

**TREE SPECIES DIVERSITY AND STABILITY IN DISTURBANCE-
DRIVEN BOREAL FOREST**

By

Daniel Yeboah

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ABSTRACT

Disturbance is a potent driver of forests. Components of disturbance such as frequency (i.e., time since last stand-replacing disturbance) and intensity (e.g., stand-replacing vs. non-stand-replacing disturbance) plays a major role in influencing plant species diversity. However, majority of studies often consider the effect of disturbance frequency alone on plant species diversity, few studies consider interactive effects between disturbance frequency and intensity of disturbance on plant species diversity. In this dissertation, my first goal was to conduct a meta-analysis to examine the relationship between overstory tree species diversity and disturbance frequency and intensity of disturbance. Across tropical and temperate biomes, tree species richness was greatest at intermediate disturbance frequency with intermediate intensity of disturbance (i.e., non-stand-replacing disturbance).

Furthermore, research on diversity-disturbance relationships (DDRs) often exclude other critical factors such as climate and local site conditions and thus limit understanding on DDR. Using observational data from a natural forest in Canada, I examine DDR, under the influences of climate and local site conditions. I found that the most important factor regulating tree species diversity was disturbance frequency and local site conditions, indicating that they are important factors in maintaining biodiversity in the boreal forest landscape.

Empirical evidence often show that wildfire frequency is strongly influence by local site factors, but broad-scale driver of fires such as climate is rarely considered. I evaluated effects of local site factors and climate on fire regimes across a large natural boreal forest (about 892,000 ha) with no commercial forest harvesting activity; as such, human influences on wildfire is relatively little. My results indicated that mean annual temperature and precipitation were the two most crucial factors driving fire regime in the natural boreal forest studied.

Species diversity has often been linked to temporal stability of ecosystem functions; however, forest stand development, species composition and soil resource availability may affect community stability, but these predictors are often overlooked. I investigated whether community stability (measured as stand level basal area) relates to tree species diversity, forest stand development, tree species composition and soil resource availability. Temporal stability was measured as coefficient of variation, which is a principal component of ecosystem stability. I used repeated measurement plot data from a central boreal forest, which is often associated with non-stand-replacing disturbances such as spruce budworm and forest tent caterpillar outbreaks, which selectively kill trees. I highlighted that temporal stability of stand basal area is influenced by forest stand development and species composition depending on the type of insect outbreak.

Key-words: climate, composition, diversity-stability relationships, intermediate disturbance hypothesis, soil drainage class, species diversity, structural equation models, time since fire.

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NOTE

The chapters of this dissertation were written to satisfy publication requirements of selected peer-reviewed journals; as such formatting and reference styles may differ slightly between chapters.

Chapters:

2. Yeboah, D. and Chen, H.Y.H. 2015. Diversity-disturbance relationships in forest landscapes. *Landscape Ecology* doi:10.1007/s10980-015-0325-y.

3. Yeboah, D. Chen, H.Y.H. and Steve, S. 2015. Tree species richness decreases while evenness increase in a natural boreal forest landscape. *Ecology and Evolution* 6:842-850.

Yeboah, D. and Chen, H.Y.H. 2015. Spatial and temporal variation of wildfire in a natural boreal forest landscape — (In preparation).

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CHAPTER 1: GENERAL INTRODUCTION

Disturbance is an integral part and a critical driver of global forest ecosystems (Bowman et al. 2009). In boreal forest of North America, both wildfire disturbance (Johnson 1996, Wang et al. 2014) and insect outbreaks are common (Fleming et al. 2002), affecting ecosystem processes and regulating biodiversity (Johnson et al. 1995). Time since fire (TSF) is a principal regulator of plant species richness and succession (Grandpré et al. 2000, Clark et al. 2003, Taylor and Chen 2011).

In spite of the importance of disturbance, its effect on species coexistence is still poorly understood. Intermediate disturbance hypotheses (IDH) is a widely investigated concept explaining how disturbance influences species coexistence (Connell 1978). Even though Connell is often credited as the originator of the IDH, other researchers such as Grime (1973) had previously discussed higher diversity at intermediate level of disturbance (Wilkinson 1999). The IDH predicts that species diversity peaks at intermediate frequency, intensity and/or extent of disturbance. However, patterns of diversity and disturbance relationships (DDRs) can be variable, with hump-shaped (Mayor et al. 2012) and U-shaped patterns occurring (Gosper et al. 2013). A possible explanation for the contrasting relationships is that previous studies only consider frequency of disturbance, and not disturbance intensity and thus provide partial information on DDR. Another explanation is the exclusion of local site conditions and climatic factors which are primary determinants of DDR. For example, previous study consider disturbance as a sole predictor of plant species richness (Bongers et al. 2009). But, in forest ecosystems local site conditions and climate variables such as mean annual temperature and precipitation have been shown to strongly influence plant species diversity (Francis and Currie 2003, Zhang et al. 2014).

Fire regimes in the boreal forest are spatially dependent on a variety of factors, including topography, drainage, proximity to water bodies, soil surficial deposits, latitude and longitude (Larsen 1997, Cyr et al. 2007). Temporally, fire regimes are also influenced by changes in mean annual temperature, precipitation and drought frequency (Parisien et al. 2011). Although wildfire is recognized as a critical disturbance process in many forests, causal relationship between large fires and the climatic factors, has been rarely investigated in most studies (Westerling et al. 2006, Cyr et al. 2007). For example, Westerling et al. (2006) found a strong positive association between large fire frequency and mean summer temperature. However, mechanistic link between climatic factors and wildfire was not considered, partly because the forest landscape was highly fragmented by logging and agriculture activities which make it difficult to partition the relative contribution of climate and anthropogenic factors to the fire frequency. Here, we studied a natural boreal forest landscape, having limited road access combined with absence of timber harvesting. Such a less fragmented landscape provides a unique opportunity to study spatial and temporal fire regime with minimum local influences by humans.

Plant species richness strongly influences ecosystem functions, including temporal stability of ecosystem functions (Tilman et al. 2006). A measure of temporal stability, defined as coefficient of variation in abundances of plant species, decreases as species richness increases (Tilman 1996, Morin et al. 2014). Other factors such as species composition, stand developmental stage and soil resources availability are potent factors influencing ecosystem stability (Huston 1997) and other ecosystem processes (Hooper and Vitousek 1998). Despite the critical importance of understanding the role of these factors in influencing ecosystem stability (Huston 1997), most studies focus on species richness, and ignore species

composition, forest stand development, and soil resource availability in natural systems (DeClerck et al. 2006, Xu et al. 2014). Understanding forest ecosystem stability to non-stand-replacing disturbance, which constitutes majority of forest disturbance worldwide (Edwards and Laurance 2013), is of critical importance especially in the boreal forest where increases in insect outbreaks and range expansion are occurring (Pureswaran et al. 2015), and that could affect the provision of goods and services which human derives from the forest.

The overall purpose of this study is to improve understanding regarding how disturbance and local environmental factors influence plant species diversity and stability, as well as test if fire regimes vary with spatial and temporal factors. Specifically, this dissertation was compiled to address the following (1) to examine the influence of disturbance frequency and intensity on tree species richness; (2) to examine the response of species richness to TSF, local site conditions, mean annual temperature and precipitation; (3) to test how fire frequency varies as a result of local environmental factors, such as soil drainage, latitude and longitude, and how mean annual temperature, mean annual precipitation, and mean annual drought may have affected fire frequency; and (4) to test whether CV of forest stand basal area relates to tree species diversity, stand development, composition and soil resource availability. Chapter two reviews published studies on disturbance frequency and intensity of disturbance and examines their effects on tree species diversity; Chapter three presents a field study of the relationship between tree species diversity and disturbance frequency, while controlling for climate and local site conditions; Chapter four examines the causes of spatial and temporal variation of wildfire; and Chapter five focuses on diversity and stability relationship.

CHAPTER 2: DIVERSITY–DISTURBANCE RELATIONSHIP IN FOREST LANDSCAPES

2.1 Abstract

Despite decades of research, there is an intense debate about the consistency of the humped-shaped pattern describing the relationship between diversity and disturbance as predicted by intermediate disturbance hypothesis (IDH). Previous meta-analyses have not explicitly considered interactive effects of disturbance frequency and intensity of disturbance on plant species diversity in terrestrial landscapes. Here we conducted meta-analyses to test the applicability of IDH by simultaneously examining the relationship between species richness, disturbance frequency (quantified as time since last disturbance as originally proposed) and intensity of disturbance in forest landscapes. The effects of disturbance frequency, intensity, and their interaction on species richness were evaluated using a mixed-effects model.

We found that species richness peaks at intermediate frequency after both high and intermediate disturbance intensities, but the richness-frequency relationship differed between intensity classes.

Our study highlights the need to measure multiple disturbance components that could help reconcile conflicting empirical results on the effect of disturbance on plant species diversity.

2.2 Introduction

The relationship between disturbance and plant species diversity has been studied for decades (Connell 1978, Huston 1979, Sousa 1984), but there is still a debate about the patterns of diversity and disturbance relationships (Mackey and Currie 2001, Svensson et al. 2012). A popular theory explaining the linkage between disturbance and diversity, the intermediate

disturbance hypothesis (IDH), predicts that low disturbance frequency, intensity, or extent (i.e., area disturbed) would enhance dominance of late-successional species, high disturbance frequency, intensity, or extent would favor early-successional species, whereas intermediate disturbance frequency, intensity, or extent would lead to co-existence of both late and early-successional species, and thus promote overall high diversity (Connell 1978).

Nonetheless, there is still no general empirical consensus in support of IDH. For example, Mackey and Currie (2001) used a vote counting method and found that of 116 species richness-, 53 Shannon's index-, and 28 evenness-disturbance relationships published between 1985 and 1996, only 16, 19, and 11% of relationships supported IDH. However, performing a meta-analysis of 28 studies focusing on IDH analyses, Svensson et al. (2012) reported that the relationship between species richness and disturbance showed a hump-shaped pattern, supporting the IDH.

Multiple disturbance components (i.e., disturbance frequency, intensity or extent) operate interactively and could account for differences in diversity response to disturbance in terrestrial landscapes (Moloney and Simon 1996, Paine et al. 1998, Shea et al. 2004). For example, it has been theorized that the coexistence of two species peaks at low, intermediate or intensity of disturbance depending on disturbance frequency (Miller et al. 2011). Previous meta-analyses and empirical studies of diversity-disturbance relationships (DDRs) reveal that considering only one component of disturbance, most commonly disturbance frequency, has led to conflicting results, general confusion regarding DDRs (Mackey and Currie 2001, Mayor et al. 2012, Svensson et al. 2012). A potential cause for this discrepancy is that the responses of diversity to disturbance frequency differ with disturbance intensity. Here, we conducted meta-analyses to test the IDH for the relationship between species richness and

disturbance frequency and intensity. We also examined whether the relationship between species richness and disturbance frequency may be dependent on the type of disturbance such as fire *vs.* logging.

2.3 Materials and methods

2.3.1 Definition of terms

We used species richness as a measure of diversity, defined as the number of overstory tree species within a forest stand. We defined disturbance as any event that killed individuals within a stand (Sousa 1984). Disturbance frequency was measured as time since last disturbance (age in years), assuming that all stands originated from the last stand-replacing disturbance (Clark et al. 2003, Brown and Gurevitch 2004, Zhang et al. 2014). We considered two levels of disturbance intensity; high disturbance intensity (i.e., > 60-100% stand basal destroyed) and intermediate intensity (i.e., up to 60% stand basal area destroyed (Schweitzer and Dey 2011, Taylor and Chen 2011, Edwards and Laurance 2013)).

