5	83.3	76.9
<i>Rubus</i> spp.	○	302.8	1236.8	13.7	440.6
<i>Salix</i> spp.	○	37.1	1.3	-	7.4

Table 3.4. Canonical correlation coefficients between significant environmental variables and the first four ordination axes for Redundancy Analysis examining species-environment relationships for each study location (Critical value for t-statistic = 1.96; $P < 0.05$; ns indicates non-significance).

Site Location and Environmental Variable	Axis	Axis	Axis	Axis
	1	2	3	4
Temiskaming-Abitibi				
Windthrow	-0.70	-0.33	ns	ns
Annual rainfall (mm)	0.75	-0.39	ns	ns
Coarse woody debris density (ha ⁻¹)	0.27	ns	-0.66	ns
North Shore				
Latitude	0.57	ns	ns	ns
Elevation (m)	-0.18	ns	0.24	0.39
Annual rainfall (mm)	-0.19	0.35	ns	ns
Coarse woody debris density (ha ⁻¹)	ns	0.24	-0.25	0.39
Windthrow	-0.10	-0.01	-0.43	ns
Gaspé Peninsula				
Conifer-dominated stand prior to disturbance	0.54	ns	ns	ns
Coarse woody debris density (ha ⁻¹)	0.51	ns	-0.30	ns
Decay class ¹	-0.29	-0.34	-0.31	ns
Spruce budworm outbreak	0.28	ns	ns	0.30
Elevation (m)	ns	-0.44	ns	ns

¹from Imbeau and Desrochers (2002).

Table 3.5. Estimates of alpha (α), gamma (S), and beta (β) diversity, in addition to Shannon's (H') and evenness (J) according to location and regeneration layer. Testing for differences in α , H' , and J among locations for each vegetation layer was made using ANOVA. Within a column, values with post-script indicate significant differences were observed for the particular vegetation layer - where unlike letters between locations for the vegetation layer in question indicate significant differences at $p < 0.05$.

Site location and vegetation layer	α	S	β	H'	J
Temiskaming – Abitibi					
All woody vegetation	8.5 ab	28	3.0	1.3	0.5
Canopy trees	3.7	11	2.2	0.6	0.5 ab
Sub-canopy tree & shrubs	4.7 ab	17	3.6	1.0 ab	0.7
North Shore					
All woody vegetation	9.2 a	22	2.7	1.4	0.5
Canopy trees	3.7	6	2.2	0.5	0.4 a
Sub-canopy tree & shrubs	5.8 a	16	2.8	1.2 a	0.6
Gaspé Peninsula					
All woody vegetation	7.5 b	19	3.6	1.2	0.5
Canopy trees	3.4	8	2.5	0.7	0.6 b
Sub-canopy tree & shrubs	4.1 b	11	4.4	0.8 b	0.6
Regional					
All woody vegetation	8.3	33	3.1	1.3	0.5
Canopy trees	3.6	12	2.3	0.6	0.6
Sub-canopy tree & shrubs	4.8	21	3.6	1.0	0.6

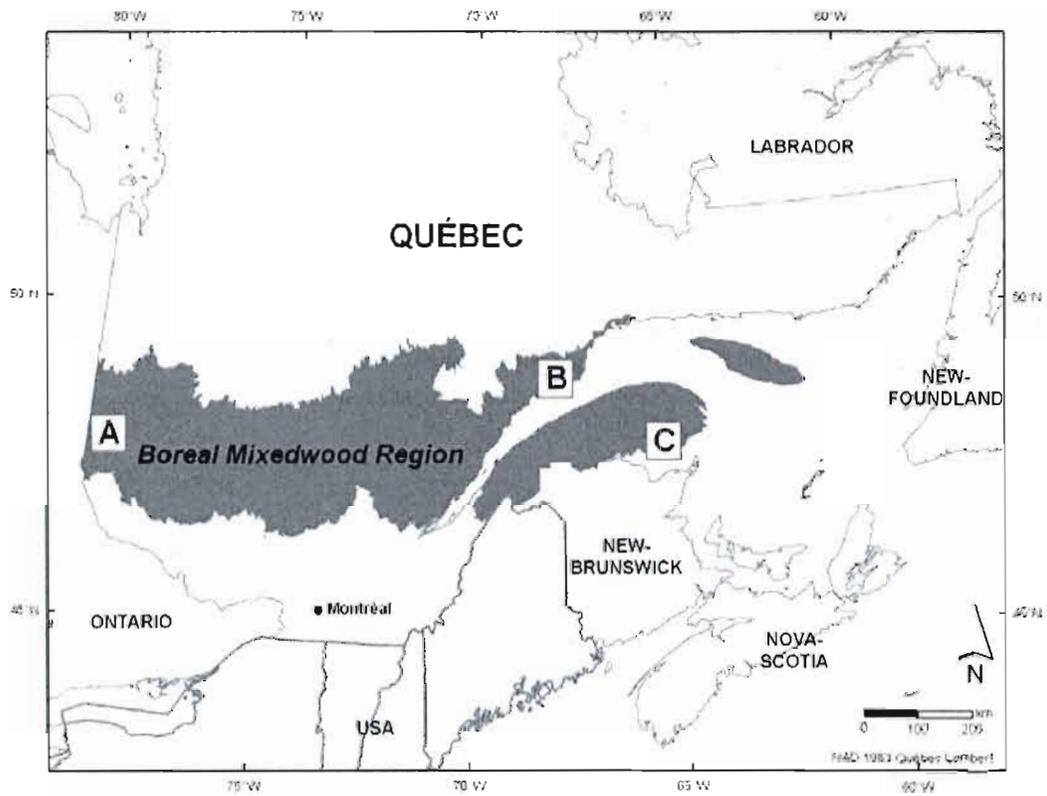


Figure 3.1. Study locations within the boreal mixedwood region of Quebec, Canada: (A) Temiskaming-Abitibi, (B) the North Shore, (C) the Gaspé Peninsula.

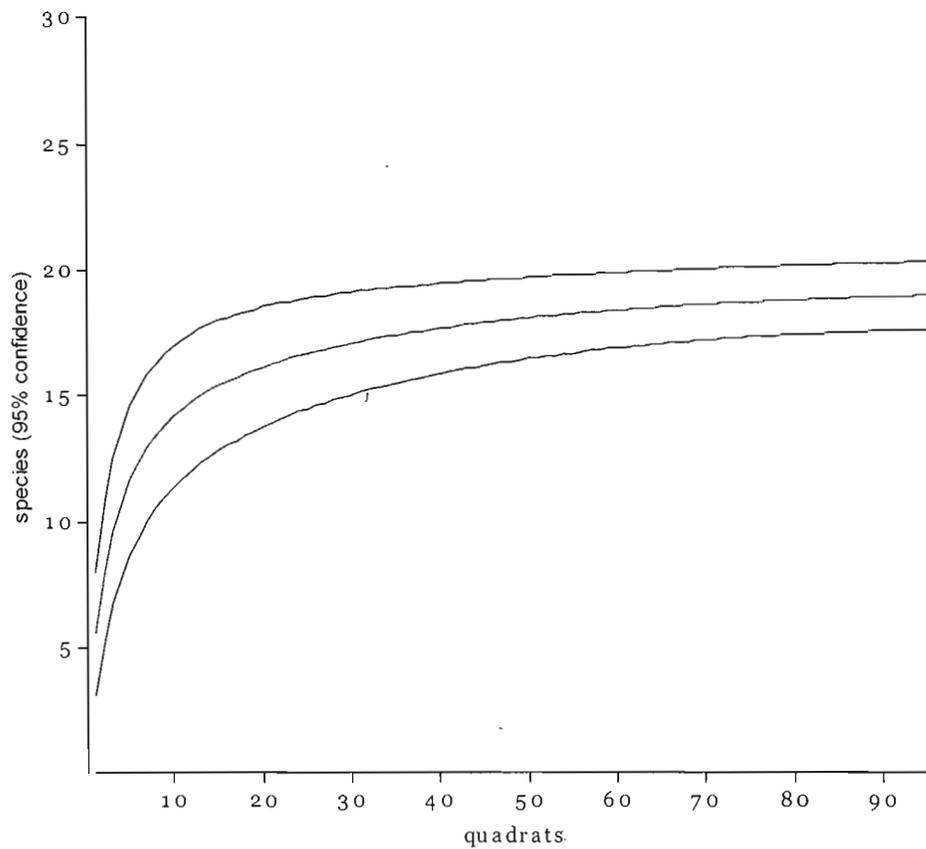
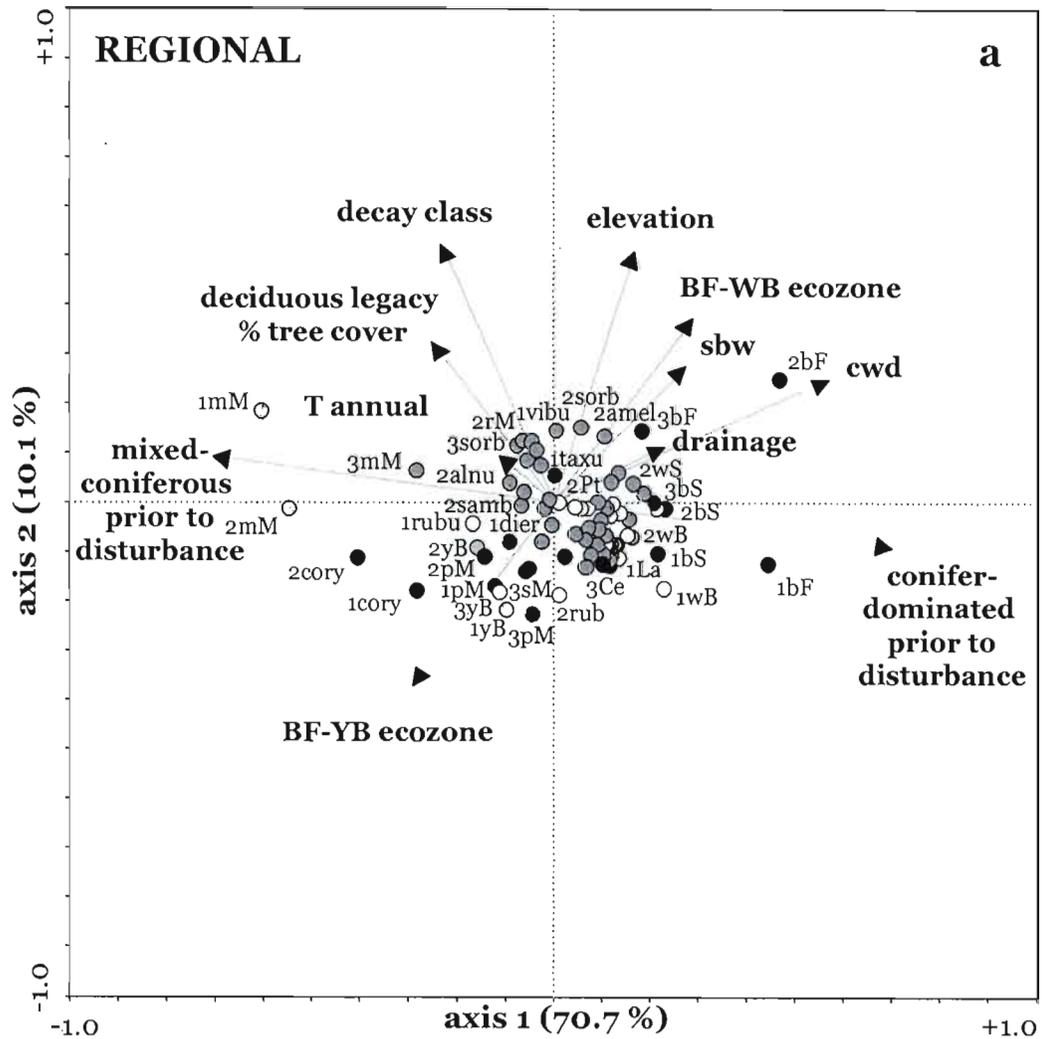
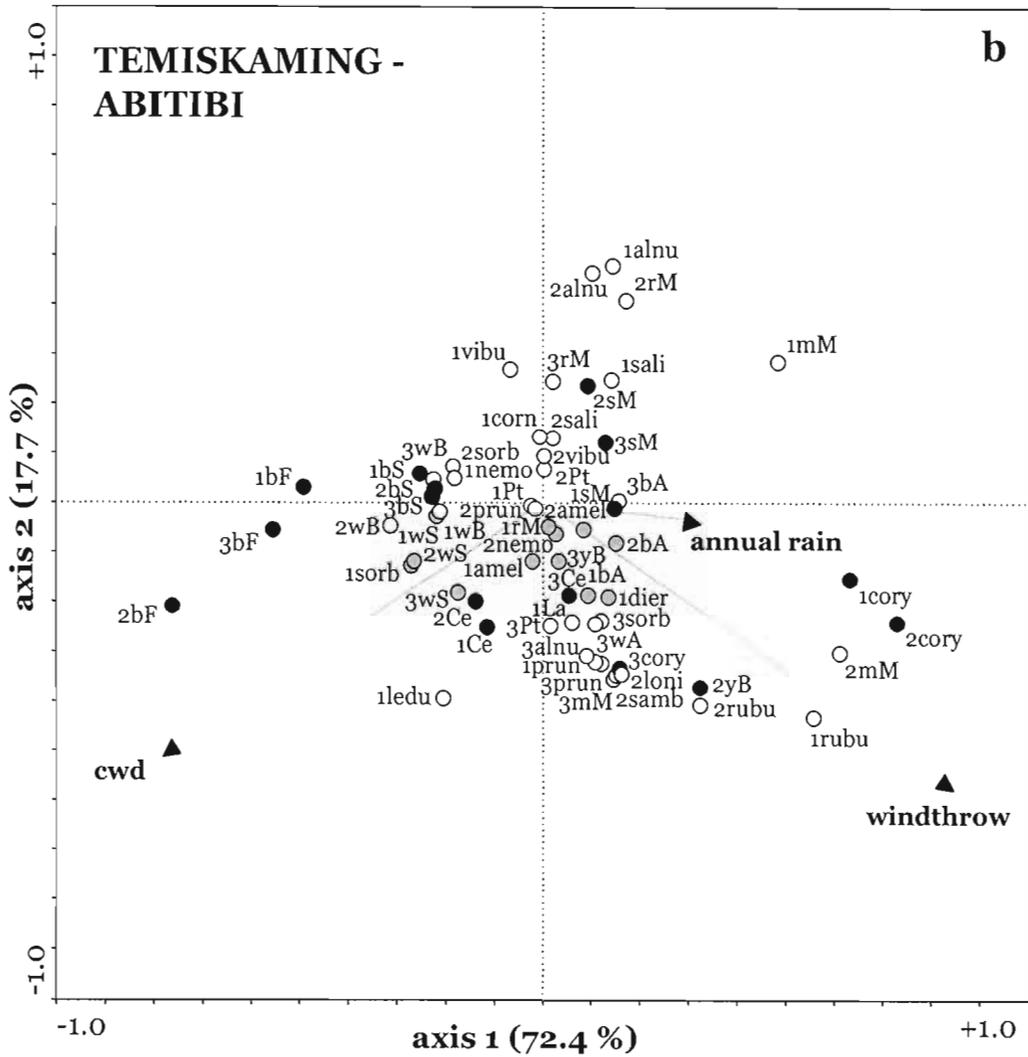
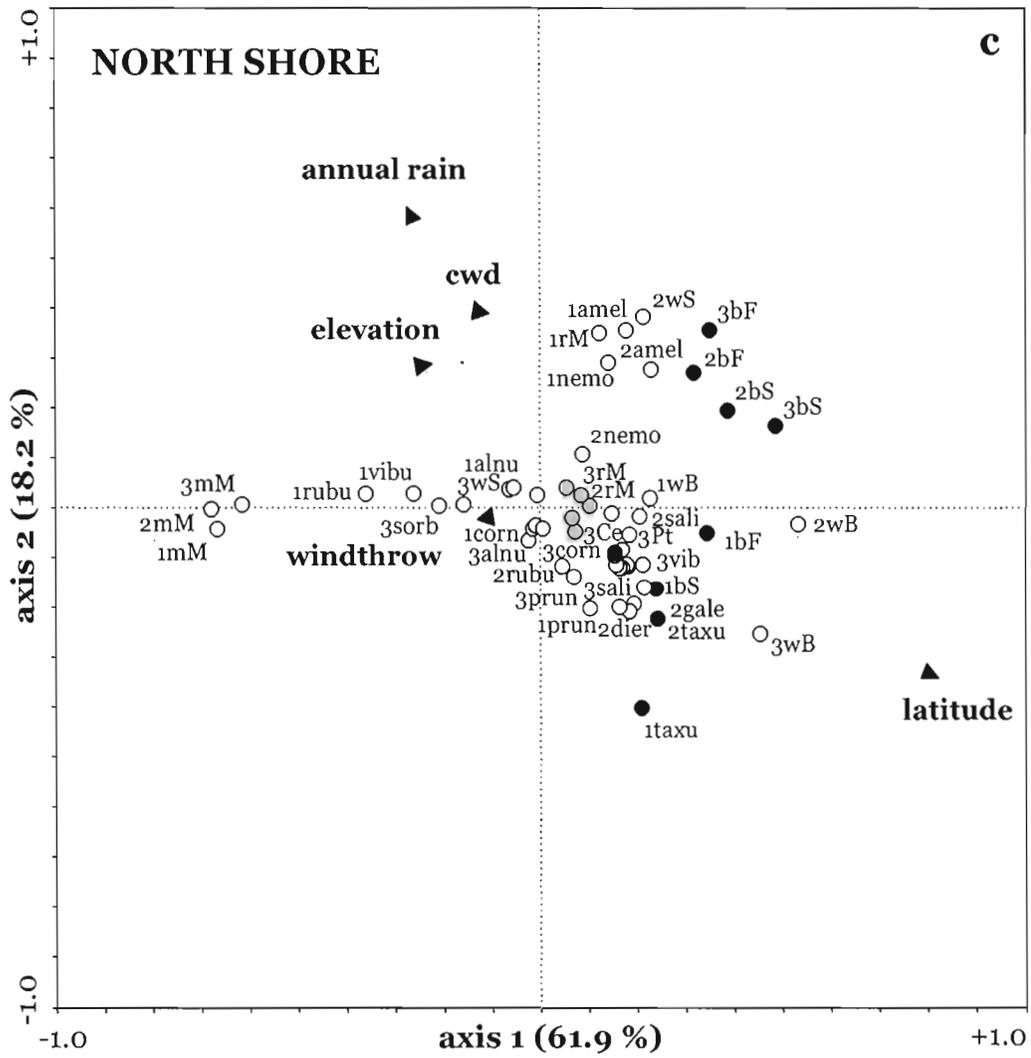