2.3.2 Data collection and selection criteria

We compiled a database of studies that reported on overstory tree species richness and gradients of disturbance. Our literature search covered a broad range of studies that tested the IDH and reported species richness. We included studies published from 1950 to 2013 catalogued in ISI Web of Knowledge, Google Scholar, Forest Science Database, and Biological Abstracts. The first topic keywords were always intermediate disturbance and diversity. The next keywords were forests, plants, or a combination of forests and plants to search within studies from those initially selected from the search results obtained from the first keywords. Shannon's index and species evenness were not considered in the final meta-

analyses as only 11 studies were found providing insufficient data to perform meaningful analyses.

Studies selected for analyses satisfied four conditions: (1) measured overstory tree species (i.e., trees having ≥ 10 cm diameter at breast height, dbh); (2) involved forest biomes; (3) examined both disturbance frequency and intensity; and (4) provided information on mean richness, standard deviation and sample size. Disturbance frequency was quantified as time since last disturbance as originally defined by Connell (1978). Disturbance intensity was classified as high (stand replacing) and intermediate based on the descriptions from original studies. A total of 41 studies that satisfied the criteria were retrieved for tropical and temperate biomes (Supplementary Table S2.1). However, we found no studies involving boreal forests that satisfied the selection criteria. Note that studies on understory layers were excluded from our search because DDRs differ among understory and overstory layers (Zhang et al. 2014). Two studies including all trees ≥ 5 cm in DBH were included in our dataset. Analysis with or without these two studies did not alter qualitative results, so they were included in our final analysis to avoid loss of information.

2.3.3 Data analysis

Most measures of effect size (ES) require a control to determine response ratio (Hedges et al. 1999), but here we introduce a new measure of effect size based only on multiple independent observations. We calculated the ES of disturbance on species richness

$$\text{as: } ES_{ij} = \frac{D_{ij}}{U_i} \quad (1)$$

where D_{ij} ($i = 1, 2, \dots, 41$; $j = 1, 2, \dots, n_i$) is the mean richness of the j^{th} observation in the i^{th} study and U_i is the grand mean of all observations within each study. By using this calculation of

ES, we were able to include a larger number of studies than if other metrics, such as Shannon's index or evenness had been used. The corresponding sampling variance (s_{ij}^2) and sample size (n_{ij}) for the ES were derived from the original studies. Each ES_{ij} was then weighted by the inverse of s_{ij}^2/n_{ij} in subsequent analyses.

We checked publication bias by performing regression tests of asymmetry and found no publication bias in the data. We developed a mixed effects, multiple linear regression model for richness in which we evaluated the effects of disturbance frequency, intensity, and their interaction on ES (Hall et al. 2012). The response variables were the E_{ij} . The full model included all the predictors including a quadratic term for disturbance frequency in a mixed-effects model with study as a random factor. To achieve the most parsimonious model, we used Akaike Information Criterion (AIC) to choose among all alternative models as subsets of the full model. We considered the model to be the most parsimonious when its AIC was smallest. The regression coefficients for the fitted mixed-effects model were considered significant at $\alpha = 0.05$. As recommended (Mittelbach et al. 2001, Chase and Leibold 2002), the significance of quadratic relationship was further confirmed with a Mitchell-Olds and Shaw (1987) test. We performed analysis in package *metafor* 1.6 (Viechtbauer 2010) in R 3.1.0 (R Development Core Team 2014) as well as linear mixed effect models by R package *lme4* (Bates et al. 2013), and both analyses produced the same results. We consequently reported the results from linear mixed effect models.

2.3.4 Assessing possible problems with methodology

A variety of disturbance types, such as selective logging, stand-replacing fire, clearcutting, windthrow, and hurricanes were included in the dataset. Wildfire and logging disturbances have different effects on tree species diversity (Taylor et al. 2013) as some tree species may

respond differently to wildfire and logging (Ilisson and Chen 2009). Consequently, we conducted separate analyses for studies involving logging and wildfire. Disturbance by logging consisted of 23 studies with 91 observations and wildfire were 15 studies with 51 observations. Unfortunately, fewer than 13 studies were found involving all remaining disturbances, so no meaningful analyses could be performed on these studies. Species diversity could be influenced by variation in sampling plot sizes because the number of species increases with plot size (Rosenzweig 1995). Thus, we tested the association between weighted ES and plot size by using Kendall's Tau correlation. The Kendall's correlation showed no significant relationship between the ES and the plot sizes ($P = 0.7$), indicating that differences in the plot sizes, which ranged from 0.1 ha to 1.5 ha, had negligible effect on ES.

2.4 Results

We found an overall significant quadratic relationship between effect size and disturbance frequency (Table 2.1; Fig. 2.1), indicating that species richness increased initially with time since disturbance, but declined in old forests. With high and intermediate disturbance intensity analyzed separately, effect size peaked at intermediate disturbance frequency after both high and intermediate disturbances. However, the magnitude of the estimate maximum richness and the age at which this maximum occurred was lower for intermediate than for high disturbance intensity (Fig. 2.1), as well as weaker significance of the quadratic term for intermediate disturbance intensity (Table 2.1).

Table 2.1 Relationships between effect size and disturbance frequency (measured as years since disturbance) overall ($n = 175$) and following high intensity of disturbance ($n = 68$), and intermediate intensity of disturbance ($n = 107$) across tropical and temperate biomes.

Model	Predictor	Estimate	Standard error	P-value

Overall relationship	Intercept	0.64060	0.06897	<0.001
	Frequency	0.01182	0.00259	<0.001
	Frequency ²	-0.00004	<0.00001	<0.001
High intensity of disturbance	Intercept	0.53670	0.09427	<0.001
	Frequency	0.01428	0.00163	<0.001
	Frequency ²	-0.00004	<0.00001	<0.001
Intermediate intensity of disturbance	Intercept	0.5814	0.09768	<0.001
	Frequency	0.01707	0.00587	0.005
	Frequency ²	-0.00010	0.00005	0.048

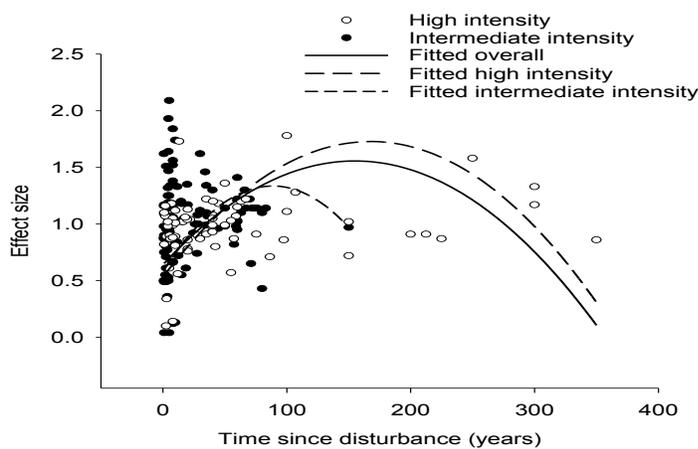


Fig. 2.1 Relationships between effect size and disturbance frequency (measured as time since disturbance in years) overall ($n = 175$) and following high intensity of disturbance ($n = 68$), and intermediate intensity of disturbance ($n = 107$) across tropical and temperate biomes. Fitted models are presented in Table 2.1.

When data were analyzed by disturbance types (fire or logging), the full model with disturbance intensity and frequency exhibited differing levels of significance of predictors

(Table 2.2). By AIC, we found that the most parsimonious models were the ones without a frequency term as a predictor, indicating that the full models (Table 2.2) were over-fitted. The effect size on average was smaller after intermediate intensity fire than high intensity fire (Fig. 2.2a). Similarly, the effect size was smaller after intermediate intensity logging than high intensity logging. However, the effects of disturbance intensity resulted partially from different disturbance frequencies associated with disturbance intensities, i.e., higher ranges of frequencies associated with high intensities (Figs. 2.2b and 2.2d).

Table 2.2 The effects of disturbance intensity and frequency on effect size for disturbance by fire ($n = 58$) and by logging ($n = 91$) in tropical and temperate biomes.

Model	Source	Sum of square	F	P
Disturbance by fire	Intensity	0.377	11.549	0.001
	Frequency	0.302	9.245	0.004
	Frequency ²	0.269	8.233	0.006
	Frequency×Intensity	0.310	9.490	0.003
	Intensity×Frequency ²	0.272	8.340	0.006
Disturbance by logging	Intensity	0.677	6.039	0.016
	Frequency	0.334	2.983	0.088
	Frequency ²	0.462	4.121	0.045
	Frequency×Intensity	0.410	3.660	0.059
	Intensity×Frequency ²	0.494	4.410	0.039

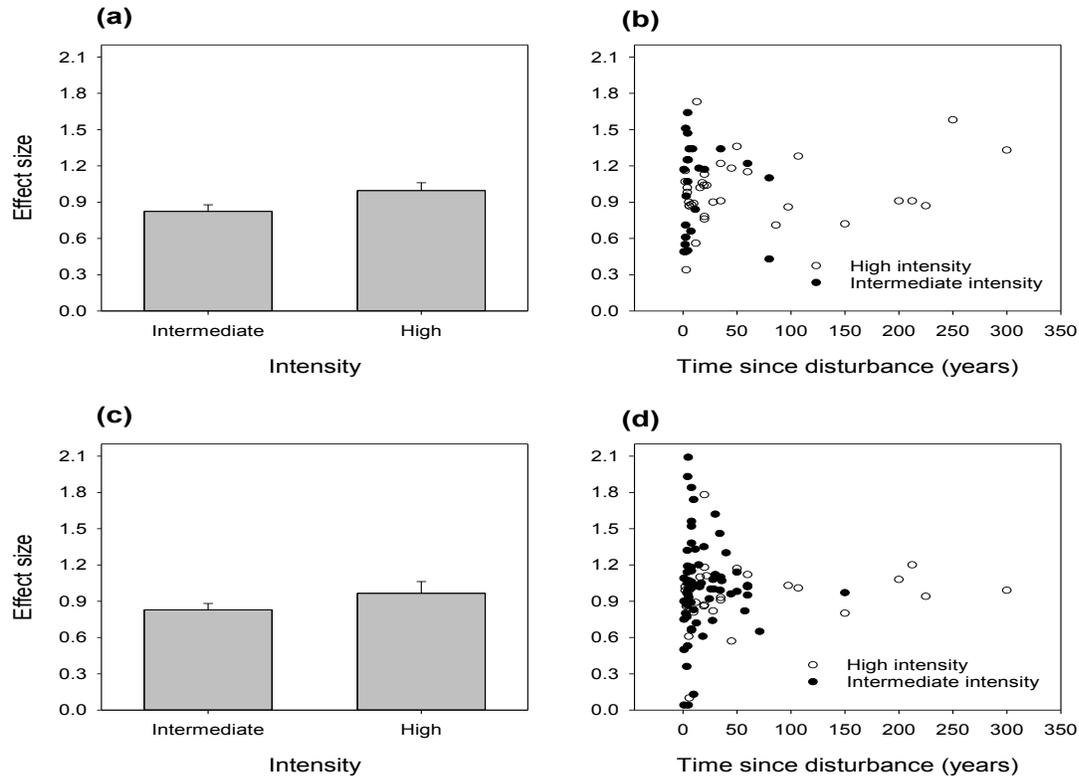


Fig. 2.2 Relationship between effect size, disturbance intensity and disturbance frequency following fire ($n=58$) and logging ($n=91$). (a) The effect of intermediate intensity vs. high intensity fire. (b) The response of effect size to disturbance frequency following fire. (c) The effect of intermediate intensity vs. high intensity logging. (d) The response of effect size to disturbance frequency following logging.

2.5 Discussion

Our meta-analysis has demonstrated a quadratic relationship between species richness and disturbance frequency following high intensity of disturbance. We also found a quadratic relationship between species richness and disturbance frequency following intermediate intensity of disturbance with the decline of species richness occurring sooner than following high intensity of disturbance. The original prediction of the IDH is that plant species diversity peaks at an intermediate level of disturbance (Connell 1978), but it does not consider how interactions among components of disturbance can influence the shape of DDRs. Our work builds upon the IDH, showing that the responses of species richness to disturbance frequency

are dependent on disturbance intensity. Theoretical (Miller et al. 2011, Miller et al. 2012) and experimental research have also reported interactive effects between disturbance frequency and intensity on species diversity (Collins et al. 2001, Hall et al. 2012), but ours is the first study that provides empirical support for the theoretical predictions. The interactive effects between components of disturbance on species diversity has also been noted in a narrative review (Shea et al. 2004). While a recent review (Svensson et al. 2012) supports the IDH (Connell 1978), Mackey and Currie (2001) questioned the general validity of the IDH, identifying that the lack of support for the IDH is likely attributed to an insufficient range of disturbance frequency. We provide a different perspective on DDRs by simultaneously considering disturbance frequency and intensity and demonstrate that species richness peaked at intermediate disturbance frequency following both high and intermediate intensity disturbance, but the maximum richness and the age or frequency at which it occurred differed between intensity classes. The empirical evidence from our work provides a unique insight into how disturbance components can interactively influence the shape of DDRs and help reconcile conflicting empirical results on the effect of disturbance on species diversity summarised by Mackey and Currie (2001).

We found that the relationship between species richness and disturbance frequency with intermediate intensity of disturbance showed a humped-shaped pattern of diversity, as suggested by Miller (1982). We speculate that colonisation and competitive exclusion could be the primary mechanisms for the pattern of diversity. For example, at the mid successional stage, intermediate disturbance intensity in forest ecosystems, which may selectively remove size-classes or specific species, may decrease species diversity (Cooke and Roland 2007, Clark and Covey 2012). Our data, analyzed separately by fire and logging origins, confirm

that species diversity decreases following intermediate intensity fire and logging without sufficient time for recovery. Given sufficient time for recovery, the decrease in species diversity after intermediate disturbance may be offset by colonisation from seed sources of new or the resident late successional species, or by vegetative reproduction, regeneration from seedbanks, or advanced regeneration of the late successional species. Longer-term monitoring will be needed to fully understand the recovery process following intermediate disturbance intensity.

Tree species diversity may respond differently to disturbance types (Taylor et al. 2013), another potential source of the debate regarding the IDH (Bongers et al. 2009, Kershaw and Mallik 2013). The different responses to disturbance frequency between wildfire and logging could be attributed to the fact that logging, in particular selective logging, leaves behind advance regeneration of trees, whereas stand-replacing wildfire kills trees non-selectively (Attiwill 1994, Ilisson and Chen 2009). However, the limited number of existing studies has precluded us from reaching a firm conclusion on how disturbance origins such fire *vs.* logging can alter the response of species diversity to disturbance frequency. The choice of diversity measure, and the influence of unmeasured factors such as stand productivity could also influence the shape of DDRs (Kondoh 2001, Svensson et al. 2012, Zhang et al. 2014), but they are beyond the scope of this study. Research into the influence of the components of diversity and stand productivity on DDRs would further resolve the debate over the validity of the IDH.

A global decrease in species diversity is having negative impacts on ecosystem function (Vitousek et al. 1997, Barnosky et al. 2011). A possible resolution to the concerns about global biodiversity loss is that forest management strategies can utilize the concept of

IDH, by manipulating disturbance frequency and intensity of applied disturbances to maximise diversity in managed forests. Management strategies incorporating the concept of IDH could be applied extensively (Keddy 2005) because selective logging after major fire disturbance is a common forestry practice worldwide, especially in tropical forest (Edwards and Laurance 2013).

2.6 Conclusion

Overall, we found that multiple disturbance components act interactively to influence the shape of DDRs of overstory tree species, providing a deeper understanding of the IDH. Nonetheless, several other factors are also likely to affect the shape of DDRs, such as species diversity of understory plants (Zhang et al. 2014), and understanding these effects would further enhance our understanding of the IDH. Future studies should design large scale experiments to investigate patterns of plant species diversity and the possible underlying mechanisms driving those patterns. Specifically, multiple disturbance components deserve considerable research attention to provide broad assessment of the effects of disturbance on plant species diversity in forest landscapes.

CHAPTER 3: TREE SPECIES RICHNESS DECREASES WHILE SPECIES EVENNESS INCREASES WITH DISTURBANCE FREQUENCY IN A NATURAL BOREAL FOREST LANDSCAPE

3.1 Abstract

Understanding species diversity and disturbance relationships is important for biodiversity conservation in disturbance-driven boreal forests. Species richness and evenness may respond differently with stand development following fire. Furthermore, few studies have simultaneously accounted for the influences of climate and local site conditions on species diversity. Using forest inventory data, we examined the relationships between species richness, Shannon's index, evenness, and time since last stand-replacing fire (TSF) in a large landscape of disturbance-driven boreal forest. TSF has negative effect on species richness and Shannon's index, and a positive effect on species evenness. Path analysis revealed that the environmental variables affect richness and Shannon's index only through their effects on TSF while affecting evenness directly as well as through their effects on TSF. Our results demonstrate that species richness and Shannon's index decrease while species evenness increases with TSF in a boreal forest landscape. Furthermore, we show that disturbance frequency, local site conditions, and climate simultaneously influence tree species diversity through complex direct and indirect effects in the studied boreal forest.

3.2 Introduction

The relationships between disturbance and plant species diversity have been studied for decades, since Connell (1978) proposed the intermediate disturbance hypothesis (IDH), which predicts plant species diversity to peak at intermediate levels of disturbance

frequencies, intensities and extents (i.e., area disturbed). However, the patterns of diversity and disturbance relationships and the possible mechanisms driving those patterns remain the subject of debate (Mackey and Currie 2001, Shea et al. 2004, Svensson et al. 2012). For example, Mackey and Currie (2001) reviewed 116 species richness-, 53 Shannon's index-, and 28 evenness-disturbance relationships in studies published from 1985 through 1996, and found support for the IDH in only 16% of richness, 19% of Shannon's index, and 11% of evenness relationships, respectively. Theoretical research has even concluded that the IDH should be abandoned because the three proposed mechanisms that support IDH are logically invalid (Fox 2013). However, recent field studies continue to provide evidence of support for the IDH in tropical (Bongers et al. 2009) and boreal forests (Mayor et al. 2012). Patterns of diversity and disturbance relationships are more frequently reported to be positively or negatively linear than the IDH predicted hump-shaped relationship (Mackey and Currie 2001). The negative linear relationship is consistent with initial floristic composition hypothesis, which states that all species occur immediately after disturbance and temporal changes in diversity and succession are driven by local extinction of species from overstory vegetation through differential rates of growth, competition and longevity (Egler 1954).

There are several reasons for the different outcomes in the testing of the IDH. Firstly, the range of disturbance frequency and intensity may influence the outcomes. For example, if only the range from high to intermediate disturbance frequencies are considered in the IDH, a positive diversity and disturbance relationship would be expected. The positive relationship, however, would be inappropriate in rejecting the IDH (Mackey and Currie 2001). Secondly, the relationships between different components of diversity and disturbance may differ (Mackey and Currie 2001, Zhang et al. 2014). Despite the crucial importance of

understanding the role of species evenness in ecosystem function (Hillebrand et al. 2008, Zhang et al. 2012), substantially fewer studies have examined species evenness-disturbance relationships in natural systems, and mechanisms responsible for species presence and absence and their relative abundance may differ with forest stand development (Chen et al. 2009, Chen and Taylor 2012). Lastly, diversity is strongly influenced by climatic factors (Francis and Currie 2003) and local site conditions (Huston 1993, Zhang et al. 2014). Failing to consider the influences of climatic factors and local site conditions may also contribute to the outcomes of testing the IDH.

Some of the disparities in disturbance—diversity relationships (DDR) may be resolved by considering the multiple interacting mechanisms that influence plant coexistence in natural forests (Shea et al. 2004, Grace et al. 2007). Stand-replacing fire disturbance is widespread, particularly in the boreal forest (Bowman et al. 2009). Time since fire (TSF) plays an important role in influencing plant coexistence, succession and/or other ecosystem processes (Johnson 1996, Grandpré et al. 2000, Clark et al. 2003, Wardle et al. 2008). Fire regimes in boreal forest vary spatially due to local site conditions, such as soil drainage, which imposes differential fuel moisture levels among locations, and thus moderate the spread of incidence fire (Larsen 1997, Cyr et al. 2007, Mansuy et al. 2010). Fire regimes are also influenced by climate such as changes in mean annual temperature and precipitation (Parisien et al. 2011). Given the importance of multiple ecological interactions (Grace et al. 2007), testing the IDH requires untangling the multiple mechanisms that influence plant diversity.

Here, we examined the relationships between species richness, Shannon's index, evenness and TSF in the central boreal forest, where stand-replacing fire is frequent (Senici et

al. 2010, Senici et al. 2013). We examined how each measure of diversity responded to TSF using boosted regression trees by simultaneously accounting for the effects of climate and local site conditions. We also explored the multiple relationships among tree species diversity, TSF, local site conditions, and mean annual temperature using structural equation models (SEMs). In the SEMs, we tested (1) the effects of temperature and local site conditions on TSF and (2) the effects of TSF, local site conditions and temperature on species richness, Shannon's index and evenness. Since most tree species can re-establish immediately following fire in the western and central boreal forest of North American (Gutsell and Johnson 2002, Chen et al. 2009, Ilisson and Chen 2009), we hypothesize species richness to decrease with TSF since local extinction may occur for early-successional, shade-intolerant species such as *Pinus banksiana* that are incapable of regenerating under canopy (Chen and Popadiouk 2002). We predict that Shannon's index will decrease with TSF, suggested by the theory of initial floristic composition (Egler 1954). We also hypothesize species evenness to increase with TSF because dominance of early-successional species tends to decrease with stand development (Bergeron 2000, Chen and Taylor 2012, Bergeron et al. 2014).

3.3 Materials and methods

3.3.1 Study area

This study was located in Wabakimi Provincial Park in northwestern Ontario (Supplementary Fig. S1). The study area is a remote wilderness park with minimal road access, virtually no human activity, and the absence of commercial forest harvesting. Hence, the park provides an ideal landscape to test the effects of relatively natural fire frequency on species diversity. This park is the second largest in Ontario, covering a total area of 892,000 ha and situated within the boundaries of 50°00'N to 51°30'N and 90°30'W to 88°30'W. Mean annual temperature

and annual precipitation recorded, from 1971 to 2010, at the nearest climate station in Armstrong, were -1.3 °C, and 700 mm, as suggested by (Environment Canada 2011). Elevation is between 328 to 462 m above sea level (Soil Landscapes of Canada Working Group 2010). Soils consist of sand, silt and clay types, and the predominate soil orders are Brunisol and Podzol (Soil Landscapes of Canada Working Group 2010). Common tree species within the park include: *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Populus balsamifera* (L.), *Betula papyrifera* March., *Picea mariana* (Mill) Britton, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., and tamarack (*Larix laricina* (Du Roi) K. Koch).

3.3.2 Sampling strategy

Stratified random sampling was employed to quantify the forest composition and productivity associated with diverse local site conditions and stand age classes based on interpreting aerial photographs, by the Ontario Ministry of Natural Resources. A total of 1018 sample plots were spatially interspersed across the park with a distance of at least 500 m between the closest sampled plots, in order to avoid the effects of spatial autocorrelation (Legendre and Legendre 2012). For each plot, a transect of 200 m was laid, and prism sweeps were taken at ten points of 20 m apart using a wedge prism with a basal area factor of two. At every sampling point, living trees with diameter at breast (dbh, 1.3 m above root collar) ≥ 10 cm were tallied by tree species and used to determine the stand basal area and tree species composition (Avery and Burkhart 2002).