Figure 3.2. Sample rarefaction analysis to determine if differences in species richness estimates were associated with variation in sampling effort. A total of 35, 57, and 95 quadrats (20 x 20 m) were used in Temiskaming-Abitibi, the North Shore, and the Gaspé Peninsula, respectively. Curves above and below mean species values represent 95 % confidence intervals.







indicate stronger associations. Only the environmental variables having significant relationships with axes 1 or 2 are shown. Some species names near the origin were removed to reduce clutter. Numbers preceding species codes indicate the following regeneration size classes: (1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 m), (3) 4 to 8 cm dbh. Species and environmental variable codes are as follows: wA = *Fraxinus americanus*, bA = *Fraxinus nigra*, wB = *Betula papyrifera*, yB = *Betula alleghaniensis*, Ce = *Thuja occidentalis*, bF = *Abies balsamea*, La = *Larix laricina*, mM = *Acer spicatum*, pM = *Acer pensylvanicum*, rM = *Acer rubrum*, sM = *Acer saccharum*, Pt = *Populus tremuloides*, wP = *Pinus strobus*, bS = *Picea mariana*, wS = *Picea glauca*, alnu = *Alnus* spp., amel = *Amelanchier* spp., corn = *Cornus stolonifera*, cory = *Corylus cornuta*, dier = *Diervella lonicera*, gale = *Myrica gale*, kalm = *Kalmia angustifolia*, ledu = *Ledum groenlandicum*, loni = *Lonicera* spp., nemo = *Nemopanthus mucronata*, prun = *Prunus* spp., rubu = *Rubus* spp., sali = *Salix* spp., samb = *Sambucus* spp., sorb = *Sorbus* spp., vibe = *Viburnum edule*, vibu = *Viburnum cassinoides*, taxu = *Taxus canadensis*, BF-WB = *Abies balsamea*-*Betula papyrifera* Ecozone, BF-YB = *A. balsamea*-*B. alleghaniensis* Ecozone, and cwd = coarse woody debris. Shade tolerance: ● high, ● mid, ○ low.

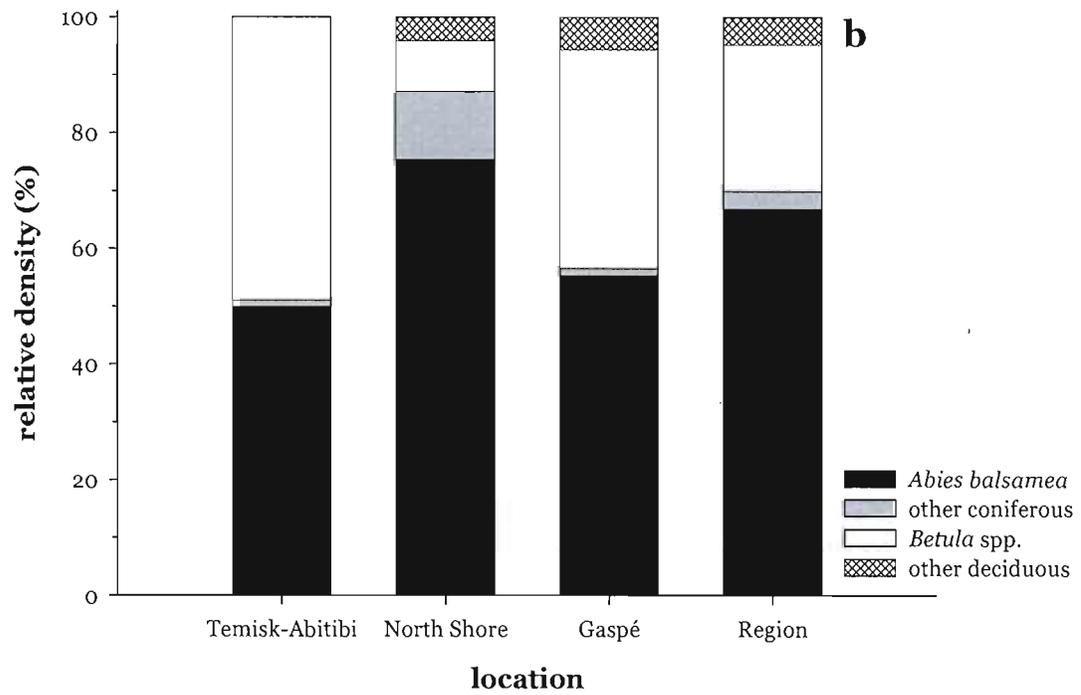
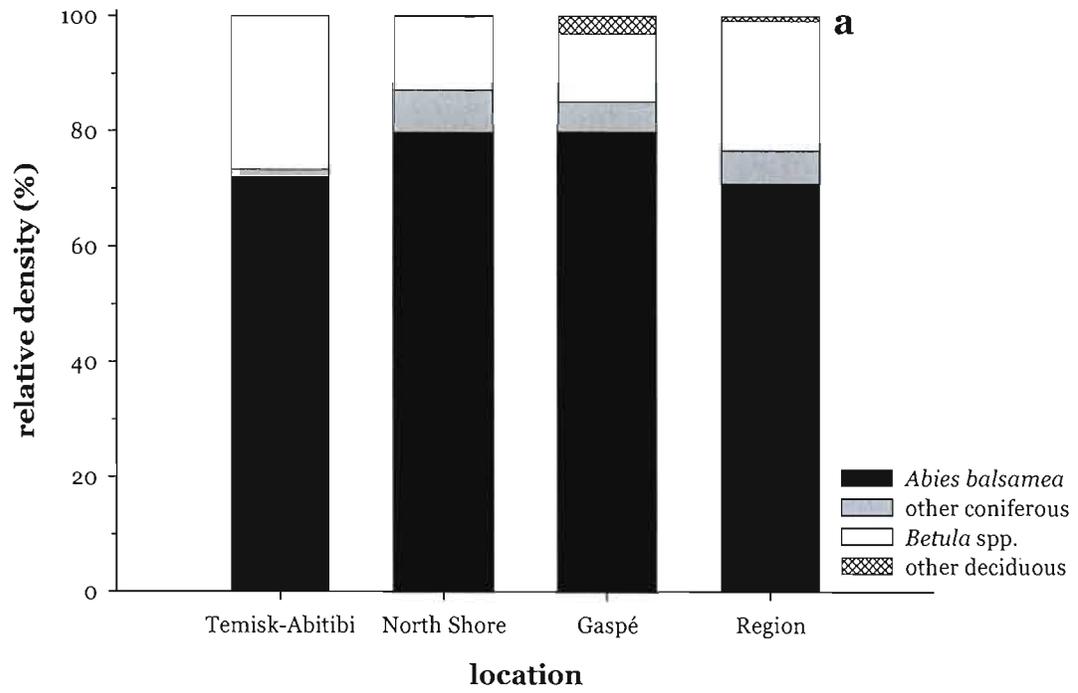


Figure 3.4 a-b. Relative densities of principal canopy tree species regeneration for each location and across the entire boreal mixedwood study region for (a) conifer-dominated stands (≥ 75 % conifer canopy prior to disturbance) and (b) mixed-coniferous stands (50-74 % conifer canopy) prior to disturbance.

PROLOGUE TO CHAPTER IV

It appears that different suites of factors determine woody vegetation responses after moderate-severity disturbances across the boreal mixedwood region. I now wish to determine how important moderate-severity disturbances are in the context of a range of natural disturbances, in terms of amount of mortality caused, that are most prevalent in the region. I compare vegetation responses to moderate-severity disturbances relative to canopy gap and catastrophic fire disturbances. Please note that this version has been slightly modified from that submitted to the *Journal of Vegetation Science*. The version here includes revisions suggested by the examining committee during my dissertation, which I believe has improved the manuscript considerably.

CHAPTER IV

**CHANGES IN WOODY VEGETATION ABUNDANCE AND DIVERSITY
AFTER NATURAL DISTURBANCES CAUSING DIFFERENT LEVELS OF
MORTALITY**

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and Alain Leduc**

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4.1. Abstract

- 4.1.1. Question:** How does woody vegetation abundance and diversity differ after natural disturbances causing different levels of mortality?
- 4.1.2. Location:** *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands of south-eastern Quebec, Canada.
- 4.1.3. Methods:** Woody vegetation abundance and diversity were quantified and compared among three disturbance-caused mortality classes: canopy gap, moderate-severity disturbances, and catastrophic fire, using redundancy analysis, a constrained linear ordination technique, and diversity indices.
- 4.1.4. Results:** Substantial changes in canopy tree species abundance and diversity occurred only after catastrophic fire. Shade-tolerant, late-successional conifer species remained dominant after canopy gap and moderate-severity disturbances whereas shade-intolerant, early-successional colonisers dominated the canopy tree regeneration after catastrophic fire. Density and diversity of mid-tolerant and shade-intolerant understory tree and shrub species increased as the amount of mortality increased. Highest species richness estimates were observed after catastrophic fire, with several species establishing exclusively under these conditions. Relative abundance of the canopy tree regeneration was most similar after canopy gap and moderate-severity disturbances. For the sub-canopy tree and shrub community, relative species abundances were most similar after moderate-severity disturbances and catastrophic fire. Vegetation responses to moderate-severity disturbances thus had commonalities with both extremes of the disturbance-caused mortality gradient, but for different regeneration layers.

4.1.5. Conclusions: Current spatio-temporal parameters of natural disturbances causing varying degrees of mortality promote the development of a complex, multi-cohort forest condition throughout the landscape. The projected increase in time intervals between catastrophic fires may lead to reduced diversity within the system.

4.1.6. Key words: disturbance-caused mortality; canopy gap disturbance; moderate-severity disturbance; catastrophic fire; natural regeneration; *Abies balsamea*-*Betula papyrifera* forests.

4.1.7. Nomenclature: Gleason & Cronquist (1991)

4.1.8. Abbreviations: MSD = moderate-severity disturbance; RDA = redundancy analysis; R = species richness; H' = Shannon's diversity index; β = Sørensen's similarity index.

4.2. Introduction

Variation in levels of disturbance-caused mortality is a key factor in determining successional pathways. The range of conditions created by the variety of disturbance agents occurring within boreal mixedwoods allows a number of different species to dominate after disturbance, depending on the amount of mortality caused. Large, severe disturbances cause extensive overstory and understory mortality, and drive succession back to conditions wherein seral species dominate (Turner et al. 1997, Gromtsev 2002). Conversely, canopy gap disturbances affect one to a few overstory trees, and facilitate the regeneration and growth of late-successional species (Kneeshaw & Bergeron 1998). Conditions after moderate-severity disturbances (defined here as an abiotic or biotic disturbance that is intermediary between canopy gap and catastrophic fire in terms of amount of mortality caused), are less predictable. Moderate-severity disturbances have been shown to drive succession back, perpetuate existing conditions, drive change towards an alternate stable state, or drive succession towards old-growth conditions (Frelich & Reich 1999; Bergeron 2000; Reyes & Kneeshaw 2008).

Catastrophic fire has historically been the prominent large, severe disturbance driving stand dynamics in *Abies balsamea*-*Betula papyrifera* boreal mixedwood forests of north-eastern North America (Bergeron et al. 2001). But with a recent climatically-induced decrease in catastrophic fire frequency (Bergeron et al. 1998), other smaller and/or less severe disturbance types such as those caused by spruce budworm (*Choristoneura fumiferana*) outbreaks, windthrow, and their interactions can become more important in shaping landscape structure and species distribution patterns. Moderate-severity disturbances, in particular, can cause profound change, as they can affect 10s to 100s of hectares of forest (Clinton & Baker 2000; Gray et al. 2000, Nagel & Diaci 2006), and can occur relatively frequently in the absence of fire. Spruce budworm outbreak, for example, has occurred on a 20 to 50 year cycle in north-eastern North America since the end of the Little Ice Age (~1850) (Blais 1983; Bouchard et al. 2006). However, although similar in spatial extent to catastrophic fire, unlike catastrophic fire, moderate-severity disturbances leave the regeneration layer relatively intact, and are thus less severe.

Successful establishment occurs where a species' life history strategies are compatible with the prevailing establishment or regeneration conditions generated by the disturbance regime (Grime 1977). Different functional groups often show divergent responses to disturbance (Oliver 1981; Roberts 2004; Kennard & Putz 2005). Early-successional, light-demanding species are usually associated with larger, more severe disturbances whereas late-successional, shade-tolerant species often dominate the regeneration layer after smaller, less severe disturbances (Frelich 2002, Gromtsev 2002). Species diversity tends to increase after disturbance (Peterson & Pickett 1995), and is also affected by variation in the amount of disturbance-caused mortality (Peltzer et al. 2000). Highest diversity estimates are hypothesized to occur at intermediate levels (Connell 1978; Miller 1982).

Given variability in species responses to disturbance, the ability to predict regeneration patterns after different types of natural disturbances causing varying degrees of mortality would significantly contribute to our understanding of boreal mixedwood stand dynamics. Further, although the early/late succession species classification is useful to predict species abundance and diversity after canopy gap

versus large, catastrophic disturbances, species responses to moderate-severity disturbances remain unclear. Past research in boreal mixedwoods has focused on either end of the disturbance impact spectrum (e.g., Leemans 1991; Kneeshaw & Bergeron 1998; Bergeron & Dansereau 1993), with little consideration of patterns of recovery across a range of disturbance-caused mortality.

The objectives of our study are to examine and compare woody species regeneration abundance and diversity after natural disturbances causing varying degrees of mortality. Specifically, we aim to: (1) determine if significant changes in relative abundances of the principal canopy species occur after canopy gap, moderate-severity, and large, catastrophic fire disturbances; and (2) examine the variation in woody species diversity in relation to these disturbance-caused mortality classes.

4.3. Study area

The study was conducted within *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands located in the Chaleur Bay region of the Gaspé Peninsula, Quebec, Canada (between 48°10' to 48°35'N and 65°45' to 66°15' W). Total surface area of the study area is approximately 6 480 km². These *Abies balsamea*-*Betula papyrifera* stands are a part of a transitional boreal mixedwood bioclimatic domain bounded by boreal forests to the north and cool-temperate deciduous forests to the south. Consequently, the forest canopy consists of a mix of evergreen conifer and broad-leaved deciduous species. *Abies balsamea*, a shade-tolerant, evergreen conifer species characteristic of late-succession conditions in these forests, and *Betula papyrifera*, a shade-intolerant broad-leaved deciduous coloniser, dominate the forest landscape. Species of lesser importance include the shade-tolerant *Picea glauca*, *Picea mariana*, and *Thuja occidentalis*, the mid-tolerant *Acer rubrum*, *Betula alleghaniensis*, and *Pinus strobus*, and the shade-intolerant *Populus balsamifera* and *Populus tremuloides*. The general transition of species after catastrophic fire is from a broad-leaved deciduous canopy followed by a mixed coniferous-deciduous canopy that can persist for several generations, which transitions to a conifer-dominated climax community in the absence of fire (Bergeron 2000).

Climate for the region is humid-continental. Mean minimum daily temperature in January is -15.8 °C while mean daily maximum in July is 22.6 °C. Mean annual precipitation is 984 mm, with approximately 79 % falling as rain (Environment Canada 2004). General topography is rolling to montane, as the region is part of the Appalachian mountain chain that extends in a west-southwest direction into the southeastern United States. Elevations range from 80 to 600 m (mean 285 m). Soils originate from glacial tills, glacio-lacustrine, fluvio-lacustrine, or alteration deposits (Robitaille and Saucier 1998). Soil drainage ranges from imperfect to rapid. Very few lakes are present although several rivers are interspersed throughout the region.

The current fire cycle, estimated to be between 170 and 250 years (Lauzon et al. 2007), allows many stands to escape catastrophic disturbances for long periods of time. Subsequently, canopy gap and moderate-severity disturbances may have large impacts on the regeneration composition if occurring more frequently than fire. Return interval estimates were 30 and 39 years for canopy gap and moderate-severity disturbances, respectively (calculated using methods described in Canham & Loucks 1984; Runkle 1992; Zhang et al. 1999). Return interval estimates were consistent with estimates from associated research undertaken within the eastern boreal mixedwood region of Quebec, Canada (De Römer et al. 2007; Bouchard et al. 2006).

4.4. Methods

4.4.1. Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Stands were surveyed during the summer of 2004. Relative species composition of the tree canopy can be quite variable among *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands. To isolate differences in regeneration patterns due to variation in disturbance-caused mortality, we selected mature (≥ 89 y old) *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands having similar relative canopy species composition and densities prior to disturbance, general topography, elevation, and soil moisture and drainage regimes (as determined from various Government of Quebec forest inventory and land classification maps). Thus, we

sampled from mesic sites having 75:25 conifer to deciduous tree species ratios prior to disturbance, were well stocked, occurring on relatively flat terrain, and having good to rapid drainage. Ground-truthing of sites (quantifying live and dead canopy trees within the disturbed area) verified that conifers represented at least 75 % of the tree canopy density prior to disturbance, of which *Abies balsamea* accounted for at least 60 % of all conifer trees. *Betula papyrifera* was the most abundant deciduous species, accounting for at least 60 % of all deciduous canopy trees. Sampling protocols for each disturbance-caused mortality class were as follows:

4.4.2. Canopy gap disturbances

Canopy gap disturbances were differentiated from moderate-severity disturbances according to the spatial extent of the mortality caused to the tree canopy. Disturbances affecting between 0.0004 and 0.2 ha of contiguous tree canopy (i.e., from canopy edge rather than 'expanded' to tree base) were classified as canopy gap disturbances. One to three transects of variable length (approx. 100 to 400 m) were randomly established within each of five mature *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands (≥ 89 y old) to quantify vegetation regeneration abundance and diversity after canopy gap disturbances. Canopy gaps were caused by a number of disturbance agents (including mortality caused by the spruce budworm, windthrow, and senescence). Canopy gaps wherein the cause of gap formation could not be determined (i.e., no sign or presence of gap makers) were not included in our study. Transects started and ended at least 30 m from the nearest logging road or forest edge, and followed a straight trajectory. A total of 46 gaps were sampled. Various gap characteristics were quantified for each canopy gap traversed by the transect line. Length and width of each gap were measured using the longest north-south distance affected by gap disturbance in conjunction with the longest distance in an east-west direction that intersected the north-south vector. Gap size was determined using the following equation (Runkle 1992):

$$\text{Area} = \pi (\text{length} \times \text{width}) / 4 \quad [1]$$

Gap age (i.e., time since disturbance) was determined using annual ring counts measured at ground level from five shade-intolerant *Prunus pensylvanica* or *Betula papyrifera* seedlings established within each gap, as it was expected that shade-intolerant species established soon after gap formation. In the absence of these species, timing of release of *Abies balsamea* was determined using the same methods, as we assumed that release from suppression of *Abies balsamea* occurred within a few years after gap formation (Fraver & White 2005; Metslaid et al. 2005). Tree, sub-canopy tree, and shrub regeneration density (all individuals ≤ 8 cm dbh) were quantified along the north-south vector used to measure gap length, within an area 2 m of each side of the vector. Thus, sampling effort was a function of gap size. Mean gap size was 0.004 ha and ranged from 0.0005 to 0.02 ha. With more than half the gaps smaller than the mean, this necessitated using a different sampling protocol from moderate-severity disturbances and catastrophic fire.

4.4.3. Moderate-severity disturbances

Spruce budworm outbreak, windthrow, and interaction disturbances (defined as spruce budworm outbreak followed by windthrow prior to complete canopy recovery) fall within our moderate-severity disturbance class when causing more than 0.2 ha of continuous canopy mortality. An upper spatial limit was not initially firmly specified, as moderate-severity disturbances can be quite extensive, differing with catastrophic fire primarily in relation to effect on the regeneration layer. Nonetheless, the largest disturbed area examined was 95 ha (mean = 24 ha, smallest = 0.03 ha). Eleven stands affected by moderate-severity disturbances were sampled. Three to six, 20 x 20 m quadrats were examined within each disturbed stand. A total of 43 quadrats were sampled. All quadrats were at least 40 m from the nearest intact forest edge and 30 m from the nearest logging road to avoid edge effects. In every quadrat, regeneration density was determined for all tree, sub-canopy tree, and shrub species using a nested plot design: density of seedlings < 1 m tall were tallied in a 2 x 10 m area, those between 1 and 2 m tall, in a 5 x 10 m area, and regeneration > 2 m tall and ≤ 8 cm dbh, using the entire 20 x 20 m area. Time since disturbance was determined with the same methods used for canopy gap disturbances.

4.4.4. Large catastrophic fire disturbances

Stand-level effects of catastrophic fire can be highly variable (e.g., Lampainen et al. 2004). Unlike canopy gap and moderate-severity disturbances, catastrophic fire can affect stands in young, early successional stages. Moreover, divergent successional trajectories have been shown to occur when stand ages differed prior to disturbance (Heinselman 1973; Johnstone & Chapin III 2006). To make meaningful comparisons with the effects of the other disturbance-caused mortality classes, we limited our sampling to severely affected areas (extensive mortality to both canopy and regeneration layers) that were mature *Abies balsamea*-*Betula papyrifera* stands prior to a catastrophic fire that burned 59 ha of forest in 1988. Note that we did not account for variation in severity of catastrophic fire damage to the organic or mineral soil layers. Given that we sampled 16 years after fire, most of the differences among sites have become difficult to detect. Thus, we only ensured that we sampled in areas wherein >75 % mortality of the pre-fire regeneration layer occurred. This was verified in the field by determining the age of the regeneration from annual ring counts at ground level of ten of the largest seedlings within each quadrat. Pre-disturbance stand compositions and stand age classes were determined using Government of Quebec forest inventory maps of the region produced prior to 1988, and were verified in the field with identification (mostly to species, but at least to conifer *versus* deciduous) and annual ring counts of remnant stumps. Tree and shrub regeneration density was assessed in ten, 20 x 20 m quadrats using the moderate-severity disturbance protocol.

4.5. Analyses

4.5.1. Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Canonical ordination analyses were used to examine the role of variation in disturbance-caused mortality (canopy gap *vs.* moderate-severity *vs.* large catastrophic fire) on the response of regenerating tree, sub-canopy tree, and shrub species, in terms of absolute densities, with CANOCO 4.02 software (ter Braak & Smilauer 1998). Disturbance types (spruce budworm outbreak, windthrow, interaction, or other) were initially included in analyses as dummy variables, to

examine responses of vegetation to each of these factors. An initial run using Detrended Correspondence Analysis (DCA) showed data to have a linear distribution (all gradient lengths were <2.2 standard deviations for axes 1 to 4). Therefore, Redundancy Analysis (RDA), a direct gradient analysis approach, was used to examine relationships between disturbance-caused mortality, disturbance type, and regeneration abundance and diversity. The forward selection option was implemented to rank the importance of each environmental variable, and to remove any environmental variables that did not significantly contribute to the observed variation. Monte Carlo permutation tests were used to evaluate the significance of each environmental variable (at $\alpha = 0.05$ to enter or stay in model, 200 permutations for each run). While canopy gap, moderate-severity, and large catastrophic fire disturbances were significantly associated with differences in regeneration abundance and diversity (all $p < 0.05$) using the forward selection procedure, none of the various disturbance types had significant effects (all $p > 0.05$). Thus, only outputs comparing relationships between each disturbance-caused mortality class and regeneration composition and abundance are shown. A set of analyses separating regeneration size classes (seedlings <1 m tall, those between 1 and 2 m tall, and regeneration >2 m tall and ≤ 8 cm dbh) was also run. Because our results did not appreciably differ from that with regeneration size classes pooled, only results showing pooled size classes are shown. Further, only sites that had undergone disturbances within a few years of one another were included in analyses to ensure that differences in species composition and abundance among disturbance-caused mortality classes were not a result of large discrepancies in time since disturbance. Thus 23, 33, and 10 of the canopy gap, moderate-severity disturbance, and catastrophic fire plots, respectively, were included in analysis. Time since disturbance for canopy gap, moderate-severity, and catastrophic fire disturbance were 15 ± 0.6 SEM, 19 ± 0.8 SEM, and 16 years, respectively.

4.5.2. Species richness and diversity in relation to variation in disturbance-caused mortality

Differences in species richness among severity classes were examined by randomly selecting 10 plots from each of the canopy gap (two from each site) and MSD (one each from ten of the 11 sites) classes and analysing these against the 10 catastrophic fire plots. Species richness (R), defined as the total number of tree, sub-canopy tree and shrub species, and Shannon's diversity index (Shannon and Weaver 1949):

$$H' = - \sum p_i \ln p_i \quad [2]$$

where p_i = proportion of the total sample belonging to species i (in this case the relative density of a species), were determined for the regeneration layer for each plot, and compared among disturbance-caused mortality classes using ANOVA (SPSS 10.0 1999). The Student-Newman-Keuls multiple range test ($\alpha = 0.05$) was used for post-hoc comparisons. Data transformation was unnecessary for R as data met the parametric assumptions of normality and homogeneity of variances among treatment groups (Zar 1996), whereas H' data were ln transformed prior to analyses. Sørensen's similarity index (Sørensen 1948):

$$\beta = 2c / (S_1 + S_2) \quad [3]$$

was used to compare species diversity among disturbance-caused mortality classes. S_1 is the total number of species in disturbance class 1, S_2 is the total number of species in disturbance class 2, and c is the number of species common to both disturbance-caused mortality classes. Similarity index values close to one indicate that classes have most of their species in common while dissimilar classes will have values close to zero.

Species richness (R) is partly a function of spatial scale (Palmer & White 1994; Kallimanis et al. 2008). We acknowledge that differences in R may be an artefact of quadrat size both within the canopy gap disturbance mortality class and between canopy gap disturbance and the other two disturbance-caused mortality classes, given the different protocols used to quantify R . To examine effects of spatial differences in sampling effort on R within the canopy gap disturbance class we used linear regression analyses to examine the effect of the area sampled for each gap on R (at $p < 0.05$). No significant relationship was observed between sampling area and R for tree ($R^2 = 0.06$, $F_{1,22} = 1.32$, $p = 0.26$), sub-canopy tree and shrub ($R^2 = 0.03$, $F_{1,22} = 1.75$, $p = 0.20$), or for total woody vegetation ($R^2 = 0.05$, $F_{1,22} = 1.21$, $p = 0.28$). A second series of linear regression analyses was subsequently undertaken to test for sampling area relationships with R for all samples among the three disturbance-caused mortality classes. No significant sampling area-species R relationships were observed: R for tree ($R^2 = 0.01$, $F_{1,64} = 0.65$, $p = 0.42$), sub-canopy tree and shrubs ($R^2 = 0.05$, $F_{1,64} = 3.27$, $p = 0.07$), or for total woody vegetation ($R^2 = 0.04$, $F_{1,64} = 2.65$, $p = 0.11$). Given these results, we felt that making comparisons of diversity estimates among disturbance-caused mortality classes was a valid undertaking.

4.6. Results

4.6.1. Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Variation in disturbance-caused mortality resulted in distinct changes in woody species abundance and diversity. Canopy gap and moderate-severity disturbances caused minor changes to the relative abundance and diversity of canopy tree species in relation to pre-disturbance conditions ($\geq 75\%$ conifer overstory), whereas substantial changes were observed after catastrophic fire (Fig. 4.1 a & b). Most sub-canopy tree and shrub species increased in absolute abundance after catastrophic fire (Fig. 4.1 c & d). The first two axes in Redundancy analysis explained 26 and 5 % of the total variance in species composition among sample plots, respectively (Fig. 4.2). Catastrophic fire was the environmental variable most strongly correlated with axis 1 (canopy gap: $r = -0.43$, moderate-severity disturbance: $r = -0.24$, catastrophic fire: $r = 0.91$) while canopy gap and moderate-severity

disturbances were more strongly correlated to axis 2 (canopy gap: $r = 0.63$, moderate-severity disturbance: $r = -0.69$, catastrophic fire: $r = 0.12$). Early-succession, post-fire species segregated to the right along axis 1 whereas late-succession, shade-tolerant species pooled to the left with the canopy gap and moderate-severity disturbances. The second axis mainly differentiated mid to high shade-tolerance species (in the upper left quadrant of the ordination diagram) from mid to low shade tolerant species (in the lower half of the ordination diagram) between canopy gap and moderate-severity disturbances.

Abies balsamea, a shade-tolerant conifer species, was strongly associated with both canopy gap and moderate-severity disturbances (Fig. 2). *Abies balsamea* accounted for 92 and 81 % of all seedlings after canopy gap and moderate-severity disturbances, respectively (Fig 1a & 1b). *Betula papyrifera*, a shade-intolerant deciduous species, dominated the tree regeneration after catastrophic fire, accounting for 54 % of all seedlings established (Fig. 1b). Other shade-intolerant and mid-tolerant tree species such as *Pinus strobus*, *Populus balsamifera* and *Populus tremuloides* clustered to the right along axis 1 in ordination space, and thus were more strongly associated with catastrophic fire.