3.3.3 Species diversity

We considered diversity indices including tree species richness, Shannon's index, and species evenness. Species richness pertained to the number of species that were observed in each

sample plot. Shannon's index was calculated by utilizing the basal area proportions of the constituent species within each sample plot. We used the inverse of Simpson's dominance index as the measure of species evenness, which is considered to be independent of species richness and a preferred index over Shannon's index (Smith and Wilson 1996). The evenness index was also determined using the basal area proportions of the constituent species.

3.3.4 Explanatory variables

To understand DDR, we assessed the effects of TSF, mean annual temperature, average annual precipitation and local site conditions on species richness, Shannon's index, and evenness. Disturbance frequency was measured as TSF (age in years) as originally proposed by Connell (1978). The TSF was determined by using either fire data from Ontario fire history maps, which document all fires ≥ 200 ha since 1921, or by coring trees. We used these fire records to initially determine TSF for fires that occurred since 1921. Because of potential inaccuracy of fire maps due to escaped patches, as well as the lack of records for fires < 200 ha, field validation was conducted by coring the dominant trees to the pith at the dbh from three dominant trees (Bergeron 1991, Senici et al. 2010). In cases where there was a discrepancy in the TSF between the fire map and the ring counting, we used TSF estimated from the latter approach for analyses. For fires occurring before 1921, we used tree ages to determine TSF. In the field, tree species known to regenerate immediately post fire (Bergeron and Brisson 1990) were preferentially selected in the following order: *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera*, and *Picea mariana* (Chen and Taylor 2012). All acquired cores were returned to the laboratory where the rings were counted under a dissecting microscope until an identical count was obtained in triplicate. From the tree ring counts, TSF was determined by adding 7, 8, or 17 years when ring counts were from *Pinus*

banksiana, *Populus* sp. (or *Betula papyrifera*), or *Picea mariana* (Vasiliauskas and Chen 2002). For stands dominated by shade tolerant species such as *Picea glauca* or *Thuja occidentalis*, it was assumed that the trees of shade intolerant species present at the sites did not regenerate immediately post-fire. In such cases, the age of the oldest tree was used regardless of the tree species as an approximation of the stand age (Senici et al. 2010). The mean stand age was 89 years (Supplementary Table S3.1).

Soil drainage class (SDC), which is comparable to soil moisture regime and nutrient regime classification (Chen et al. 2002), was used to represent local site conditions. SDC represents a composite measure of overall site quality, which is assessed from soil texture, soil thickness, and topographic position, soil permeability, depth of water table, and organic layer depth. SDC was determined on site using soil pits to the parent material, or 120 cm deep. SDC was ranked from 0 to 9, which represent dry, moderately fresh, fresh, very fresh, moderately moist, moist, very moist, moderately wet, wet, and very wet soil, respectively.

To determine the effects of temperature and precipitation on species diversity, we derived long-term (1921-2010) climate estimates from BioSIM R: produced in Quebec, Canada (<https://cfs.nrcan.gc.ca/projects/133>), which generates scale-free climate data based on latitude, longitude, and elevation (Hogg 1997). The climate estimates were used to calculate mean annual temperature (MAT) and mean annual precipitation (MAP).

3.3.5 Statistical analysis

We developed individual models for measures of diversity through the use of TSF, SDC, MAT, and MAP as predictors. We employed generalized linear model and boosted regression trees (BRT) to examine the effects of these predictors on diversity indices. Both modelling

approaches yield similar results. For simplicity, we reported the results from the generalized linear models.

We also constructed separate SEM models for diversity indices. SEM possesses a unique strength for analyzing complex relationships, in that the same variable may be treated as a predictor and as a response variable (Grace et al. 2007, Grace et al. 2010). Goodness-of-fit for the model was determined from the maximum likelihood χ^2 test, and the model was judged as having a good fit if $P > 0.05$, which indicates that the model is consistent with the data (Rosseel 2012). The chi-square test can be influenced by sample size, therefore, we also reported the comparative fit index (CFI) which is least affected by sample size (Bentler and Bonett 1980, Bentler 1990, Rosseel 2012). In a preliminary model, we included MAP as a predictor in SEMs; however, the model did not yield a good fit. Accordingly, as recommended (Grace et al. 2007, Grace et al. 2010), we modified SEMs to include the effects of MAT and SDC, on TSF, and TSF, MAT and SDC on diversity, with or without the quadratic term for SDC. We treated SDC as a regular numeric variable in SEMs since SDC is an ordinal variable and we were interested whether species diversity could be quadratically related to SDC (Rosseel 2012, Zhang and Chen 2015). We determined the magnitude of direct effect from SEM coefficients. We also estimated the total effects of a given exogenous variable on different components of diversity by adding standardized direct and indirect effects. The statistical significance for the SEM coefficients were evaluated using a bootstrap method, as bootstrapped estimates do not assume any particular distribution and thus, are often suitable for non-normal data such as the number of species (Bollen and Stine 1992).

3.4 Results

The final generalized linear models explained the 18, 21, and 21% variation of tree species richness, Shannon's index, and evenness, respectively (Table 3.1). TSF and SDC were the strongest predictors, whereas MAT and MAP were less important in all models (Table 3.1). Species richness decreased with TSF, increased with MAT and MAP, and was higher in intermediate SDC (Fig. 3.1). Species evenness, however, increased with TSF, decreased with MAT and MAP, and was higher in very moist and moderately wet sites than other SDCs. Shannon's index had similar relationships to the predictors as species richness (Fig. 3.1).

Table 3.1. Percent variance explained by time since fire (TSF, years), soil drainage class (SDC), mean annual temperature (°C), and mean annual precipitation (mm) on tree species richness, Shannon's index, and species evenness ($n = 1018$). Percent variance explained by each individual predictor is calculated as the sum of squares associated with the predictor divided by the total sum of squares for each model. The reported models including TSF, SDC, MAT, and MAP as predictors are better than the models with a quadratic term of TSF as an additional predictor based on Akaike information criterion; for all diversity indices, the quadratic term of TSF was statistically insignificant ($P > 0.05$).

Diversity index	TSF	SDC	MAT	MAP	Error distribution	R ²
Richness	11.13	5.53	0.01	0.86	Poisson	0.18
Shannon's index	11.72	8.52	0.07	0.78	Gaussian	0.21
Evenness	12.42	7.77	0.11	1.01	Gaussian	0.21

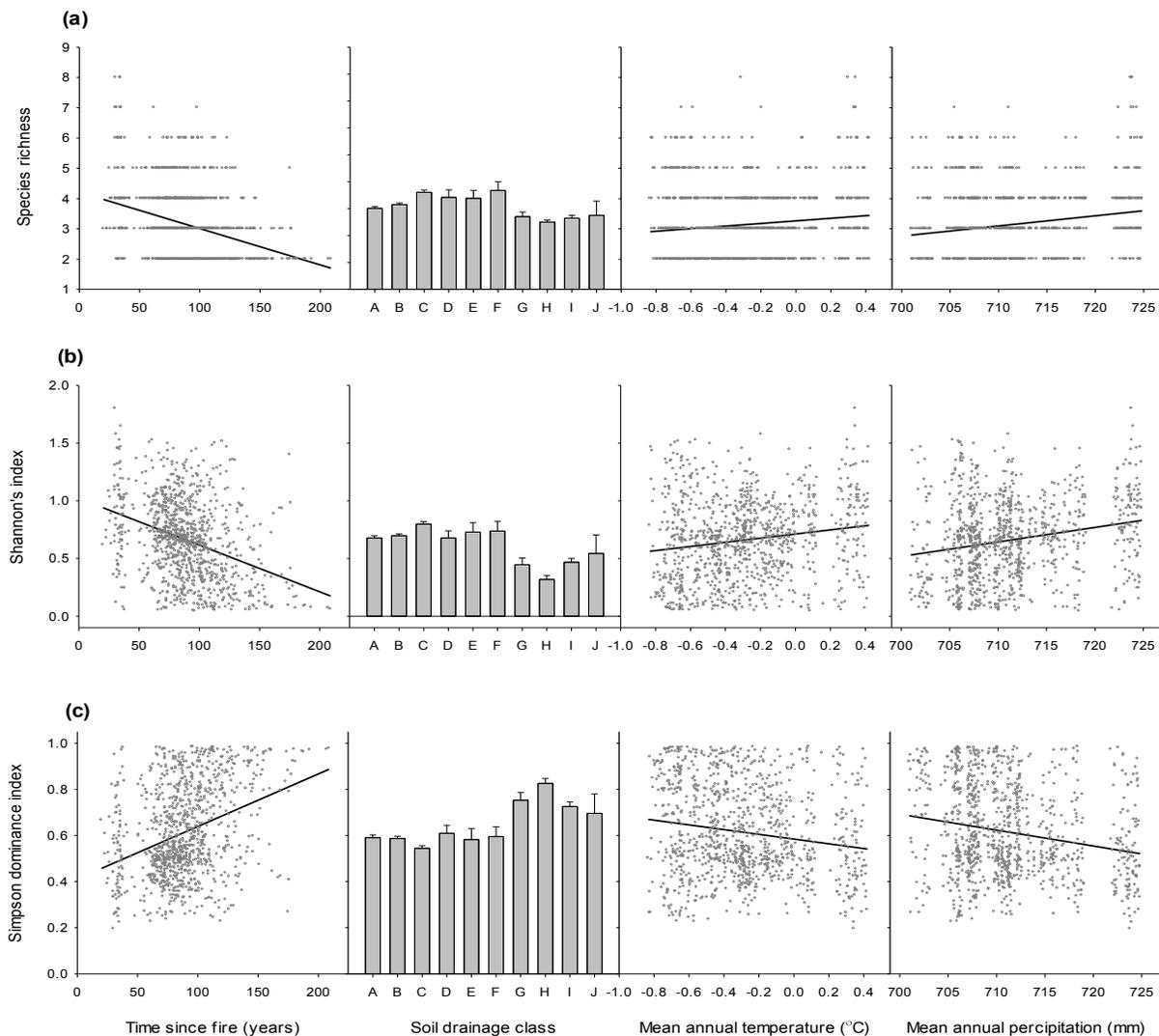


Fig. 3.1 Bivariate relationships between diversity indices and time since fire, soil drainage class, mean annual temperature and mean annual precipitation. (a) Species richness. (b) Shannon's index. (c) Species evenness. Soil drainage classes from A to J represent dry, moderately fresh, very fresh, moderately moist, moist, very moist, moderately wet, wet, and very wet soil, respectively. Values in the figures associated with soil drainage classes are mean + 1 s.e.m. Dots and lines in other figures are observed values and fitted linear regressions.

The SEM models with the quadratic term of SDC yielded an inadequate fit of data to the model for species richness ($P < 0.001$, $df = 1$, CFI = 0.931), Shannon's index ($P < 0.001$, $df = 1$, CFI = 0.938) and evenness ($P < 0.001$, $df = 1$, CFI = 0.938). As recommended (Grace

et al. 2010), these models were modified by eliminating non-significant direct effects of the quadratic term of SDC. The modified model yielded adequate fit of data for species richness ($P > 0.05$, CFI = 1), Shannon's index ($P > 0.05$, CFI = 1) and evenness ($P > 0.05$, CFI = 1). There was a significantly negative direct effect of TSF on richness and Shannon's index, but a positive effect on evenness (Fig. 3.2). MAT had a negative direct effect and SDC had a positive direct effect on TSF in the richness model (Fig. 3.2). SDC had a negative indirect influence on species richness through TSF (Table 3.2).

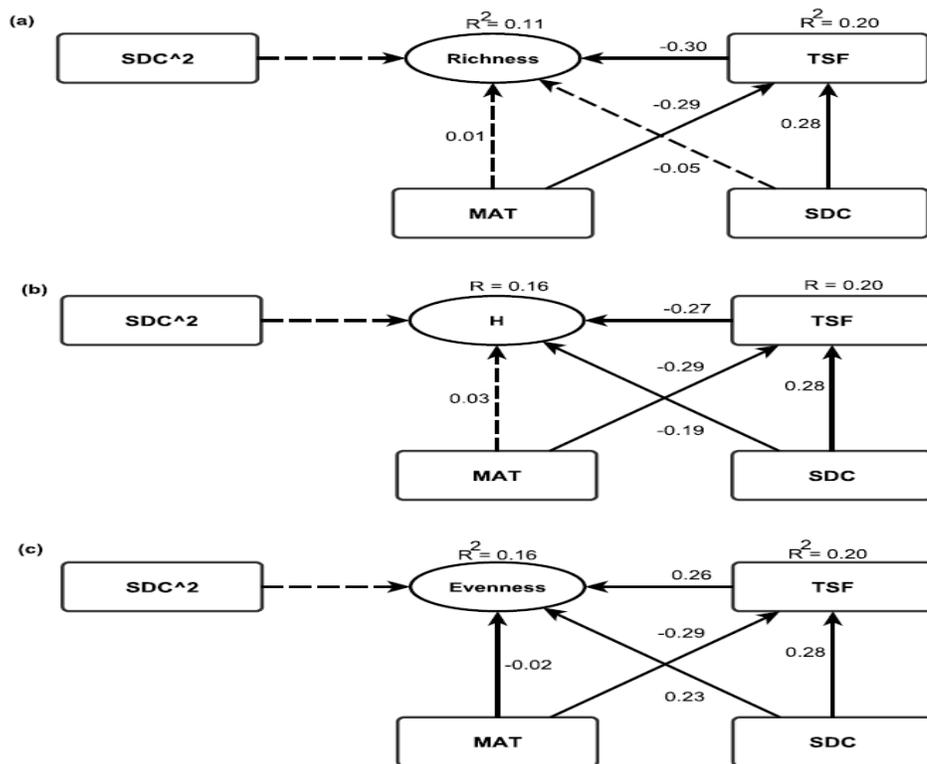


Fig. 3.2 Results of structural equation modelling (SEM) relating tree species diversity to disturbance frequency. Solid lines represent significant ($P < 0.05$) SEM coefficients and dashed lines represent insignificant ones ($P \geq 0.05$). (a) Species richness. (b) Shannon's index (H). (c) Species evenness. TSF, MAT and SDC represent time since last fire (years), mean annual temperature ($^{\circ}$ C) and soil drainage class, respectively.

Table 3.2 The direct, indirect, and total standardized effects on tree species richness, Shannon's index and evenness based on structural equation models (SEM). The total effect was estimated by adding standardized direct and indirect effects.

SEM model	Predictor	Pathway to each component of diversity	Effect	P-value
Model for species richness in Fig. 3a	Time since fire	Direct	-0.3	<0.001
		Indirect effect	-	-
		Total effect	-0.3	<0.001
	Soil drainage class	Direct	-0.05	0.103
		Indirect effect through time since fire	-0.1	<0.001
		Total effect	-0.15	<0.001
	Mean annual temperature	Direct	0.01	0.887
		Indirect effect through time since fire	0.11	<0.001
		Total effect	0.12	<0.001
Model for Shannon's index in Fig. 3b	Time since fire	Direct	-0.27	<0.001
		Indirect effect	-	-
		Total effect	-0.27	
	Soil drainage class	Direct	-0.19	<0.001
		Indirect effect through time since fire	-0.1	<0.001
		Total effect	-0.29	<0.001
	Mean annual temperature	Direct	0.05	0.121
		Indirect effect through time since fire	0.12	<0.001
		Total effect	0.17	<0.001
Model for species evenness in Fig. 3c	Time since fire	Direct	0.26	<0.001
		Indirect effect	-	-
		Total effect	0.26	<0.001
	Soil drainage class	Direct	0.23	<0.001
		Indirect effect through time since fire	0.09	<0.001
		Total effect	0.32	<0.001
	Mean annual temperature	Direct	-0.05	0.114
		Indirect effect through time	-0.11	<0.001

since fire	
Total effect	-0.16 <0.001

3.5 Discussion

Despite a wide range of stand ages included in our study, our analysis demonstrated that species richness of overstory trees decreased with time since fire in the studied boreal forest. Based on the prediction of IDH, a recently disturbed forest stand would consist of early successional species, and shade tolerant species would grow into the stand, and eventually outlast early-successional species. This succession process would result in young stands consisting of early-successional species, old stands consisting of late-successional species, and intermediate aged stands having both early- and late-successional species-diversity peaks in intermediate aged stands. However, in boreal forests, most tree species can re-establish immediately following fire (Gutsell and Johnson 2002). The decrease of species richness over time is attributable to age-dependent local extinction of short-lived early successional, shade-intolerant species (Chen and Popadiouk 2002, Luo and Chen 2011).

By contrast, other empirical studies conducted in forests with long stand-replacing disturbance intervals indicate that species richness and/or Shannon's index peaks at intermediate stand age (Zhu et al. 2009, Zhang et al. 2014). These contrasting findings appear to be attributable to long-term ecosystem-specific adaptive responses to disturbance frequencies: In fire-frequent western and central boreal forests of North America (Weir et al. 2000, Senici et al. 2010), evolutionary selection has resulted in a pool of tree species that can establish immediately after fire (Johnson 1996, Gutsell and Johnson 2002), whereas in forests with long stand-replacing disturbance intervals, as originally hypothesized by (Connell 1978), late-successional species establish after local site environments have been modified by early-

successional species (Zhu et al. 2009, Zhang et al. 2014). Furthermore, disturbance and species richness relationships are dependent on whether understorey species are considered. For example, Gosper et al. (2013) found a ‘U’-shaped diversity – time since fire relationship with species from all forest strata considered because the species of subdominant functional types are suppressed under intensive resource competition during self-thinning stage of stand development.

We found a positive linear evenness-TSF relationship. This result is consistent with our hypothesis. The increase in species evenness with stand age is attributable to that the dominance of early-successional species, i.e., *Pinus banksiana*, *Populus* spp., decreases with stand development (Taylor and Chen 2011, Chen and Taylor 2012, Bergeron et al. 2014).

Previous studies have demonstrated that tree species diversity is strongly influenced by disturbance frequency alone, advancing our understanding of DDRs (Brown and Gurevitch 2004, Gosper et al. 2013), which could be explained by controlling for a single factor, rather than multiple factors. However, in a large landscape other drivers (e.g., local site conditions) contribute to plant species diversity, and thus, we partitioned the effect of stand age from SDC, MAT and MAP, and found that TSF and SDC are equally important factors in regulating tree species diversity, which is coherent with previous work (Zhang et al. 2014). SDC contributes significantly to tree species diversity (Huston 1993, Roberts and Gilliam 1995, Zhang et al. 2014), such that topographic soil moisture (Moeslund et al. 2013) and soil nutrient supply (Huston 1993, Cornwell and Grubb 2003) may directly control plant species diversity patterns. Previous studies have shown that climate exerts a potent influence on DDRs, particularly at regional and global levels (Francis and Currie 2003, Mayor et al. 2012); however, we observed that through TSF, SDC indirectly influenced tree species richness and

evenness. These findings reflect the important role of SDC in influencing plant coexistence, and therefore deserve attention in DDR (Roberts and Gilliam 1995, Zhang et al. 2014).

Theoretical studies often acknowledge that plant species coexistence is not attributable to a single mechanism, but rather, are the outcome of complex interacting mechanisms (Shea et al. 2004, Agrawal et al. 2007, Hughes et al. 2007), albeit empirical evidence is lacking. Thus, we have built on theoretical work by providing empirical insights on DDR, in which we explored multiple mechanisms underlying tree species diversity patterns using SEM. The SEM results demonstrated that in natural forest ecosystem subject to complex causal factors, several processes act simultaneously to influence plant species diversity. For example, we found a strong direct effect of SDC and MAT on TSF, while through TSF, MAT indirectly influenced species richness and evenness. These results provide a deeper understanding of DDR and provide some resolution to the disputes surrounding the IDH.

3.6 Conclusion

In conclusion, our results demonstrated that tree species richness decreases, while species evenness increases with time since fire in a boreal forest landscape. These results are attributed to the establishment of most trees species soon after fire and the decline of dominance of early-successional, shade-intolerant species with stand development. Moreover, our results demonstrated complex causal links between climate, local site condition, time since fire and measures of species diversity in the boreal forest.

CHAPTER 4: SPATIAL AND TEMPORAL VARIATION OF WILDFIRE IN A NATURAL BOREAL FOREST LANDSCAPE

4.1 Abstract

Previous studies often show that climate strongly correlate with fire regimes, but cause-and-effect relationships are rarely considered, because it is difficult to separate contribution of climate to fire regimes from human activities. Furthermore, the relative contribution of climate to fire regimes compared with local environmental factors is poorly understood. Our objective was to test how mean annual temperature (MAT), mean annual precipitation (MAP), drought (measured as climate moisture index), and local environmental factors (including soil drainage and firebreaks) may have affected spatial variation in fire frequency. We evaluated the spatial and temporal variation in fire frequency across a large natural boreal forest (about 892,000 ha), where human impact on forest wildfire is relatively little because of absence of timber harvesting and no other human activities with minimal road access. Fire history was reconstructed using fire records and dendroecological survey. We tested the effects of numerous local environmental factors (e.g., soil drainage and firebreaks), MAT, MAP, CMI on spatial variation of fire frequency, using survival analyses. We conducted Akaike information criterion (AIC) analyses to determine best fit model, selecting the model with smallest AIC as most parsimonious model. We found that model with MAT and MAP as predictors were the most parsimonious model. Fire frequency increased with MAT and decreased with MAP. Overall, our results suggest that across very large forest landscape future changes in climate could lead to increase wildfire disturbance.

4.2 Introduction

Wildfire is one of the most common natural disturbance processes in forest ecosystems worldwide (Bowman et al. 2009, Wang et al. 2014). In the boreal forest, fire regimes are predicted to be substantially altered by global climate change (Kasischke and Turetsky 2006, Jolly et al. 2015). Given these potential changes in fire regimes, determination of direct causal factors controlling wildfire at multiple spatial and temporal scale is important because of its profound consequences on forest ecosystem functions (Cyr et al. 2007, Bond-Lamberty et al. 2014). For example, increase fire occurrence can lead to significant release of carbon through direct combustion of biomass, affecting global carbon cycle (Amiro et al. 2001, Bond-Lamberty et al. 2007).

Previous fire-history studies in North America have reported higher fire frequency in western (Weir et al. 2000) than the eastern boreal forest (Bergeron et al. 2001), likely explained by the contribution of temperature and precipitation variation in the respective regions (Krawchuk et al. 2009). Even though fire frequency has increased temporally in North America (Westerling et al. 2006, Flannigan et al. 2009), temporal changes in humid air masses circulation and precipitation have historically (i.e., since 1800s period of the little ice age) correlated with a reduction in fire frequency in some forests in the western (Larsen 1996, Weir et al. 2000) and eastern boreal forests of Canada (Bergeron et al. 2004). Within a particular region, fire frequency is influenced by variation in local environmental factors, including proximity to water bodies, soil drainage, elevation, latitude and longitude, and surficial deposits (Cyr et al. 2007, Mansuy et al. 2010). Fire regimes also vary significantly due to effects of human activities such as timber harvesting and fire suppression in the 1900s (Weir et al. 2000, Taylor and Scholl 2012).