The shade-intolerant *Corylus cornuta* and *Prunus pensylvanica* dominated the sub-canopy tree and shrub component after catastrophic fire, but were present in only very low densities after canopy gap and moderate-severity disturbances. *Rubus* spp., which are rapidly colonising, shade-intolerant shrubs, were abundant after both moderate-severity disturbances and catastrophic fire, and absent after canopy gap disturbances. *Salix* spp. established only after catastrophic fire while the mid-tolerant *Acer rubrum* and the high shade-tolerant *Acer pensylvanicum* pooled towards the upper left in ordination space, indicating greater abundance after canopy gap disturbances. *Acer spicatum* was able to successfully regenerate under all post-disturbance conditions, suggesting that its distribution is mediated by other factors more so than variation in the amount of disturbance-caused mortality. *Corylus cornuta*, *Rubus* spp., and *Acer spicatum* exhibited aggregated distributions, and produced dense thickets that precluded establishment of other species.

Nemopanthus mucronata, *Sorbus* spp., and *Amelanchier* spp. pooled to the left along axis 1, but more towards moderate-severity disturbances along axis 2.

4.6.2. Species richness and diversity in relation to variation in disturbance-caused mortality

Twenty-two tree and shrub species were observed within the system (Table 4.1). Tree species richness (R) was lowest after moderate-severity disturbances and greatest after catastrophic fire (Table 4.2). Sub-canopy tree and shrub R and total woody plant species R was highest after catastrophic fire. Greater R after catastrophic fire relative to either canopy gap or moderate-severity disturbance is attributable to the influx of early-successional, shade-intolerant species. Shannon's diversity index (H') for canopy trees was similar among disturbance-caused mortality classes (Table 4.2). Sub-canopy tree and shrub H' and total woody plant species H' were lower after moderate-severity disturbances relative to either canopy gap or catastrophic fire disturbances. Canopy tree species compositions were most similar after canopy gap and moderate-severity disturbances while sub-canopy tree and shrub regeneration was most similar after moderate-severity disturbances and catastrophic fire disturbances (Table 4.3). Thus, moderate-severity disturbances shared commonalities with both extremes of the disturbance-caused mortality gradient, but for different forest regeneration layers. Canopy gap and catastrophic fire disturbed sites shared the least number of common species for all woody vegetation layer comparisons of β . Irrespective of the amount of disturbance-caused mortality, canopy tree regeneration was dominated by one or two species, whereas sub-canopy tree and shrub regeneration was more evenly distributed among component species (Fig. 4.1). Five species established exclusively after catastrophic fire (*Betula aleghaniensis*, *Pinus strobus*, *Populus balsamifera*, *Populus tremuloides*, *Salix* spp.), one after moderate-severity disturbances (*Nemopanthus mucronatus*), while no tree, sub-canopy tree, or shrub species were exclusive to canopy gap disturbances (Table 4.1).

4.7. Discussion

4.7.1. Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Distinct regeneration patterns were observed after canopy gap, moderate-severity, and catastrophic fire disturbances. Marked changes from pre-disturbance conditions, wherein shade-tolerant conifer species dominated the tree community, only occurred after catastrophic fire. The abundance of advance regeneration facilitated cyclical regeneration patterns after canopy gap and moderate-severity disturbances while destruction of most of the regeneration layer after catastrophic fire facilitated the establishment of more shade-intolerant species. For example, the shade-intolerant *Betula papyrifera* dominated the tree community after catastrophic fire, but was only a minor component after canopy gap and moderate-severity disturbances. *Betula papyrifera* densities were similar and low after canopy gap and moderate-severity disturbances despite large differences in the spatial extent among many of the canopy gap and moderate-severity disturbances examined here (disturbances ranged from 0.0005 to 95 ha).

Given that the moderate-severity disturbances examined in this study caused more than 75 % contiguous canopy mortality, and that the spatial extent of some moderate-severity disturbances was larger than that after catastrophic fire, greater changes in the tree community after such disturbances might be expected (e.g., Miller 1982; Peterson 2000). Yet despite major structural changes, relative tree species composition was not substantially altered from pre-disturbance conditions. This was the case irrespective of the type of moderate-severity disturbance, be it spruce budworm outbreak, windthrow, or their interaction, and despite the presence of shade-intolerant tree species in nearby clearcut or fire-originated stands functioning as potential seed sources. So while the spatial extent and degree of canopy tree mortality of some moderate-severity disturbances can be similar to or greater than that of catastrophic fire, severity between these disturbance types differs considerably. Much of the regeneration layer remains intact, more residual material is present, and proximity to legacy trees that function as seed sources is generally closer after moderate-severity disturbance. Thus, potential for recovery to pre-

disturbance conditions is greater, and the time needed for this recovery is reduced relative to after catastrophic fire; this appears to be true even for relatively extensive disturbances as long as the regeneration layer is intact. Our results are consistent with those of Kneeshaw & Bergeron (1998), Webb & Scanga (2001), and Rich et al. (2007) who found that smaller and/or less severe disturbances can hasten or maintain stand development towards late-succession conditions by favouring shade-tolerant species. Splachtna et al. (2005) observed similar general patterns, although the mechanisms involved were different, as canopy closure was also the result of lateral expansion of deciduous canopy trees.

The presence of a mostly intact regeneration layer likely had the greatest impact in retaining late-successional species dominance after both canopy gap and moderate-severity disturbances. In this forest system, *Abies balsamea* and *Picea glauca* seedlings establish and persist in the understory as advance regeneration for long periods of time until a canopy disturbance occurs (Morin & Laprise 1997). *Abies balsamea* advance regeneration, in particular, already occupied much of the available growing space. Many shade-intolerant tree species in our study region that can regenerate from seed require exposed mineral soils or recently burned organic soils to establish; e.g., *Populus tremuloides*, *Pinus banksiana* (Zasada et al. 1992). Seed dispersal constraints (Le Page et al. 2000) and low-pre-disturbance densities of canopy tree species that can regenerate via root suckering may also have played a role (e.g., *Populus spp.*); moreover, seeds of the canopy tree species in the region do not persist in the soil seed bank for more than a few years (Frank & Safford 1970; Greene et al. 1999), suggesting that the soil seed bank had little role in tree regeneration patterns.

High densities of coarse woody debris can affect seedling establishment (Reyes & Kneeshaw 2008). In our sites, downed logs inhibited germination by physically covering potential establishment sites, and by reducing light availability to the surface. Conversely, downed logs can act as nurse sites when sufficiently decomposed (Stevens 1997; Iijima et al. 2007). However, the advance regeneration in our study sites had already grown over the majority of these potential regeneration sites, negating any potential benefits (such as reduced competition) that nurse sites

can provide. Species regenerating from seed may thus be limited to establishing on exposed mineral soil resulting from tree uprooting after windthrow, and in areas with lower densities of advance regeneration and coarse woody debris (Reyes & Kneeshaw 2008). The importance of advance regeneration on post-disturbance dynamics has also been reported elsewhere (Leemans 1991; Ban et al. 1998; Grassi et al. 2004). Nevertheless, the deciduous component in mixedwood stands is often maintained after moderate-severity disturbance (Bergeron 2000; Dery et al. 2000). Although *Betula papyrifera* did not increase in relative abundance after moderate-severity disturbances in our study, the species maintained its importance in the canopy. Thus, moderate-severity disturbances may also act to slow successional trajectories towards late-succession conditions or to stabilize the current landscape structure over many generations (Bergeron 2000; Woods 2004; Papaik & Canham 2006).

While tree regeneration was similar after canopy gap and moderate-severity disturbances, considerable differences in the sub-canopy tree and shrub community were observed. Differences in establishment success of sub-canopy tree and shrub species between canopy gap and moderate-severity disturbance are related to different life-history characteristics of the component species and the availability and use of specific resource requirements. Certain species such as *Prunus pensylvanica* and *Rubus* spp. were quick to respond to ephemeral resources, and could take better advantage of subtle microenvironment differences between canopy gap and moderate-severity disturbances. *Rubus* spp., in particular, is a disturbance specialist that can remain dormant for many years in the seedbank, and does not require exposed mineral soils for germination (Lautenschlager 1991; Palmer et al. 2000). Further, nitrate (NO_3) pulses generally occur in forest soils one to two years after more severe disturbances (e.g., fire, soil scarification) (Truax et al. 1994), which can trigger germination of dormant *Rubus* spp. seeds (Jobidon 1993). Greater abundance of intolerant sub-canopy tree and shrub regeneration within larger gaps has also been observed elsewhere in the boreal mixedwood region (Kneeshaw & Bergeron 1998).

4.7.2. Species richness and diversity in relation to variation in disturbance-caused mortality

Our study supports the view that groups of species differing in important life history characteristics exhibit different responses across a range of disturbance-caused mortality. However, for the range of natural disturbances occurring in eastern boreal mixedwoods, our results for species richness and diversity of the woody plant community did not follow Connell's intermediate disturbance hypothesis (1978). In contrast to Miller (1982), large spatial differences between canopy gap and moderate-severity disturbances did not equate to significant increases in species richness or diversity. Richness and diversity estimates were, in fact, similar or lower after moderate-severity disturbances relative to both disturbance-caused mortality extremes. Our results show that the predictions of the intermediate-disturbance hypothesis are not always observed when catastrophic fire is the primary severe disturbance. Schwilk et al. (1997) obtained comparable results after fires in Mediterranean-climate shrublands, finding lowest plant diversity estimates at intermediate fire frequencies. Mackie & Currie (2001) and Sasaki et al. (2009) also show that the unimodal pattern of diversity characteristic of the intermediate-disturbance hypothesis is not always realised in other terrestrial systems.

Although generally similar in composition, some differences in the sub-canopy tree and shrub community were observed between canopy gap and moderate-severity disturbances, while several species were unique to catastrophic fire. Proliferation of disturbance specialists and shade-intolerant species, along with persistence of shade-tolerant, late-successional species, resulted in higher species richness estimates after catastrophic fire. The absence of several mid-tolerant and shade-intolerant species after canopy gap disturbances suggests that some of these species would be extirpated from the system without periodic moderate-severity or catastrophic fire disturbances. Thus, variation in disturbance-caused mortality is crucial to creating habitat diversity, allowing different species functional groups to persist across the landscape. Further, change in the vegetation community from canopy gap to the catastrophic fire range of disturbances is not a linear, continuous

species replacement process. Moderate-severity disturbances have distinct attributes, and subsequently effects, on regeneration abundance and diversity. The difficulty in characterising disturbances within the moderate-severity range is that vegetation responses have important similarities (and differences) to both disturbance-caused mortality extremes, depending on the vegetation layer examined.

4.8. Conclusions

Natural disturbances can have lasting and distinctive effects on the landscape. Expected changes in global climate will have considerable effects on mortality, recruitment patterns, and disturbance regimes. While fire cycles are expected to shorten and the incidence and severity of insect disturbances predicted to increase in much of the boreal region (Stewart et al. 1998; Volney and Fleming 2000), eastern North American boreal mixedwood fire cycles have been lengthening (Bergeron et al. 2001; Lauzon et al. 2007). Current return interval lengths for the various disturbances in *Abies balsamea*-*Betula papyrifera* boreal mixedwood forests is consistent with a disturbance regime characterised by relatively frequent partial events and rare catastrophic events. Given that canopy gap and moderate-severity disturbances do not appreciably change relative species composition of the canopy tree layer from pre-disturbance conditions, convergence towards late-successional forest conditions is promoted throughout the landscape. The projected increase in time intervals between catastrophic fires may lead to reduced diversity within the system.

4.9. Acknowledgements

Jean-Francois Liquidrano-Gagnon, Isabelle Nault, Mathieu Bouchard, David Saucier, Jonatan Belle-Isle, Steve Bujold, Julie Messier, and Maude Beauregard were important contributors to data collection and integral in either keeping me from losing my sanity in the field or accelerating the process :). Additionally, this study would not have been possible without financial and/or technical support from TEMREX, NSERC-CFS and the SFMN.

4.10. References

Please see the General Citation List (pp 133-154).

Table 4.1. Species shade tolerance, presence/absence (+/-), and richness (*R*) estimates (via presence/absence data from all sites) in relation to amount of disturbance-caused mortality for *Abies balsamea*-*Betula papyrifera* boreal mixedwood stands. Shade tolerance levels were obtained from Sack and Grubb (2002) and Humbert et al. (2007).

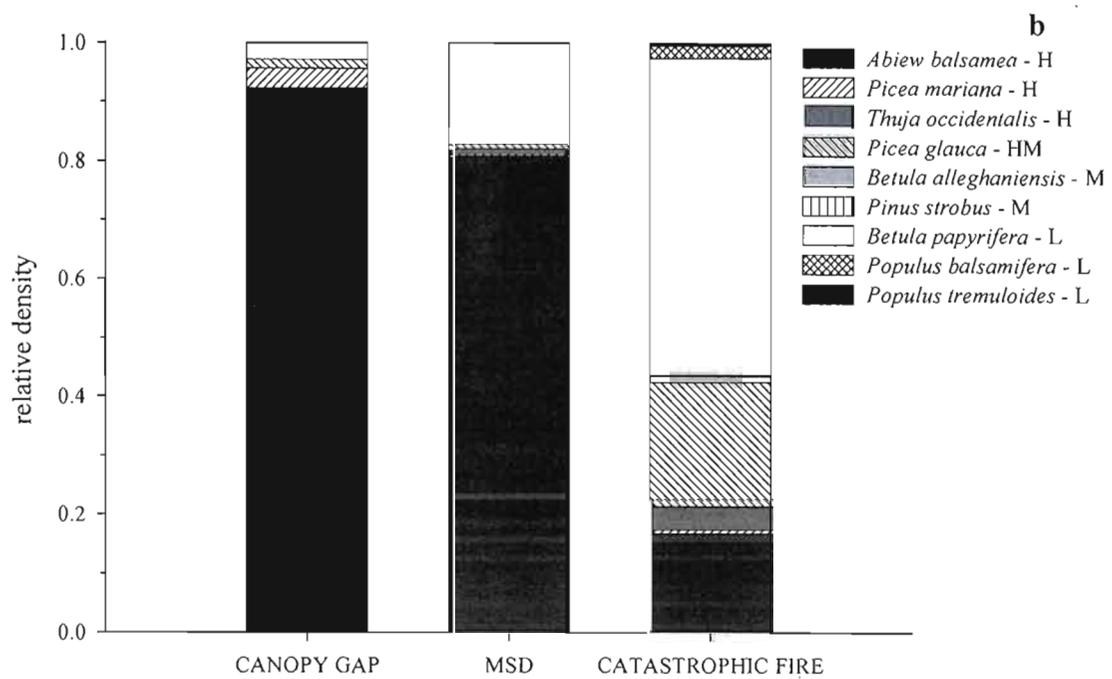
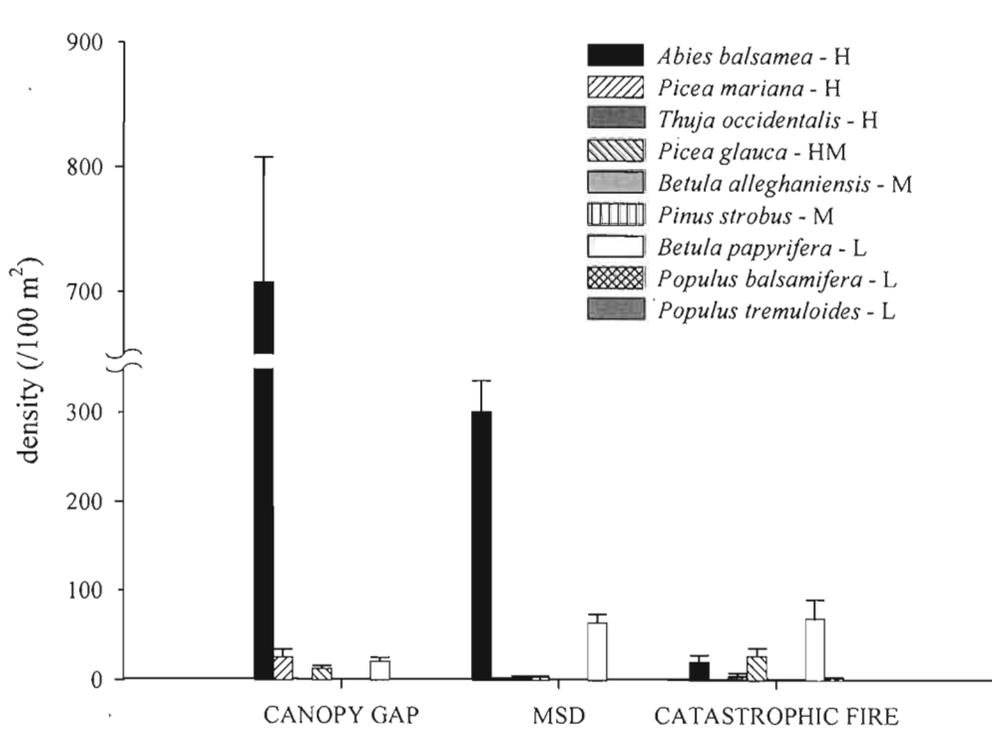
Species	Shade tolerance	Canopy gap disturbance	Moderate-severity disturbance	Catastrophic fire
Canopy trees				
<i>Abies balsamea</i>	High	+	+	+
<i>Picea mariana</i>	High	+	+	+
<i>Thuja occidentalis</i>	High	-	+	+
<i>Picea glauca</i>	High to mid	+	+	+
<i>Betula alleghaniensis</i>	Mid	-	-	+
<i>Pinus strobus</i>	Mid	-	-	+
<i>Betula papyrifera</i>	Low	+	+	+
<i>Populus balsamifera</i>	Low	-	-	+
<i>Populus tremuloides</i>	Low	-	-	+
Sub-canopy tree & shrubs				
<i>Acer pensylvanicum</i>	High	+	+	-
<i>Corylus cornuta</i>	High	+	-	+
<i>Acer rubrum</i>	Mid	+	+	+
<i>Acer spicatum</i>	Mid	+	+	+
<i>Diervella lonicera</i>	Mid	+	-	+
<i>Nemopanthus mucronatus</i>	Mid	-	+	-
<i>Sambucus</i> spp.	Mid	-	+	+
<i>Sorbus</i> spp.	Mid	+	+	+
<i>Viburnum edule</i>	Mid	+	+	+
<i>Amelanchier</i> spp.	Mid to low	+	+	+
<i>Salix</i> spp.	Low	-	-	+
<i>Prunus pensylvanica</i>	Low	-	+	+
<i>Rubus</i> spp.	Low	-	+	+
Canopy tree richness (<i>R</i>)		4	5	9
Sub-canopy tree and shrub <i>R</i>		8	10	11
All woody vegetation <i>R</i>		12	15	20
Number of unique species		0	1	5