In contrast to local environmental factors, spatial variation in climate is a broad-scale factor controlling fire regimes (Drever et al. 2008, Fauria and Johnson 2008, Parisien et al. 2011). In particular, drought frequency, changes in mean annual temperature (MAT) and precipitation (MAP) are the most critical drivers of fire regimes in forest ecosystems (Amiro et al. 2004, Girardin et al. 2006, Parisien et al. 2014). For instance, Westerling et al. (2006) found a strong positive association between fire frequency and mean summer temperature in western US. In the Canadian boreal forest, strong effects of the local environmental factors on fire regime have been observed, together with the decreasing fire frequency in eastern (Bergeron et al. 2004) and an increasing fire frequency in northwestern Ontario (Senici et al. 2010). Most of the studies often suggest that the changes in frequency is attributed to climate, but empirical evidence is lacking (Senici et al. 2010). Thus, more research into the relative contribution of climate and the local environmental factors to fire regimes is needed, as well as investigation on climate-fire relationship to improve our understanding on how changes in climate may have affected fire regimes differently among forest ecosystems in North America.

Although strong correlation between climate (i.e., spring and summer temperature) and wildfire has been recognized (Westerling et al. 2006), cause-and-effect relationship were overlooked. The lack of causality could be attributed to the challenge of partitioning climate control on fire regimes from other anthropogenic factors, which typically affect fire regimes in disturbance-driven boreal forest of North America (Cyr et al. 2007, Senici et al. 2010). Here, our objective was to understand how numerous local environmental factors (e. g., soil drainage, elevation, latitude and longitude) and spatial variation in mean annual drought (quantified as climate moisture index), mean annual temperature and mean annual

precipitation affect fire frequency (i.e., broad-scale climate *vs.* local site factors). We also tested if fire frequency has change temporally, and how the temporal changes in fire frequency relates to temporal changes in climate. Our study was conducted in a large natural boreal forest landscape, i.e., Wabakimi Provincial Park, where land-use histories have relatively little effect on fire regimes because of the absence of timber harvesting activities, combined with very limited road access. We expect a trend of temporal increase in fire frequency similar to observations in central boreal region of Ontario, due to increase dryness in the region which strongly correlate with occurrence of large forest fires (Wotton et al. 2003, Beverly and Martell 2005).

4.3 Materials and methods

4.3.1 Study area

We conducted this study in Wabakimi Provincial Park in northwestern Ontario. The park covers an area of 892,000 ha and is located within the boundaries of 50°00'N to 51°30'N and 90°30'W to 88°30'W. Mean annual temperature is -1.3 °C and mean annual precipitation is 700 mm, suggested by Environment Canada (2011). The park is a well known remote wilderness park with no exploitation of timber and was used by aboriginal people for fishing and animal hunting purposes until 1983 when the park was created (Beverly 1998, Peter et al. 1998). There are many water bodies which provide relatively cool summer and warm winter temperatures due to moderating lake effect of Lake Nipigon or Whitewater Lake (Figure 1). Elevation varies between 328 to 462 m above sea level (Soil Landscapes of Canada Working Group 2010). Sand, silt and clay are common in the park and the dominant soil orders are Brunisols and Podzols (Soil Landscapes of Canada Working Group 2010). The Brunisols are associated with glaciofluvial deposits which have rapid drainage, such as excessive to very

well-drained classes. But the Podzols are mostly located on morainal deposits with moderate drainage class (Soil Landscapes of Canada Working Group 2010). The forest is characterized by the following tree species: *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Populus balsamifera* (L.), *Betula papyrifera* March., *Picea mariana* (Mill) Britton, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill., and tamarack (*Larix laricina* (Du Roi) K. Koch).

4.3.2 Fire history

Fire history of the park was reconstructed by either utilizing existing fire data from Ontario fire history maps or by dendrochronological analyses. The fire data consist of fire dates, location and spatial extent of large fires (≥ 200 ha) since 1921. But, we only obtained fire records from 1964 to 2011 because of uncertainties associated with fire detection in the isolated and remote areas. Fires occurring in the period before 1964 were assessed by coring trees to determine the amount of time elapsed since the most recent fire.

The fire history reconstruction started with constructing a preliminary TSF map for the park in ArcGIS (ESRI, Redland, Canada); by using the fire dates from the available fire records. A systematic plan was used to sample the park after constructing the TSF map. The park was divided into hexagons of 40 km² each, resulting in a total of 292 hexagon sampling units of gapless network throughout the park (Figure 1). A total of 112 (38%) hexagons were assigned TSF based on known fire records for the period from 1964 to 2011. For hexagons burnt by multiple fires, the TSF was weighted based on the proportional areas burned by fire and the terrestrial land area within each hexagon.

4.3.3 Field sampling

A total of 180 remaining hexagons that required field sampling, we used tree ages to determine TSF. A transect of 200 m was laid and coring of dominant trees to the pith at the dbh (diameter at breast height, 1.3 m above root collar) was done from three dominant trees (Bergeron 1991, Senici et al. 2010). Canopy tree species of pioneers were given preference in selection based on their ability to regenerate immediately post fire (Bergeron and Brisson 1990). These trees were selected according to the following sequence: *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera*, and *Picea mariana* (Chen and Taylor 2012). The increment cores were all returned to the laboratory, placed under a dissecting microscope, and tree rings counted until an identical count was obtained in triplicate. From the tree ring counting, TSF was determined by adding 7, 8, and 17 years to *Pinus banksiana*, *Populus* sp. (or *Betula papyrifera*), and *Picea mariana*, respectively, allowing us to correct for underestimation of tree ages (Vasiliauskas and Chen 2002). In forest stand dominated by *Picea glauca*, *Thuja occidentalis* or *Abies Balsamea*, we assumed that trees of shade intolerant species present at the sites did not regenerate immediately post fire. In such cases, TSF for a hexagon corresponded to the age of the oldest tree sampled, which is considered as minimum age (i.e., censored observation) because the exact date of the last fire is unknown (Senici et al. 2010).

4.3.4 Explanatory variables

Spatially, fire frequency is influenced by soil texture, surficial deposits (coded as dummy variables), aspects, elevation, soil drainage, latitude and longitude (in decimal degrees) and distance (in meters) to fire breaks. The surficial deposits, aspects, elevation, soil drainage class were adapted from Soil and Landscape of Canada (Soil Landscapes of Canada Working

Group 2010), which comprise of all the key soils and their characteristics based on series of GIS coverage for the land of Canada. The soil types included clayey, sandy or loamy types, evaluated following protocol used in Ontario's forest inventories (Ontario Ministry of Natural Resources 2015). The distance to fire breaks was calculated as the mean distance to a water body, considered as any nearby river or lake from a randomly generated points during field sampling in each hexagon, measured in all cardinal directions and their intermediates represented on a 1:250000 topographic map (Cyr et al. 2007, Senici et al. 2010). To examine effect of aspect on fire frequency, we converted aspect into x and y coordinates. Each aspect class, north, north-east, east and south was positioned on a trigonometric circle of radius 1 and then centered at the origin where the angle is equivalent to azimuth of the dominant aspect of the slope, so that the horizontal axis corresponds to the west-east axis, whereas the vertical axis was represented by the south-north axis. The following coordinates represented each aspect class: north (0, 1), south (0, -1), east (1, 0), west (-1, 0), north-east (0.7071, 0.7071), south-east (0.7071, -0.7071), north-west (-0.7071, 0.7071), south-west (-0.7071, -0.7071) where $\sin(45^\circ) = \cos(45^\circ)$.

To understand climate-fire relationship, we derived long-term (1921-2011) climate estimates for the park, from BioSIM produced in Quebec, Canada, providing scale-free climate estimates that were derived based on latitude, longitude and elevation of plot within each hexagon (<https://cfs.nrcan.gc.ca/projects/133>). The climate estimates were used to calculate annual temperature (MAT), mean annual precipitation (MAP) and climate moisture index (CMI; mean annual precipitation - annual potential evapotranspiration) (Hogg 1997).

4.3.5 Statistical analyses

Fire frequency and fire cycle was estimated using several methods. The fire frequency (burn rate) means annual percent area burned and it is inversely related to fire cycle. The fire cycle is defined as the time required to burn a given area equal in size to that area. During 1964-2011 when fire records were available, fire cycle was estimated by dividing the total terrestrial land area (i.e., 768,000 ha) by the average annual area burnt in that time period (Heinselman 1973). The burn rate method of calculating fire cycle precludes us from estimating fire cycle prior to 1964. Thus, fire cycles for different time periods (including 1883-2011) were calculated to examine if fire cycle has remained constant over time, using survival analysis. Based on the survival analysis, we developed Cox regression model and then extracted cumulative fire hazards (i.e. the accumulation of hazard over time) with `coxph` and base hazard functions (Tsiatis 1978). The hazard function means instantaneous probability of fire frequency and is statistically equivalent to the fire frequency. From the accumulation of hazard over time, we estimated fire cycle by averaging all the hazard over a specified time period, so that the inverse of the hazard represented the fire cycle (Johnson and Gutsell 1994).

Survival analyses has unique strength for analyzing censored data (Allison 2011). The effect of environmental variables on fire frequency was tested by developing a suite of models, using Cox regression which is estimated by partial likelihood (Cox 1972). Cox regression analysis do not make any assumption that burning increases with stand age because baseline hazard of burning is derived from empirical TSF distribution (Allison 2011). We developed a Cox regression model, with climate and local site factors included in same model. We also developed 14 alternative models as subsets of the full model. We conducted Akaike

information criterion (AIC) analyses to evaluate model performance, selecting the model with smallest AIC as the most parsimonious model. From the best model, we tested the significance of each predictor with the base hazard function. That is, hazard ratios from the selected model was estimated as the percentage change in the hazard for every one-unit increase in a predictor (Allison 2011). To understand climate control on temporal changes in fire frequency, TSF was converted into decades, and the TSF for each decade determined. A cumulative function analyses with cumulative TSF as dependent variable, and TSF for each decade as a predictor was developed, so that we can estimate predicted values of cumulative TSF for entire park. This analysis was done using generalized linear model. The long-term climate data for MAT for the same period as the decadal fire data was used to examine the climate-fire relationship. We tested the association between cumulative TSF and MAT, using Kendall's Tau correlation. Statistical analysis was performed in R with survival package, using `coxph` and `basehaze` functions from the package (R Development Core Team 2015).

4.4 Results

The total area burnt from 1964 to 2011 was 105,515 ha, corresponding to about 12% of the landscape burnt. Fire burned an average of 2245 ± 644 ha (mean + 1 SD) per year, representing 0.29% of fires annually. The 1990s was the most active fire decade, whereas the 1960s was the least active decade (Fig 4.1). There was a fire cycle of 342 years for the 1964-2011 time period (Table 4.1).

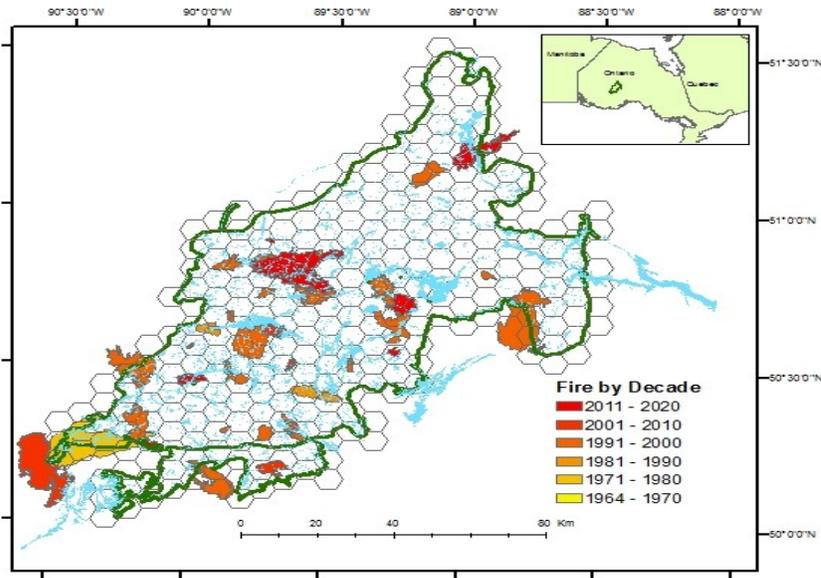


Fig. 4.1 Location of Wabakimi Provincial Park in the boreal forest of Ontario, Canada.

Table 4.1 Fire cycle calculation for Wabakimi Provincial Park in Ontario, Canada.

Method	Time period investigated	Fire cycle (years)
Burning rate	1964-2011	342
Inverse hazard	1964-2011	184 (178 - 190) ¹
	1883-2011	65(64 - 65)

¹95 % confidence interval in parentheses

By AIC, we found that the most parsimonious model was the one with MAT and MAP as predictors (Table 4.2). Fire frequency increase with spatial variation in MAT (Table 4.3). Spatially, fire frequency was influenced significantly by MAT and MAP, but MAT had a stronger effect than MAP (Table 4.3 and 4.4). The cumulative time since fire distribution in relation to TSF reveals that fire cycle has increased since the 1883-2011 period (Fig. 4.2). When TSF was converted into decades, cumulative time since fire distribution in relation to TSF showed that fire cycle has increased in the park (Fig.4.3). Further analyses of data reveals strong negative association between predicted cumulative time since fire distribution and temporal changes in MAT ($r = -0.36$, $P < 0.001$).

Table 4.2 Survival analyses results comparing different models

Model	AIC score
Mat	2025
Mat+Map	2016
Mat+Map+Cmi	2018
Mat+Map+Cmi+Distw	2020
Mat+Map+Cmi+Distw+Elev	2022
Mat+Map+Cmi+Distw+Elev+Lat	2022
Mat+Map+Cmi+Distw+Elev+Lat+Long	2024
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg	2023
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme	2023
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw	2025
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw+Db	2026
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw+Db+St	2034
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw+Db+St+Dra	2036
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw+Db+St+Dra+Xas	2038
Mat+Map+Cmi+Distw+Elev+Lat+Long+Dmg+Dme+Doutw+Db+St+Dra+Xas+Yas	2037

Mat, mean annual temperature (°C); Map, mean annual precipitation (mm); Cmi, climate moisture index (cm yr⁻¹); Distw, distance to waterbodies (m); Elev, elevation (m); Lat, latitude (decimal degrees); long, longitude (decimal degrees); Dmg, ground moraine, Dme, end moraine; Doutw, outwash deposit; Db, beach and aerolian deposit; St, soil texture; Dra; soil drainage class, Xas, west-east axis; Yas, north-south axis. Detail description for each predictor is provided in Table S4.1.

Table 4.3 Results from Cox proportional hazard model (n = 292) showing the effects of mean annual temperature (MAT) and precipitation (MAP) on fire frequency. The model with mean annual temperature and precipitation as predictors was better than other models based on Akaike information criterion (AIC).

Predictors	Fire frequency ratio	Final model	
		Prob > χ^2	AIC
MAT	2.711	<0.001	2016.14
MAP	0.896		

The χ^2 value is likelihood ratio test. As recommended by Allison (1995), the magnitude of effect associated with each predictor is calculated as: 100 (fire frequency ratio - 1) %. Hence, fire frequency ratio for MAT shows an increase in fire frequency with MAT.

Table 4.4 Results for partitioning of variance for each predictor

Predictors	Sum of square	F	P
MAT	21080	15.26	<0.001
MAP	17954	12.99	<0.001

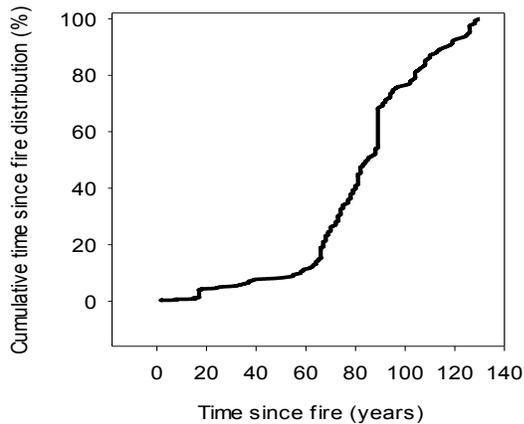


Fig. 4.2 Time since fire distribution for Wabakimi Provincial Park in northwestern Ontario, Canada.

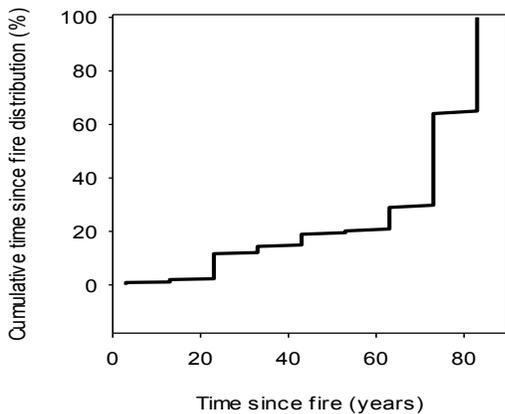


Fig. 4.3 Time since fire distribution for fires grouped into decades in Wabakimi Provincial Park, Canada.

4.5 Discussion

Our findings indicate that across a large natural boreal forest, spatial variation in climate drives fire frequency. The result indicates that MAT is one of the most important predictors of fire frequency, which is consistent with predictions for increase temperature-driven fire frequency among different locations in the North American boreal forest (Wotton et al. 2010, Parisien et al. 2011). Previous studies showed that fire frequency varies spatially due to soil

orders (Senici et al. 2010) and elevation (Cyr et al. 2007), but spatial variation in climate has often been overlooked. In contrast, we simultaneously examined spatial variation in climate and several environmental factors, and found that fire frequency is controlled primarily by broad-scale climatic factors. The result showed that temporal variation in wildfire frequency positively correlated with MAT. Strong positive correlation between wildfire frequency and mean spring or summer temperature has also been reported by Westerling et al. (2006). In spite of progress on climate-fire relationship, cause-and-effect relationship was not considered, because the study which was conducted in fragmented forest makes it difficult to separate contribution of climate to large fires from human activities. However, we studied a natural forest landscape with relatively little human influences; as such we have demonstrated that fire frequency is caused by MAT.

MAP is another important factor controlling fire frequency in the boreal forest. The result supports previous study by Whitman et al. (2015), who showed that forest fire regimes are strongly dependent on summer precipitation. There is growing recognition that fire regimes can vary significantly across the boreal forest of North America because of differences in the amount and frequency of precipitation (Amiro et al. 2004, Girardin et al. 2004). For instance, considerable change in forest area burn in British Columbia has been attributed to increases in amount of precipitation (Girardin and Wotton 2009, Meyn et al. 2013).

Our study revealed that fire cycle increased significantly over the 1883-2011 time period. The temporal increase in fire cycle is in agreement with Bergeron et al. (2004) who showed that fire cycle increased temporally in Quebec. However, fire cycle has decreased temporally in other forest of northwestern Ontario (Senici et al. 2010), but the causes of that

change are unclear. On the other hand, the temporal pattern of increasing fire cycle in our study is explained by MAT. For example, our result showed that the decade of 1990 experienced the greatest area burned in the park. In northwestern Minnesota with similar climate, fire activity also increased markedly during the 1900s, primarily due to exceptionally warm and dry conditions (Clark 1988).

Our result showed differences in fire cycle calculations between the burn rate and survival analysis method for the same time period, as reported in previous study. We speculate that the discrepancy in fire cycle is likely due to fire occurrences which were missed when creating fire maps for the park, thereby leading to a longer fire cycle using the burn rate method.

Because of the strong linkage between temporal variation in climate and fire regime, changes in climate can be a major challenge for forest management (Girardin et al. 2013). For instance, any extreme temperature experienced in the boreal forest region could increase the risk of wildfire (Beverly and Martell 2005, Jolly et al. 2015), unless it's compensated for by increase in precipitation. The longer fire cycle we observed can also lead to a potential shift towards older forest stands, affecting tree growth and mortality (Bond-Lamberty et al. 2014). As fire cycle is lengthening in the boreal forest of North America, future outbreaks of forest insects and expansion in range could render the boreal forest of North America vulnerable to extensive insect damage (Pureswaran et al. 2015).

4.6 Conclusion

We have demonstrated that fire cycle increased temporally in the natural boreal forest we studied. The increase in fire cycle was driven primarily by changes in mean annual temperature and precipitation. Additionally, spatial variation in climate was a primary driver

of fire frequency. Within the same central boreal region, the different temporal patterns of fire frequency between our natural forest and others fragmented by human activities suggest that control on fire regimes is dependent on forest type, with climate effects on fire regimes more important for the landscape we studied than the influences of local environmental factors.

CHAPTER 5: TEMPORAL STABILITY OF BOREAL FOREST STANDS ARE NOT INFLUENCED BY TREE SPECIES DIVERSITY

5.1 Abstract

Disturbances are common in boreal forest, in particular non-stand-replacing insect outbreaks, which may affect stability of ecosystem functions in response to such disturbances. Empirical evidence in manipulated grassland experiments often shows a positive relationship between species diversity and ecosystem stability. However, it remains unclear whether the effect of diversity in grassland is applicable to natural forest ecosystems where the influences of critical factors such as stand development, species composition and soil resource availability on diversity-stability relationship are often overlooked. We test if the variability (measured as coefficient of variation, CV) in stand level basal area in response to the insect outbreaks is influenced by tree species richness, evenness, stand age, species-specific compositions (e.g., *Populus* sp. or *Betula papyrifera* *Betula*, and *Picea glauca* or *Abies balsamea* basal area proportions) and soil moisture regime. We hypothesized that increase species diversity (measured as species richness or evenness) decreases variability in stand level basal area, because many randomly and independently varying species contribute to total abundance of plants, such that adding more species result in more averaging of their fluctuations and hence less variation in total abundance, as suggested by theory of statistical averaging.

Alternatively, we expect that increase species richness has no effect, but rather species composition and changes in abundance of particular species affect the variance. We used repeated measurements plots data to assess the variation in stand level basal area in responses to spruce budworm (SBW) and forest tent caterpillar (FTC) outbreaks, which selectively kill

trees in the boreal forest of Canada. Models were developed separately for SBW and FTC, using generalized linear model. We performed a multiple regression model, with tree species richness, evenness, stand age and soil moisture regime considered as predictors in the same model. We also developed alternative models by adding a quadratic term for stand age to the predictors. We conducted Akaike information criterion (AIC) analyses, selecting the model with smallest AIC as most parsimonious model. We found that tree species richness had no effect on the CV for stand level basal in responses neither to SBW nor FTC. In both models for SBW and FTC, cubic model performed better than other models. Variability in stand basal area decreased initially, i.e., up to about 100 years, increased sharply in older stands, and then slightly increased in the oldest stands. The most important factors influencing variation in stand level basal area in response to SBW were composition of *Abies balsamea* and the stand age. Our results suggest that in disturbance-driven forests, temporal stability of ecosystem is driven by stand development and species composition, depending on the disturbance agent.