Table 4.2. Comparison of species richness (R) and Shannon's diversity index (H') according to disturbance-caused mortality class at the plot level. Dissimilar letters along each row indicate significant differences among classes using ANOVA at $\alpha = 0.05$.

Richness (R)	Canopy gap disturbance	Moderate-severity disturbance	Catastrophic fire
R canopy trees	3.9 ± 0.10 a	2.9 ± 0.23 b	4.7 ± 0.21 c
R sub-canopy trees and shrubs	1.6 ± 0.58 a	2.5 ± 0.43 a	5.4 ± 0.40 b
R total woody vegetation	5.5 ± 0.62 a	5.4 ± 0.52 a	10.1 ± 0.55 b
H' canopy trees	0.58 ± 0.00 a	0.58 ± 0.0028 a	0.58 ± 0.0016 a
H' sub-canopy trees and shrubs	1.95 ± 0.001 a	1.8 ± 0.034 b	1.94 ± 0.0023 a
H' total woody vegetation	1.52 ± 0.0010 a	1.47 ± 0.015 b	1.53 ± 0.0015 a

Table 4.3. Comparison of Sørensen's similarity index (β) according to disturbance-caused mortality class at the plot level (400 m²). A value close to one indicates that species composition between sites affected by the disturbances being compared have most of their species in common whereas values close to zero indicate sites are highly dissimilar.

Vegetation community level	Disturbance class (S1)		Disturbance class (S2)	Sørensen's similarity index (β)
β canopy trees	canopy gap	<i>vs.</i>	moderate-severity disturbance	0.889
	canopy gap	<i>vs.</i>	catastrophic fire	0.667
	moderate-severity disturbance	<i>vs.</i>	catastrophic fire	0.769
β sub-canopy trees and shrubs	canopy gap	<i>vs.</i>	moderate-severity disturbance	0.571
	canopy gap	<i>vs.</i>	catastrophic fire	0.400
	moderate-severity disturbance	<i>vs.</i>	catastrophic fire	0.588
B total woody vegetation	canopy gap	<i>vs.</i>	moderate-severity disturbance	0.696
	canopy gap	<i>vs.</i>	catastrophic fire	0.519
	moderate-severity disturbance	<i>vs.</i>	catastrophic fire	0.667



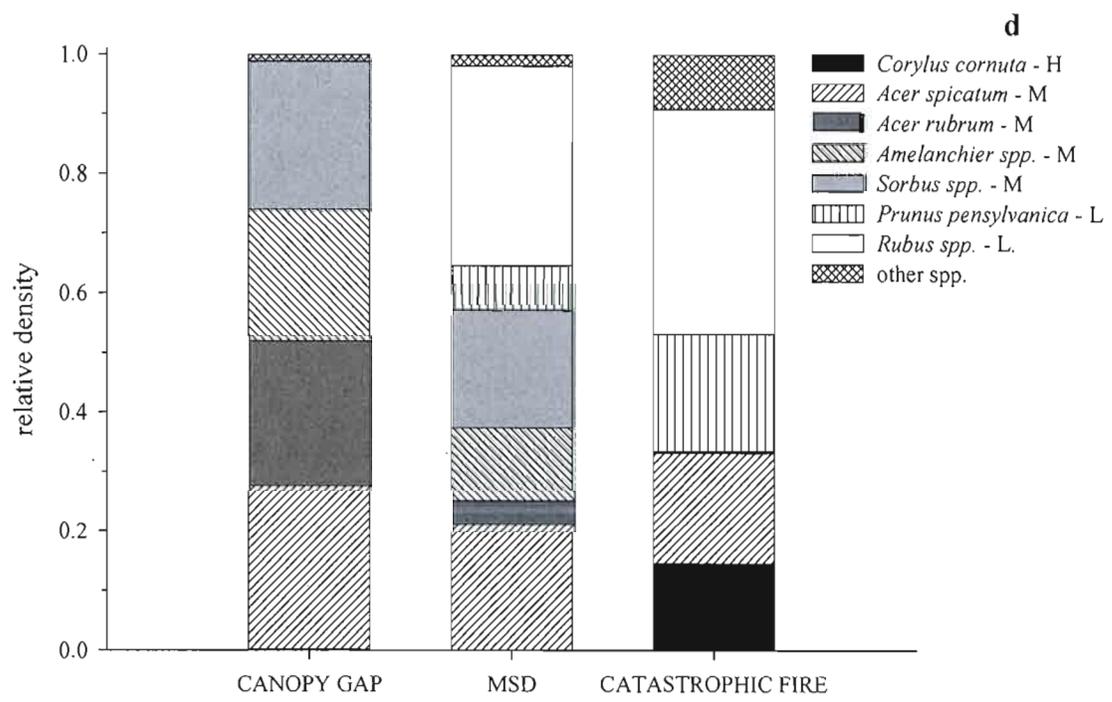
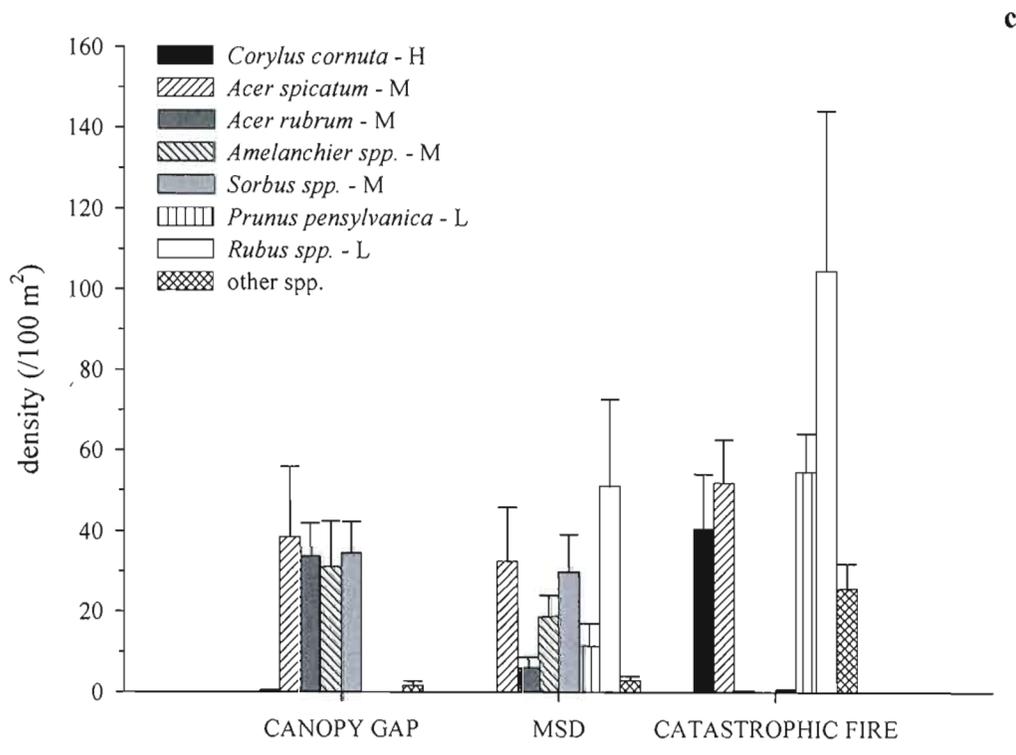


Figure 4.1a-d. Total and relative tree and sub-canopy tree and shrub regeneration density after canopy gap disturbance, moderate-severity disturbance (MSD), and large catastrophic fire in *Abies balsamea*-*Betula papyrifera* boreal mixedwood forests. Letters after species name indicate shade tolerance: H = high, HM = high to mid, M = mid, and L = low shade tolerance. Shade tolerance levels were derived from Humbert et al. (2007).

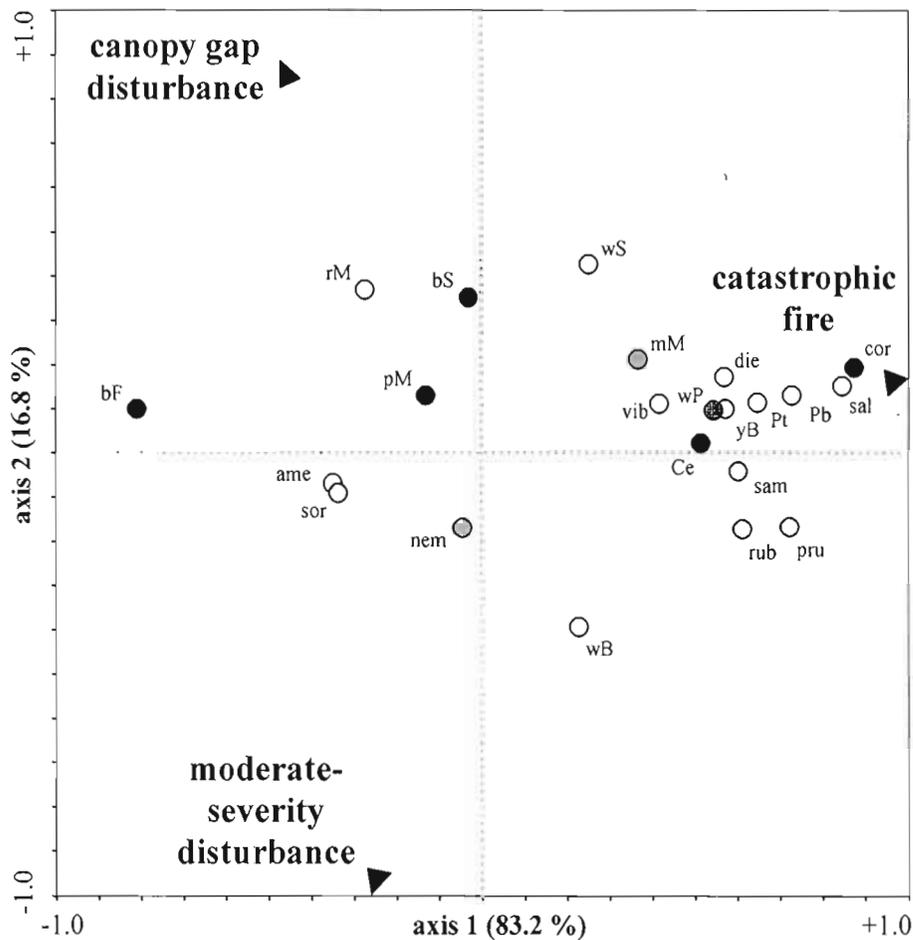


Figure 4.2. Redundancy analysis (RDA) of species density in relation to variation in disturbance-caused mortality. The first two canonical axes in RDA explained 26 and 5 % of the cumulative variance in the species data, respectively. Species codes are as follows: bF = *Abies balsamea*, bS = *Picea mariana*, Ce = *Thuja occidentalis*, mM = *Acer spicatum*, Pb = *Populus balsamifera*, Pt = *Populus tremuloides*, pM = *Acer pensylvanicum*, rM = *Acer rubrum*, wB = *Betula papyrifera*, wS = *Picea glauca*, wP = *Pinus strobus*, yB = *Betula alleghaniensis*, ame = *Amelanchier* spp., cor = *Corylus cornuta*, die = *Diervella lonicera*, pru = *Prunus* spp., nem = *Nemopanthus mucronata*, rub = *Rubus* spp., sal = *Salix* spp., sam = *Sambucus* spp., sor = *Sorbus* spp., and vib = *Viburnum edule*.

Shade tolerance: ● high, ● high to mid, ● mid, ○ mid to low, ○ low.

CHAPTER V

THE NATURAL DISTURBANCE REGIME IN BOREAL MIXEDWOODS

When first arriving in Quebec and visiting my sites, my initial impression was that the severity and type of disturbance were the principal, overriding factors determining vegetation responses, concurring with the current views on the importance of natural disturbance in driving forest dynamics (Kneeshaw and Bergeron 1998, Frelich 2002, Seymour et al. 2002). Accordingly, I developed hypotheses based on this premise. In terms of disturbance severity, clearly distinct patterns occurred between partial (canopy gap and moderate-severity disturbances) and catastrophic disturbances, whereas disturbances within the range of partial disturbances exhibited similar responses (Table 5.1). To my surprise, disturbance type, be it spruce budworm outbreak, windthrow, or their interaction, had little influence in determining post-disturbance species diversity and abundance. The various partial disturbances were important for bringing about changes in forest structure, but local biotic and environmental factors were what more strongly influenced the composition of the regeneration.

Stand composition prior to disturbance, in particular, was important. Conifer-dominated stands generally had an abundance of *Abies balsamea* advance regeneration in the understory prior to disturbance. Because partial disturbances had little impact on the regeneration layer, stand composition after disturbance was dominated by *Abies balsamea*, irrespective of disturbance type. Although an increase in deciduous shrub and sub-canopy tree species was observed in mixed coniferous-deciduous stands (particularly in areas with lower densities of *Abies balsamea* and coarse woody debris), these stands retained their relative species mixes when considering only the canopy tree layer (see Chapter 2). Canopy development may be delayed for a number of years by the influx of competing sub-

Table 5.1. General attributes and post-disturbance pathways for natural disturbances in function of increasing disturbance-caused mortality in eastern boreal mixedwoods of Quebec.

ATTRIBUTE:	DISTURBANCE-CAUSED MORTALITY GRADIENT:				Catastrophic fire
	Canopy gap	Moderate-severity disturbance:			
		budworm	windthrow	Interaction	
Post-disturbance arboreal vegetation	perpetuates existing condition; creates forest patches of different ages	benefits establishment of shade-tolerant species, particularly balsam fir; can ↑ intolerant hardwood component in the absence of balsam fir advance regeneration	can ↑ intolerant hardwood component but composition also dependent on structural conditions and density of advance regeneration; ↑ establishment from seed rain due to ↑ soil exposure, few legacy trees remain	composition dependent on density of advance regeneration; ↑ intolerant hardwood component – primarily in mineral soils from uprooted trees, but hardwood component usually lower than after windthrow	death of advance regeneration; early-succession species dominate; allows persistence of serotinous and root suckering species (e.g., jack pine, aspen)
Deadwood	one to a few standing snags and/or downed logs (cwd)	many standing snags and downed logs; white birch often subsequently die standing as well	many uprooted & snapped trees, few standing snags, high cwd densities can result in areas with very little light availability to ground, but also help to retain soil moisture	many downed logs; greater variability in terms of level of decay; few legacy trees remain as many have succumbed to subsequent windthrow	↓ cwd, but some to many standing snags left
Herbaceous	old-growth species persist	old-growth species persist but at considerably lower densities; ↑ presence of some shade-intolerant species	greater presence of shade-intolerant species, thus ↓ heterogeneity in vascular species composition	old-growth species persist but at considerably lower densities; ↑ presence of some shade-intolerant species	↑ early-successional shade-intolerant species; ↓ shade-tolerant species
Size (area)	≤ 0.2 ha	> 0.2 ha	> 0.2 ha	> 0.2 ha	> 0.2 ha
Size (range)	4.7 – 472.8 m ²	0.2 – 95.2 ha	0.2 – 41.7 ha	0.2 – 30.1 ha	*0.2 – > 80 000 ha
Mortality	one to a few canopy trees killed	canopy and sub-canopy affected, particularly balsam fir and white spruce; regeneration layer remains relatively intact	canopy, sub-canopy, and some of the regeneration layer affected because of uprooting	canopy, sub-canopy, and some of the regeneration layer affected because of uprooting	canopy, sub-canopy, and regeneration layers killed
Return interval	30 yr	*20 – 40 yr	*650 – 16 516 yr	ND	**170 – 250 yr
Landscape pattern	few patches of early succession forest embedded in matrix of primarily late-succession forest	patches of various age classes embedded in matrix of primarily late-succession forest	patches of various age classes embedded in matrix of primarily late-succession forest	patches of various age classes embedded in matrix of primarily late-succession forest	if return interval shorter than lifespan of late-succession species, few patches of late-succession forest embedded in matrix of early-succession forest

ND = no data; ↑ = increase; cwd = coarse woody debris.

*estimate is 39 years when pooling all moderate-severity disturbance types

**return interval estimate is from Lauzon et al. (2007)

canopy tree and shrub species, but they will have limited effect once the tree canopy grows beyond a few metres in height. Note that an increase in the deciduous canopy tree component was observed after windthrow in mixed coniferous-deciduous stands. This too, however, appears to be temporary as *Abies balsamea* was present in abundance in the smaller size classes and generally responds well to canopy openings. Thus, in the absence of a subsequent severe disturbance, stands should develop towards shade-tolerant, conifer dominant conditions.

I initially believed that moderate-severity disturbances would cause large changes in species diversity and relative abundances, given the spatial extent of many of these disturbances, some affecting almost 100 ha of territory, but this was not observed. Further, different vegetation responses among moderate-severity disturbance types were also expected given the temporal differences in canopy tree mortality among them. This too was not evident, as regeneration patterns were more a function of the density of advance regeneration after the various disturbance types. Moderate-severity disturbances either drove stand development towards old-growth, conifer-dominated conditions or stabilised current conditions, depending on advance regeneration density and local site characteristics. In almost no cases were stands driven back to early successional conditions. *Populus* spp., for example, were either absent or were present at very low densities after moderate-severity disturbances; and even in stands where *Betula* spp. considerably increased in abundance, *Abies balsamea* seedlings were always present in abundance as well. Catastrophic fire was the only natural disturbance that substantially altered the community composition and is, therefore, important for promoting woody species diversity across the landscape given the current return intervals of the various natural disturbances.

5.1. Regeneration pathways after natural disturbances in eastern boreal mixedwoods

My data suggest that natural regeneration pathways are contingent on both the amount of disturbance-caused mortality; i.e., severity, and the density of advance regeneration present after disturbance. Although various climate and physiographic variables can act as local modifiers, general woody vegetation responses can be conceptually modelled in the following manner:

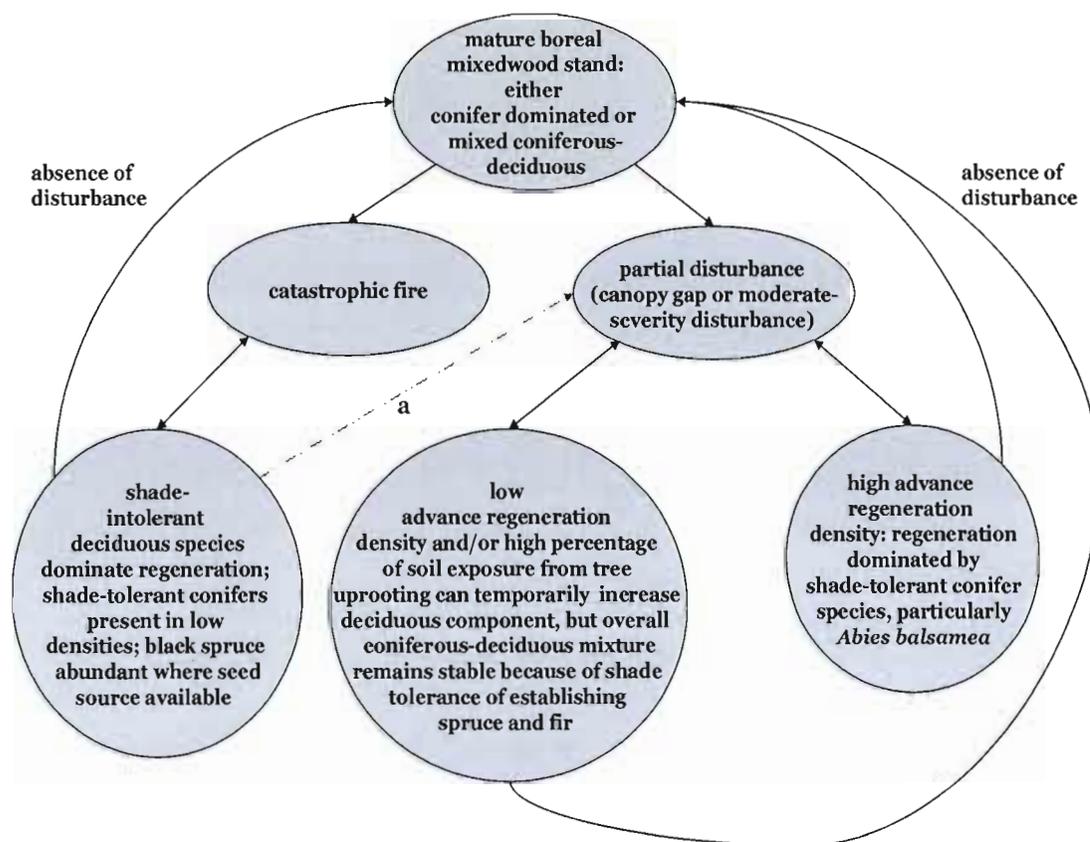


Figure 5.1. Regeneration pathways after natural disturbances in Quebec's boreal mixedwood forests.

Notes: (a) link incomplete as the deciduous-dominated forest type was not examined: it is unclear how a stand will respond if a partial disturbance occurs after catastrophic fire in stands dominated by shade-intolerant deciduous species prior to returning to mature or multi-cohort mixedwood conditions; i.e., young, deciduous stands were not examined here. Further, the link may be irrelevant as younger stands are generally not susceptible to partial disturbances until reaching a certain age or size (e.g., see Bergeron 2000).

5.2. Ecosystem management

While integrating concepts of natural disturbance ecology into ecosystem management planning can be difficult, it is clearly necessary. It entails manipulating any or all of the following to alter ecosystem vulnerability or responses: (a) pre-disturbance conditions, (b) the natural disturbance itself – if or when possible, (c) post-disturbance conditions, and (d) stand re-establishment processes (Dale et al. 1998); done in order to meet various ecological, social, and economic needs while maintaining ecosystem health. For example, if the goal is to increase the shade-intolerant hardwood component after moderate-severity disturbance, provided an adequate seed source is present nearby, tilling to expose mineral soils or burning the ground layer in certain areas within a site to remove some of the advance regeneration could be done. Note that a generalised regional-scale plan may be too insensitive to the specific nuances found at local levels, as different suites of factors were important to local species compositions. Thus, management plans that are both specific to the disturbance regime affecting a particular landscape and that meet desired management goals should be adopted (Dale et al. 1998).

5.3. Species diversity

The diversity and relative abundances of the various species in the woody vegetation community reflects the severity and frequency of the assortment of natural disturbances across the boreal mixedwood landscape. Different adaptations and abilities to respond to disturbances have resulted in the partitioning of resources according to competitive ability and niche availability. The current natural disturbance regime promotes development towards late-successional conditions; thus favouring *Abies balsamea* and other shade-tolerant woody species.

5.4. Future directions

The information gathered here provides a foundation for which to develop and address other hypotheses and questions: do understory species responses differ from woody vegetation responses? How important are other interaction-type disturbances (e.g., insect outbreak x fire) and can we model forest responses to them? Can the correlative *versus* causal nature of certain environmental factors be determined (e.g., the role of coarse woody debris)? Can patterns and mechanisms of

forest change be generalised from stand-level to regional scales, or are they fundamentally different at different scales? Is knowledge of the principal mechanisms and factors that drive forest change sufficient to create models that can generally explain boreal mixedwood dynamics or predict future stand composition? Do current stand dynamics models based on the effects of disturbance (e.g., Frelich and Reich 1998, Frelich and Reich 1999) sufficiently explain the various vegetation responses? The following are some of the major lines of investigation that should be pursued:

5.4.1. Understory species responses to natural disturbances

Research should be expanded to include the understory vegetation community, as responses of understory species to natural disturbances often differ from the overstory (Roberts 2004, Ramovs and Roberts 2005). Many herbaceous and bryophyte species have been shown to be sensitive to large micro-environmental changes (Soderstrom 1988, Duffy and Meier 1992, Roberts and Zhu 2002, Fenton et al. 2003), with large differences occurring even at rather small spatial scales. Shen et al. (2009), for example, observed differences in *Primula nutans* distribution at a 100 cm² scale in alpine wetlands. Further, the role of the understory in ecosystem functioning remains unclear, as is knowledge of the key environmental conditions and biotic factors affecting the distribution and abundance of many of the component species.

Changes in the frequency and scale of natural disturbances can release certain understory species from prior competitive restraints, which can subsequently result in these species rapidly occupying large expanses of the landscape (Jäderlund et al. 1997, Payette and Delwaide 2003, Nilsen et al. 2001). There is also the contention that expansion and dominance of the understory by one or a few of these aggressive species is an inadvertent outcome of forestry practices that deviate from natural disturbances (Horsley 1985, Mallik 1995, Dolling 1996, George and Bazzaz 1999). Improved knowledge of individual species responses to disturbances of varying severities will help forest managers to preemptively control for the spread of these species if desired. Some preliminary results are included in Appendix F.

5.4.2. Species – environment associations

While density of coarse woody debris was a factor strongly affecting regeneration patterns, it must be noted that the positive relationship between its density and shade-tolerant conifer species density may be an artefact of coarse woody debris simply being present in abundance after disturbance; i.e., correlation should be distinguished from *causation*. The role of coarse woody debris in affecting regeneration patterns needs to be clarified with further study. Comparisons of regeneration patterns after moderate-severity disturbance and/or catastrophic fire with and without salvage logging could be performed, for example.

5.4.3. Interaction disturbances

While an additive response was observed for the spruce budworm x windthrow interaction disturbance examined here (see chapter 2), for many other interaction disturbances, it remains unclear whether their effects are also additive, synergistic, or are multiplicative in nature (Paine et al. 1998, Kulakowski et al. 2003, Asbjornsen et al. 2004, Bigler et al. 2005, Alba-Lynn and Detling 2008). Both natural-natural [e.g., windthrow x windthrow (Harcombe et al. 2004), fire x insect outbreak (Kulakowski et al. 2003)] and natural-anthropogenic [e.g., insect outbreak x salvage logging (Radeloff et al. 2000), windthrow x salvage logging (Rumbaitis del Rio 2006), clearcutting x ungulate herbivory (Reyes and Vasseur 2003), grazing x fire exclusion (Abella and Covington 2007)] interactions require further study. Those involving anthropogenic causes are of particular concern as novel combinations of disturbances may result in changes that are beyond the natural ranges of variability native organisms are adapted to (Paine et al. 1998). Interactions of this nature can cause cascading effects for which recovery to original conditions becomes difficult without costly intervention, and may result in other negative consequences such as the proliferation of exotic species (Simberloff 2000, Timoney 2003). Questions also arise in terms of what spatial scales to study? Is order of events important to species re-establishment? Or how important is the interval between events? Given the increasing frequency of natural-anthropogenic interaction disturbances (Payette and Delwaide 2003), it is essential to be able to account for their impacts in management planning scenarios.

5.4.4. Ecological models

Ecological modeling can be useful for the conceptualization and measurement of complex stand dynamic patterns at different spatial and temporal scales. Ecological modeling of forest ecosystem dynamics requires information on initial stand conditions, post-disturbance pathways, return intervals, forest change probabilities, and effects of geographic locations and site conditions (Frelich and Lorimer 1991, Yemshanov and Perera 2003). A model describing some of the ecological processes involved in driving mixedwood systems can thus be developed from my research here, as much of the required information has been gathered. Theoretical analysis of effects of various environmental factors on forest growth will be useful in developing models that predict future forest conditions under different climate scenarios or for exploring the effects of various forest management objectives and strategies. For example, the STORM model proposed by Frelich and Lorimer (1991) could be modified to describe the multiple pathways that boreal mixedwood stands can develop after natural disturbance, and to predict forest structure and composition given a set of initial conditions. Simulations to examine effects of changes in disturbance frequency (e.g., 1/2, 2x, 3x historical disturbance rates) on landscape characteristics can also be made using a model based on STORM (n.b., the STORM model was designed to predict stand development after disturbance in deciduous stands based on a given set of initial conditions and knowledge of canopy growth rates). Integrating information on interaction disturbances will also prove valuable, again, given their increasing frequency due to anthropogenic causes.

5.5. Parting thoughts

Various natural disturbances operate within the boreal mixedwood ecosystem at different spatio-temporal scales. Predicting the correct responses to the array of disturbances and their interactions can be quite daunting given the number of possible successional pathways (Abrams et al. 1985, Frelich and Reich 1998, Frelich and Reich 1999, Kulakowski et al. 2003, Harcombe et al. 2004), all of which are dependent on many other interacting biotic and environmental factors also having effects at different scales (Frelich and Reich 1995, Ohmann and Spies 1998, Vanderpoorten and Engels 2002, Lorimer and White 2003). It's no wonder then

that patterns and processes occurring after natural disturbances have been described in the past as 'random, chaotic, and un-interpretable' (Shaw 1983 *in* Foster et al. 1998). Nevertheless, reducing this complexity by interpreting and characterising the nature of these patterns, determining the key factors influencing responses and under which circumstances these factors are important, as well as determining predictability in time and space is essential for understanding ecosystem dynamics, and will ultimately help in the development of sound management guidelines.

I identified some of the key factors influencing vegetation diversity and abundance after natural disturbances and outlined some areas of research requiring further attention. I stress that while disturbance is a fundamental process causing ecosystem change, various stand level characteristics prior to and after disturbance can strongly affect vegetation diversity and abundance. Pre-disturbance stand composition, and specifically the density of advance regeneration established within, had ubiquitous effects that generated predictable regeneration patterns throughout the region. Yet while these factors produced generality, a number of different environmental factors had important local influences that were important for producing variability in species diversity and abundance across the region, stressing the importance of scale when testing the influence of various environmental, compositional, structural, and functional parameters on species responses.

5.6. References

Please see the General Citation List (pp 133-154).

PROLOGUE TO APPENDIX A

Information on temporal aspects of natural disturbances is of key importance to any forest ecosystem management plan. This section of my research didn't make it to 'chapter class' due to time constraints. But I thought it necessary to at least acknowledge that the information has been gathered.

Both spatial and temporal patterns need to be addressed in order to gain full understanding of the natural disturbance regime; i.e., how important are particular disturbance types across the landscape over time? Results of this section have important ecological and management implications, as knowing the frequency of the various natural disturbances is fundamental to the development of sustainable harvesting cycles. I determine return intervals for spruce budworm and windthrow moderate-severity disturbances, as well as compare return intervals for canopy gap, moderate-severity, and catastrophic fire natural disturbances in the boreal mixedwood region of Quebec, Canada.

APPENDIX A

**VARIATION IN RETURN INTERVAL RATES FOR NATURAL
DISTURBANCES ACROSS QUEBEC'S BOREAL MIXEDWOOD
FORESTS**

AA.1. Review

Disturbance frequency can strongly affect species diversity and abundance across the landscape. Return intervals for two types of moderate-severity disturbances, spruce budworm (*Choristoneura fumiferana*) outbreak and windthrow, from three different locations (Gaspé Peninsula, the North Shore, and Temiskaming-Abitibi) across the boreal mixedwood forest region of southern Quebec, Canada were determined and compared to examine temporal differences in occurrence of moderate-severity disturbance across the region. Environmental factors strongly associated with occurrence of the various disturbance types were also assessed. Secondly, return intervals for a spectrum of natural disturbances, from canopy gap to moderate-severity to catastrophic fire, were estimated and compared to determine their relative frequencies, and thus, importance in determining species diversity and abundance across the landscape. Return intervals ranged from 20 to 40 years for spruce budworm outbreak while windthrow recurred every 650 to 16 516 years. Estimates were similar among locations for each of the moderate-severity disturbance types. Spatial aggregation of spruce budworm outbreak and windthrow was observed. Spruce budworm outbreak was correlated with the amount of mature balsam fir. Windthrow was associated with greater percent slope in coastal locations and with low-lying areas near water in more continental locations. Return interval estimates for canopy gap, moderate-severity, and catastrophic fire disturbances were 30, 39, and between 170 and 250 years, respectively. Current return interval estimates for the spectrum of natural disturbances occurring throughout the landscape indicate that convergence towards late-successional forest conditions is promoted.

AA.2. Objectives

Disturbance frequency strongly influences species composition across the landscape (Oliver 1981, Krasny and Whitmore 1992). The recent increase in catastrophic fire return intervals (Bergeron et al. 2001) suggests that canopy gap and moderate-severity disturbances may now play larger roles in shaping the vegetation community than previously observed. Our objectives were to: (1) determine return intervals for spruce budworm (*Choristoneura fumiferana*) outbreak and windthrow,

two important moderate-severity disturbance types affecting the boreal mixedwood region; (2) determine if the recurrence of these disturbances differs across the region; (3) examine the importance of various physiographic variables on the susceptibility to these moderate-severity disturbance types; and (4) compare return intervals for a spectrum of natural disturbances, from canopy gap to catastrophic fire, occurring within the mixedwood region.

AA.3. Study area

The *Abies balsamea*-*Betula* spp. boreal mixedwood zone spans east to west across southern Quebec from 46 to 50° N and 64 to 80° W (Fig. 1). It encompasses 23.8 million ha and represents 18.6 % of the forested land of the province (MRNQ 2003). *Abies balsamea*, *Betula papyrifera*, and *Betula alleghaniensis* dominate the forest canopy. *Picea glauca*, *Picea mariana*, *Acer rubrum*, *Populus balsamifera*, and *Populus tremuloides* are also present in abundance in some sites while *Thuja occidentalis*, *Pinus resinosa*, *Pinus strobus*, *Pinus banksiana*, *Larix laricina*, *Acer saccharum*, *Fraxinus americana*, and *Fraxinus nigra* are occasionally found.

Return intervals were determined for three geographically distinct locations within the boreal mixedwood region of Quebec (Fig A1.1). The continental, western sites are located in the Temiskaming and Abitibi municipalities (between 47°30' to 48°20' N and 77°30' to 79°10' W). Two eastern coastal locations, differing mainly in latitude, were examined: the North Shore is situated along the north shore of the St. Lawrence River (Haute Côte Nord and Manicouagan municipalities, between 48°30' to 50°00' N; 68°00' to 69°50' W). Stands in this area are near the northern limit of the boreal mixedwood region. The southern coastal sites are situated along the southern part of the Gaspé Peninsula, in stands located near the Chaleur Bay area of the Atlantic coast (between 48°10' to 48°35' N and 65°45' to 66°15' W).

Temperatures fluctuate more widely in the western sites. Mean January and July temperatures for the Temiskaming-Abitibi sites are -16.2 and 17.5 °C, respectively. Mean annual temperature is 2.1 °C, while mean annual precipitation is 965 mm, with 72 % falling as rain. Mean January and July temperatures are -14.1 and 16.5 °C, and -11.8, and 17.9 °C, and for the North Shore and Gaspé Peninsula sites, respectively. Mean annual temperature for the North Shore sites is 2.2°C, while

mean annual precipitation is 989 mm, with 70 % falling as rain. Mean annual temperature for the Gaspé Peninsula sites is 3.6 °C, while mean annual precipitation is 963 mm, with 75 % falling as rain. A general latitudinal decrease in precipitation and increase in temperature occurs from northern to southern latitudes along the coast. Degree growing days range from 170 to 180, 140 to 160, and 150 to 170 days for the Temiskaming-Abitibi, North Shore, and Gaspé Peninsula sites, respectively.

AA.4. Methods

A *return interval* is the average time in years between two successive disturbances in a given area. Mean return interval rate is the arithmetic average of all return intervals determined, in years, for a designated area during a specified time period. Return intervals can be expressed as a *frequency* by calculating its inverse:

$$\text{Disturbance frequency} = 1 / \text{return interval rate} \quad [1]$$

Canopy gap return intervals were determined using methods described in Runkle (1992) (see also chapter 4). Digitised inventory data from a Geographic Information System database for our study region (sampled in 1994) was used to estimate return intervals for spruce budworm outbreak and windthrow moderate-severity disturbance types. Total area affected by moderate-severity disturbances divided by total area covered by mature forest ≥ 70 y (2433.3 km²) gave an estimate of the fraction of an area affected by moderate-severity disturbances in any given year.

For both canopy gap and moderate-severity disturbances, we assumed 15 years to be the time period for which these partial disturbances could be distinguished from the surrounding canopy (Canham and Loucks 1984, Zhang et al. 1999). Thus, the inverse of disturbance frequency $\div 15$ years gave us a return interval estimate for these partial disturbances.

Return interval estimates for catastrophic fire were described and determined for our study region in an associated study by Lauzon *et al.* (2007). Note that estimates for each disturbance type are derived independently; i.e., for partial disturbances, estimates are based on currently available mature forest. Areas affected by catastrophic fire are not amenable to partial disturbances until reaching maturity.

Various physiographic variables were gathered from forest inventory maps and other government of Quebec resources to examine their potential influences on disturbance frequency.

AA.5. Analyses

Although incorporating as many attributes as possible into an ordination model can lead to important insights, it also greatly increases model complexity, potentially making interpretation rather difficult. For these reasons, principal components analysis (PCA) was used to reduce the number of factors inputted in the models into two components, and to eliminate redundant information (Joliffe 1986).

AA.6. Preliminary results and discussion

AA.6.1. Spruce budworm and windthrow return intervals

Spruce budworm outbreak and windthrow return intervals were approximately 40 and 17 000 years, respectively.

AA.6.2. Return intervals of the various natural disturbances along a disturbance-caused mortality gradient

Return intervals increased with amount of disturbance-caused mortality. Canopy gap and moderate-severity disturbances were relatively frequent, occurring every 30 and 39 years, respectively. The catastrophic fire return interval was considerably longer, occurring between 170 and 250 years (Lauzon *et al.* 2007). This suggests approximately 3.3, 2.6, and between 0.4 and 0.6 % of the landscape is affected by canopy gap, moderate-severity, and catastrophic fire disturbances per year, respectively.

Return intervals were consistent with estimates for gap dynamics research in conifer-dominated forests of north-eastern North America (De Romer *et al.* 2007) and with estimates for moderate-severity disturbances were consistent with estimates for province-wide spruce budworm outbreaks (Bouchard *et al.* 2006). Values were comparable as over 98 % of moderate-severity disturbances observed within our study region were the result of the last outbreak that occurred between 1965 and 1992 (Gray *et al.* 2000). Lorimer and White (2003) estimated similar return intervals for stand-replacing disturbances in northeastern US spruce-northern hardwoods forests.

Current return interval estimates for the various natural disturbances suggest that the disturbance regime would result in a spatially and temporally dispersed multi-cohort age structure for this system. Further increases in the length of the fire cycle may lead to the extirpation of some early-successional specialists, and implies that deciduous stands would be removed from the system across the landscape. However, Bergeron and Dansereau (1993) show that mixedwood stands could be maintained due to the shorter, periodic cycles of spruce budworm outbreak, a moderate-severity disturbance that provides some opportunity for shade-intolerant species to re-establish. This was observed in our study as well (see chapters 2, 3, 4).

Estimates for catastrophic windthrow were similar to Schulte and Mladenoff (2003), who determined a return interval range of between 465 to >10 000 years in mixedwood forests of Wisconsin, and are generally longer than the ranges observed in other studies: Canham and Loucks (1984): 1210 years for forests in Wisconsin, Zhang *et al.* (1999): 546 years in Michigan, Frelich and Lorimer (1991): > 1500 years in Michigan.

AA.7. References

Please see the General Citation List (pp 133-154).

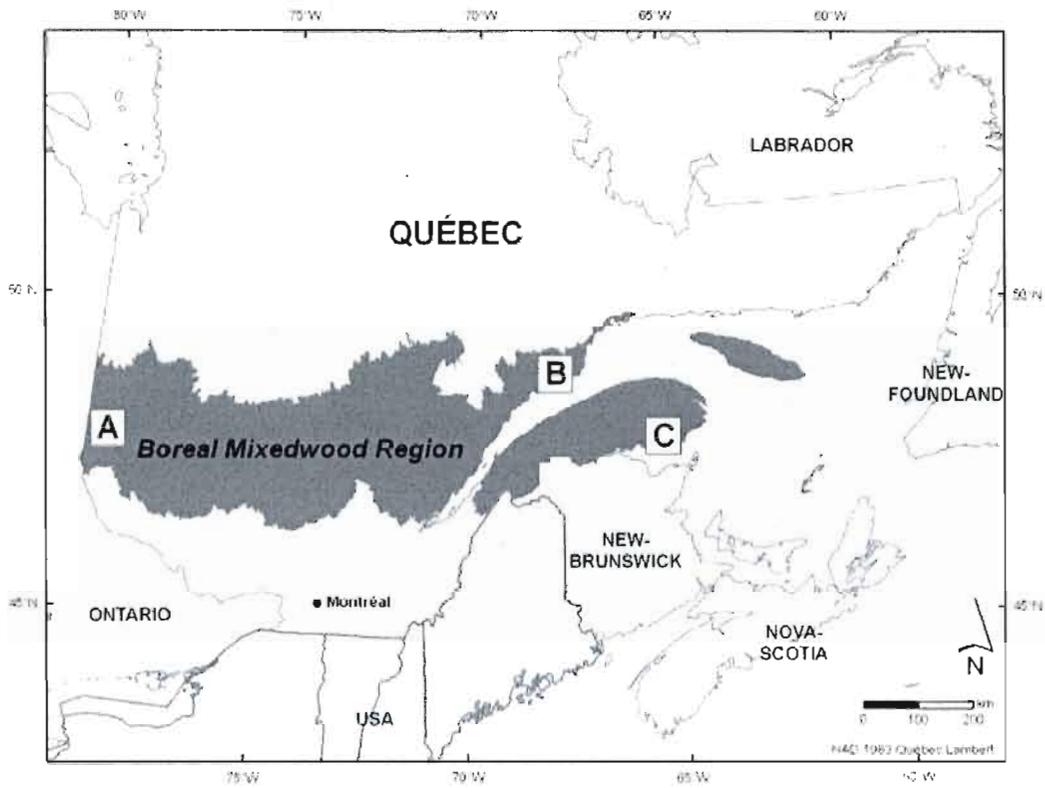


Figure AA.1. Study locations within the boreal mixedwood region of Quebec, Canada: (a) Temiskaming & Abitibi, (b) the North Shore, (c) the Gaspé Peninsula.

APPENDIX B

DEMANDE DE PRÉSENTATION D'UN MÉMOIRE OU D'UNE THÈSE PAR ARTICLES

Nom de GÉRARDO REYES Code
l'étudiant : permanent : REYG21047209
Programme : DOCTORAT EN BIOLOGIE

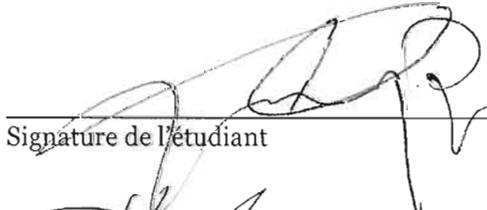
NATURAL DISTURBANCE DYNAMICS IN *ABIES BALSAMEA-
BETULA SPP.* BOREAL MIXEDWOODS OF SOUTHERN
QUEBEC: EXAMINATION OF SPATIO-TEMPORAL FACTORS
AFFECTING WOODY VEGETATION DIVERSITY AND
ABUNDANCE
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Titre de l'article, nom des coauteurs, nom du journal ou de la revue, date et numéro de
soumission ou lettre d'acceptation, ou année et numéros de volume et de pages.

- (1) Moderate-severity disturbance dynamics in *Abies balsamea-Betula* spp.
forests: the relative importance of disturbance type and local stand and
site characteristics on woody vegetation response; Reyes, G., and D.
Kneeshaw; *Ecoscience* 15(2): 241-249 (2008).
- (2) Factors causing regional variation in woody vegetation diversity and
abundance after natural disturbances; Reyes, G.P., Kneeshaw, D., and L.
De Grandpré; *Ecography*: (soumit nov 2009).

- (3) Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality; Reyes, G.P.; Kneeshaw, D.; De Grandpré, L.; and A. Leduc; *Journal of Vegetation Science* (soumit mai 2008: JVS5858).
- (4) Regional variation in return interval rates for moderate-severity disturbances in Quebec's boreal mixedwood forests; *Forest Ecology and Management* (d'être soumis dec 2009).



Signature de l'étudiant

12/12/2008

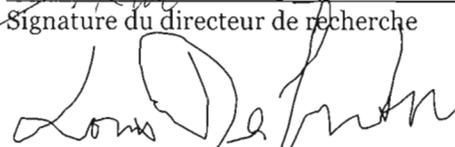
Date



Signature du directeur de recherche

15-12-2008

Date



Signature du co-directeur de recherche

19-12-2008

Date



Signature de la directrice du programme

21-12-2009

Date

APPENDIX C

PERMISSION TO WRITE THESIS IN ENGLISH

Gerardo Reyes PhD (cand)

11/12/2008

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greyes@dal.ca, reyes.gerardo@courrier.uqam.ca

Re: permission to write thesis using the English language

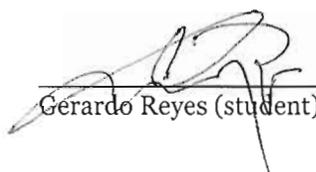
Dear Sir or Madam,

On Tuesday December 2, 2008 I spoke with Dr. Louise Brissette, Director of the PhD program in Biology for permission to write my thesis entitled:

**NATURAL DISTURBANCE DYNAMICS IN *ABIES BALSAMEA-BETULA*
SPP. BOREAL MIXEDWOODS OF SOUTHERN QUEBEC: EXAMINATION
OF SPATIO-TEMPORAL FACTORS AFFECTING WOODY VEGETATION
DIVERSITY AND ABUNDANCE**

in English. It was agreed upon that the general abstract is to be written using both the French (as per Règlement no 8, Article 8.1.4.5.1, p 33) and English languages. The format and style of my thesis will follow the UQAM guidelines for PhD theses written in manuscript form. Thank you.

Sincerely,

		
Gerardo Reyes (student)	Daniel Kneeshaw (supervisor)	Louise Brissette (director of PhD program)

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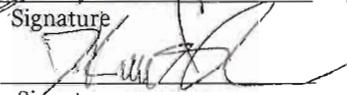
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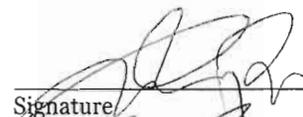
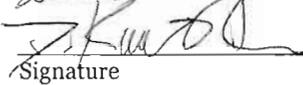
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CHANGES IN WOODY VEGETATION ABUNDANCE AND DIVERSITY AFTER NATURAL DISTURBANCES CAUSING DIFFERENT LEVELS OF MORTALITY

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APPENDIX F

UNDERSTORY VEGETATION DIVERSITY

AF.1 Introduction

Biodiversity is important for preserving habitat quality and for the maintenance of ecosystem functioning and services (Wardle et al. 2000). On a more anthropocentric level, it provides us with genetic resources for crop plants, sources of medicines, and stimulates tourism and outdoor recreation. Habitat loss, fragmentation, and altered natural processes due to climate change pose significant threats to native biodiversity. Species extinctions and drastic changes in biodiversity will alter natural resource availability, the manner in which pests and diseases are controlled, how organic wastes are broken down and recycled, food production and pollination efficiency, and water purification (Naeem et al. 1994, Tilman 1999). Thus, it is imperative that we engage in searching for a clear understanding of the ecosystems in which we live in, depend on, and effect, so that we assure at least the maintenance of the elements important for natural ecosystem functioning. This includes understanding of understory plant species responses to natural disturbances and the roles that certain factors and mechanisms play in influencing responses. Some preliminary data are presented here (see Table AF.1 and Figure Af.1).

AF.2 References

Please see the General Citation List (pp 133-154).

Table AF.1. Plant species diversity in boreal mixedwoods of Quebec, Canada.

Acronyms are as follows: sbw = spruce budworm outbreak, wt = windthrow, int = interaction, bF wB = *Abies balsamea*-*Betula papyrifera* canopy, bF yB = *Abies balsamea*-*Betula alleghaniensis* canopy.

disturbance type - stand type - ecozone	canopy trees: shade tolerant	canopy trees: shade intolerant	sub-canopy trees & shrubs	groundcover: shade tolerant	groundcover: shade intolerant	TOTAL
sbw - conifer - bF wB	5	1	10	11	6	33
sbw - mixed - bF wB	4	2	5	14	5	30
sbw - mixed - bF yB	7	2	9	20	5	43
wt - conifer - bF wB	5	1	6	17	11	40
wt - conifer - bF yB	6	1	10	17	7	41
wt - mixed - bF wB	5	1	7	ND	ND	*13
int - conifer - bF wB	3	1	9	17	10	40
int - mixed - bF wB	3	1	12	18	7	41
int - mixed - bF yB	7	1	15	17	7	47
mature mixed	7	1	16	26	9	59
mature conifer	3	1	9	16	2	31

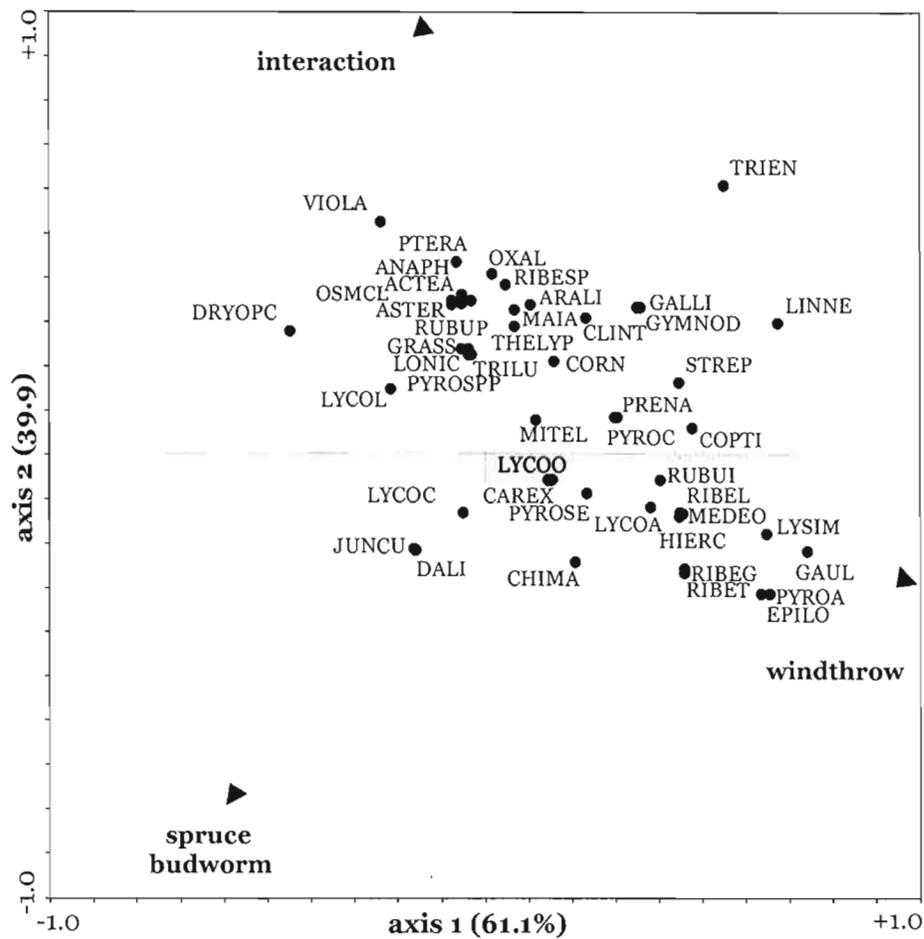


Figure AF.1. Redundancy analysis (RDA) of understory species presence/absence after different moderate-severity disturbance types in the Gaspé Peninsula. The first two canonical axes in RDA explained 14 and 9 % of the cumulative variance in the species data, respectively. Species codes are as follows: ACTEA = *Actea* spp., ANAPH = *Anaphalis margaritacea*, ARALI = *Aralia nudicaulis*, ASTER = *Aster* spp., CAREX = *Carex* spp., CHIMA = *Chimaphila umbellata*, CLINT = *Clintonia borealis*, COPTI = *Coptis groenlandicum*, CORN = *Cornus canadensis*, DALI = *Dalibarda repens*, DRYOPC = *Dryopteris spinulosa*, EPILO = *Epilobium angustifolium*, GAUL = *Gaultheria procumbens*, GRASS = Poaceae, GYMNOD = *Gymnocarpium dryopteris*, JUNCU = *Juncus* spp., HIERC = *Hieracium* spp., LINNE = *Linneus borealis*, LONIC = *Lonicera canadensis*, LYCOA = *Lycopodium annotinum*, LYCOC = *Lycopodium*

clavatum, LYCOO = *Lycopodium obscurum*, LYCOL = *Lycopodium lucidulum*,
LYSIM = *Lysimachia punctata*, MAIA = *Maianthemum canadensis*, MEDEO =
Medeola virginiana, MITEL = *Mitella nuda*, OSMCL = *Osmunda claytoniana*,
OXAL = *Oxalis montana*, PRENA = *Prenanthes altissima*, PTERA = *Pteridium*
aquilinum, PYROA = *Pyrola asarifolia*, PYROC = *Pyrola chlorantha*, PYROSE =
Pyrola secunda, PYROSPP = *Pyrola* spp., RIBEG = *Ribes glandulosum*, RIBEL =
Ribes lacustre, RIBESP = *Ribes* spp., RIBET = *Ribes triste*, RUBUI = *Rubus ideaus*,
RUBUP = *Rubus pubescens*, STREP = *Streptopus roseus*, THELYP = *Thelypteris*
phegopteris, TRIEN = *Trientalis borealis*, TRILD = *Trillium erectum*, TRILU =
Trillium undulatum, VIOLA = *Viola* spp.

APPENDIX G

AMENDMENTS TO CHAPTER 2: PUBLISHED IN *ECOSCIENCE* 15(2): 241-249

The following supplementary tables were added as clarification of information provided in Chapter II.

Table AG.1. Mean density \pm SEM (ha^{-1}) of natural regeneration in relation to moderate-severity disturbance type and stand composition prior to disturbance.

Conifer = > 75% conifer canopy; Mixed con-dec = 50-75 % conifer canopy.

Species	Spruce budworm		Windthrow		Interaction	
	Conifer	Mixed con-dec	Conifer	Mixed con-dec	Conifer	Mixed con-dec
Canopy trees						
<i>Abies balsamea</i>	1472 \pm 251	388 \pm 81	809 \pm 227	130 \pm 94	828 \pm 197	289 \pm 71
<i>Acer saccharum</i>	0	17 \pm 6	0	0	0	2 \pm 2
<i>Betula alleghaniensis</i>	14 \pm 6	24 \pm 7	105 \pm 41	164 \pm 96	0	59 \pm 17
<i>Betula papyrifera</i>	248 \pm 59	150 \pm 28	304 \pm 57	5 \pm 3	391 \pm 87	135 \pm 29
<i>Picea glauca</i>	18 \pm 8	2 \pm 1	7 \pm 3	3 \pm 3	3 \pm 2	3 \pm 2
<i>Picea mariana</i>	5 \pm 2	4 \pm 3	26 \pm 11	0	1 \pm 1	0
<i>Pinus strobus</i>	0	0	5 \pm 4	0	0	1 \pm 1
<i>Thuja occidentalis</i>	0	0	3 \pm 2	0	0	0
Sub-canopy tree & shrubs						
<i>Acer pensylvanica</i>	0	22 \pm 10	0	75 \pm 35	0	5 \pm 2
<i>Acer rubrum</i>	16 \pm 6	38 \pm 16	0	0	37 \pm 15	31 \pm 9
<i>Acer spicatum</i>	51 \pm 28	251 \pm 61	117 \pm 28	721 \pm 165	155 \pm 46	601 \pm 94
<i>Amelanchier spp.</i>	78 \pm 40	287 \pm 172	34 \pm 21	0	88 \pm 42	26 \pm 20
<i>Cornus stolonifera</i>	0	0	14 \pm 14	0	0	0
<i>Corylus cornuta</i>	0	16 \pm 11	6 \pm 5	148 \pm 50	0	174 \pm 64
<i>Lonicera canadensis</i>						
<i>Nemopanthus mucronata</i>	8 \pm 6	0	2 \pm 2	0	0	0
<i>Prunus pensylvanica</i>	52 \pm 24	1 \pm 1	3 \pm 2	0	38 \pm 14	16 \pm 6
<i>Prunus virginiana</i>	0	0	0	1 \pm 1	0	0
<i>Rubus spp.</i>	28 \pm 23	2 \pm 2	25 \pm 16	0	31 \pm 24	0
<i>Sambucus spp.</i>	1 \pm 1	2 \pm 2	2 \pm 2	0	17 \pm 12	23 \pm 6
<i>Sorbus spp.</i>	88 \pm 26	56 \pm 15	41 \pm 14	6 \pm 6	179 \pm 75	103 \pm 28

Table AG.2. Species presence/absence (+/-) in relation to moderate-severity disturbance type and stand composition prior to disturbance. Richness estimates are from all quadrats from each category pooled together.

Species	spruce budworm		windthrow		interaction	
	conifer	mixed con-dec	conifer	mixed con-dec	conifer	mixed con- dec
canopy trees						
<i>Abies balsamea</i>	+	+	+	+	+	+
<i>Acer saccharum</i>	-	+	-	+	-	+
<i>Betula</i>	+	+	+	+	-	+
<i>alleganiensis</i>						
<i>Betula papyrifera</i>	+	+	+	+	+	+
<i>Picea glauca</i>	+	+	+	+	+	+
<i>Picea mariana</i>	+	+	+	-	+	+
<i>Pinus strobus</i>	-	+	+	-	-	+
<i>Thuja occidentalis</i>	+	+	+	+	-	+
sub-canopy tree & shrubs						
<i>Acer pensylvanica</i>	-	+	-	+	+	+
<i>Acer rubrum</i>	+	+	+	+	+	+
<i>Acer spicatum</i>	+	+	+	+	+	+
<i>Amelanchier</i> spp.	+	+	+	-	+	+
<i>Cornus stolonifera</i>	-	-	+	-	-	-
<i>Corylus cornuta</i>	-	+	+	+		+
<i>Lonicera canadensis</i>	-	-	-	-	+	+
<i>Nemopanthus</i>	+	-	+	-	-	+
<i>mucronata</i>						
<i>Prunus</i>	+	+	+	+	+	+
<i>pensylvanica</i>						
<i>Prunus virginiana</i>	-	+	-	-	-	+
<i>Ribes</i> spp.	+	+	+	+	+	+
<i>Rubus</i> spp.	+	+	+	+	+	+
<i>Sambucus</i> spp.	+	+	+	-	+	+
<i>Sorbus</i> spp.	+	+	+	+	+	+
<i>Taxus canadensis</i>						
<i>Vaccinium</i> spp.	+	-	+	-	-	+
<i>Viburnum</i>	-	-	-	-	-	+
<i>cassinoides</i>						
<i>Viburnum edule</i>	+	-	+	-	-	+
<i>Viburnum trilobum</i>	-	-	-	-	+	-

Tree richness (<i>R</i>)	6	8	7	6	4	8
Sub-canopy tree & shrub <i>R</i>	11	11	14	9	11	17
Total woody vegetation <i>R</i>	17	19	21	15	15	25
Number of unique species	-	-	1	-	1	-

Table AG.3. Results of the forward selection procedure in redundancy analysis: conditional effects of the various environmental variables on vegetation distribution after moderate-severity disturbances ($\alpha = 0.05$ for entrance in the model). P-values for variables significantly affecting vegetation distribution patterns are in bold font.

Variable	F	P
Stand composition prior to disturbance	9.0	0.002
Coarse woody debris (CWD) density	4.5	0.002
Percent slope	4.0	0.002
Distance to the nearest mature coniferous stand	3.7	0.002
Drainage	3.1	0.002
Spruce budworm outbreak	2.7	0.002
Deciduous legacy tree density	2.2	0.006
Ecozone (<i>Abies balsamea</i> - <i>Betula papyrifera</i> vs. <i>A. balsamea</i> - <i>B. alleghaniensis</i>)	1.4	0.100
Distance to the nearest mature mixed coniferous-deciduous stand	1.7	0.064
Snag density	1.5	0.086
Proportion of CWD snapped	1.1	0.297
Density of coniferous legacy trees	1.0	0.411
Windthrow disturbance	0.8	0.709
Stand density prior to disturbance	0.8	0.766

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