5.2 Introduction

Understanding the relationship between species diversity and ecosystem stability has been the subject of much debate over the past several decades (MacArthur 1955, May 1973, Tilman et al. 2006, Isbell et al. 2015). However, there is now growing consensus that increasing species richness leads to greater temporal stability of ecosystem functions in grasslands (Tilman et al. 2006, Gross et al. 2014). Similarly, Isbell et al. (2015) who combined data from 46 experiments in grasslands showed strong evidence in support of positive diversity-stability relationships (DSR).

Nonetheless, whether the diversity effects reported in manipulated grassland experiment is applicable to natural forest ecosystems remains unclear (Grossiord et al. 2014).

One reason is that plant species in herb-dominated grasslands change rapidly in relative abundance among years, whereas shift in community composition occur much slower in forest typically associated with long-lived trees; such differences may contribute to the outcomes of testing the DSR (Huston 1997). Furthermore, abundance of a particular species strongly influence ecosystems functions rather than species richness (Winfree et al. 2015). Failing to consider the influence of plant species abundances may contribute to the disparities in the DSR. Even though ecosystem stability is only improved by diversity when evenness is high (Hillebrand et al. 2008), species evenness-stability relationship is often overlooked and thus limit understanding on DSR in previous studies. Thirdly, forest ecosystem stability is strongly influenced by stand development, but substantially fewer studies consider stand age effect on DSR. For example, Dovciak and Halpern (2010) found a positive linear effect of stand age on DSR for forest stands up to forty years. However, the stand stage effect on DSR over longer period (i.e., in stands > 40 years old) is unknown. Such information is important because during stand development the abundance of slow-growing coniferous species increases with stand age as fast-growing deciduous species decreases (Chen and Taylor 2012), which potentially influences DSR. Another challenge about DSR is that soil resource availability is rarely considered (Huston 1997). Some studies have partly resolved the problem by directly controlling soil moisture levels, suggesting that soil moisture levels contributes significantly to DSR (Xu et al. 2014). Understanding the effect of soil resource availability on DSR is of critical importance because of a wide range of variation in soil resource availability, which could influence functions in natural ecosystems (Zhang and Chen 2015).

Understanding DSR in forest ecosystems is crucial because societies around the world utilize forest for animal hunting, industrial wood production and other ecosystem functions (e.g., global carbon cycle). Because of these benefits, we urgently need to improve our understanding concerning how forest ecosystem may respond to potential changes in disturbance regimes, such as increasing incidence of insect outbreaks associated with global climate change (Percy et al. 2002, Boyd et al. 2013, Gray 2013). Insect outbreaks have tremendous influences on forest ecosystems, affecting about three times greater the area of fire in the North American boreal forest (<https://www.ontario.ca/page/annual-report-forest-management-2012-2013>). Spruce budworm and forest tent caterpillar outbreaks are the significant insect pests, which selectively kill *Abies balsamea* and *Populus* sp., respectively. Potential increases in such insect outbreaks and range expansion could have profound consequences on tree mortality and major losses of merchantable timber (Hennigar and MacLean 2010).

Temporal stability in plant species abundances, measured as coefficient of variation, (CV), decreases with increasing species diversity (Tilman 1996, DeClerck et al. 2006). A major theory explaining why multiple species are stable is the statistical averaging or portfolio effect, which states that if abundances of different species (each varies randomly and independently through time) contribute to total abundance of plants, then adding more species together leads to more averaging of their fluctuations and hence less variation in total abundance (Doak et al. 1998, Tilman et al. 1998). The stability of forest ecosystem functions in response to non-stand-replacing disturbance is important because majority of disturbances in global forests are non-stand replacing (Edwards and Laurance 2013), especially in Canada's boreal forest (Natural Resource Canada 2014). Our objective is to test whether CV

of stand basal area relates to tree species richness, evenness, stand development, species composition and soil resource availability. We hypothesize that CV of forest stand basal area will decrease with increase species richness, suggested the theory of statistical averaging (Doak et al. 1998). Alternative hypothesis is that species richness has no effect on CV of stand basal area, but rather species composition and changes in abundance of particular species which are most vulnerable to insect outbreaks (i.e., *Populus* sp. *Betula papyrifera*, *Abies balsamea*) drives the ecosystem function (Winfrey et al. 2015). We expect that increase in tree species evenness will decrease CV of forest stand basal area because different species contribute evenly to stand basal area. We predict that the shape of the relationship between CV for stand basal area and stand stage might be nonlinear if forest succession is ≥ 40 years, because fast growing shade intolerant species will be replaced by slow-growing late successional species (Chen and Taylor 2012). We also hypothesize that CV of stand basal area will decrease on moist and wet sites than drier sites because of higher mortality of coniferous trees such as *Abies balsamea* on drier sites than moist and wet sites (Dupont et al. 1991).

5.3 Materials and methods

5.3.1 Study area

The study was conducted in northern Ontario, where annual mean temperature is about 1.3 °C and annual mean precipitation is roughly 831 mm (Environment Canada 2011). Dominant tree species in the area include: *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* March., *Picea mariana* (Mill) Britton, *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill. The predominant natural disturbance in the area include wildfire, spruce budworm (*Choristoneura fumiferana*), forest tent caterpillar (*Malacosoma disstria*), and

windthrow, which typically affect most boreal forests in Canada (Bergeron et al. 2001, Fleming et al. 2002, Bouchard et al. 2006).

5.3.2 Sampling strategy

Stratified random sampling was utilized to select a wide range of stand compositions, ages, and site conditions based on Forest Resource Inventory by Ontario Ministry of Natural Resources (OMNR). We also acquired insect infestation maps for Ontario from Forest Insect and Disease Survey conducted using aerial photos taken annually since 1941 by Canadian Forest Service. Our study focused on sampling stands affected only by non-stand-replacing insect disturbance, which selectively kill trees in boreal forests (Maclean 1984, Cooke and Roland 2007). Disturbance by SBW and FTC were described as non-stand-replacing disturbance where up to 60 % stand basal area destroyed (Schweitzer and Dey 2011, Taylor and Chen 2011). As reported by Chen and Taylor (2012), each sampled stand was re-measured by combining ground survey and aerial photo interpretation measurement, yielding a total of 78 repeated measurements plots for the insect outbreak disturbances. Each sampled stand for our dataset was re-measured multiple times, ranging from three to six times (Chen and Taylor 2012). For each of the sampled stand, the re-measurement time interval varied among plots, over 14 to about 20 years. This time interval involves both the ground survey and the aerial photo interpretation measurement. During field data collection, a 200 m transect was laid in each sampled stand and 10 variable-radius point samples taken at 20 m apart using wedge prism with basal area factor two. Then, all living tree stems ≥ 10 cm at breast height were tallied by tree species and used to determine tree species composition based on species-specific stand basal area proportions (Avery and Burkhart 2002). In each 200 m transect, three trees were selected, with dbh, heights and ages measured. The heights

and ages of the tree samples were used to determine site index (Chen et al. 2002). Priority in sampling was given to pioneer tree species because of their ability to colonized immediately after fire (Bergeron and Brisson 1990). The sampling was prioritized according to these sequence; *Pinus Banksiana*, *Populus tremuloides*, *Betula papyrifera*, and *Picea Mariana*. Stand age was determined in the field by coring the tree samples to the pith at the dbh to extract one increment core from each of the sampled trees.

Aerial photos were taken for the sample stands and interpreted by a qualified photogrammetry technician. To interpret each sampled stand on the photo, every effort was made to precisely locate the ground survey transect line on the photo. Stand composition from aerial photos were quantified from crown cover of individual species by using a rectangular plot of 2 ha (100×200 m) located on the transect line. The following factors such as site index derived from ground survey, crown closure from photo interpretation, stand age and the proportion of individual species were combined to determine stand basal area from the photo interpretation.

5.3.3 Dependent and independent variables

The dependent variable was the CV for stand basal area, a standardized variable which allowed us to compare plots having large differences in average basal area due to different census intervals (Tilman 1996, Morin et al. 2014). As described in Taylor et al. (2000), soil moisture regime (SMR) was used as indicator of soil resource availability. The SMR is considered as a composite variable which consist of several factors including soil texture, soil thickness, and depth of water table, topographic position, and soil permeability classification (Chen et al. 1998, Chen et al. 2002). SMR was determined on site involving soil pit excavations. SMR was ranked from 1 to 3, meaning dry, moist and wet sites.

Overstory tree species richness was determined from the number of species observed in each sample plot. Other indices of diversity such as species evenness (i.e., inverse of Simpson's dominance index) were determined using the basal area proportions of the constituent species. The evenness index is considered to be independent of species richness and a preferred index over Shannon's index (Smith and Wilson 1996). Stand composition was determined by the percentage basal area of the constituent species including *Populus* sp., *Betula papyrifera*, *Picea glauca* and *Abies balsamea*.

Tree ring counting was used to determine TSF (i.e., stand age) or by using fire date from Ontario fire history maps which provide record of all fires ≥ 200 ha since 1921. Using the fire date to determine TSF could potentially be inaccurate due to residual stands that escape fire and small fire < 200 ha. Field validation was thus performed for all sampled stands by coring the three tree samples to the pith at the dbh (diameter at breast height, 1.3 m above root collar). In the event where discrepancy occurs in TSF between fire date and the ring counting, the TSF from the ring counting was used for analyses. TSF for all stands originated before 1921 was determined from tree ring counts. All cores were sent back to the laboratory and the rings counted with hand held magnifier until the same count was obtained three times. The following corrections were made to tree ages from ring count by adding 7 years to the ages at diameter at breast height (dbh) if stand was dominated by *Populus* sp. or *Betula papyrifera*, 8 years if dominated by *Pinus Banksiana*, 17 years if dominated by *Picea Mariana* or other shade tolerant species, based on empirical model developed specifically for our region (Vasiliauskas and Chen 2002).

5.3.4 Statistical analysis

We tested the effects of species richness, evenness, stand age, stand composition, and SMR on the temporal stability, using GLM. We performed a multiple regression model including all variables, with richness and evenness considered in the same model. Gaussian distribution was assigned in the GLM (Zuur et al. 2009). We also developed alternative models by adding a quadratic term for stand age to the predictors. Further analyses of data included interaction terms in the model, but were removed in the final model because none was significant. Model performance was evaluated by conducting Akaike information criterion (AIC) analyses, selecting the model with smallest AIC as most parsimonious model. Because disturbance by SBW and FTC selectively kill *Picea mariana* and *Populus tremuloides*, models were developed separately for SBW and FTC insect outbreaks. Stand age is often related to species richness; thus, we assessed potential correlation among predictors, using Spearman's rho correlation. There was significant correlation between stand age and species richness ($P < 0.05$). This problem can be resolved using different approaches. Firstly, we included all predictors in one model without assigning priorities. Secondly, we use residual and sequential regression by assigning priority to one predictor, and then modeling the effect of the other predictor on the residual (Graham 2003). Lastly, we reversed the priority in the second approach. There was no logical or theoretical basis for prioritizing one variable over the other, and thus included all important variables in our analysis, as in previous study (Chen and Luo 2015). Assigning priority to stand age would marginalize richness effect, whereas stand age would be marginalized if we consider richness as a priority, thereby leading to spurious conclusions (Brown et al. 2011).

5.4 Results

The final models for SBW and FTC explained 45 and 28% variation in CV of stand basal area, respectively (Table 5.1). The cubic model was better than quadratic one in the model for SBW (Supplementary Table S5.2). Species richness was unrelated to CV for stand basal area in all models (Fig. 5.1). Stand age and abundance of *Abies balsamea* significantly influence CV for stand basal area in response to SBW. Temporal stability of stand basal area increased initially, i.e., stands age up to about 100 years, and decreased in stand ages > 100 (Fig. 5.2). There was a positive linear relationship between CV for stand basal area and composition of *Abies balsamea* (Fig. 5.3).

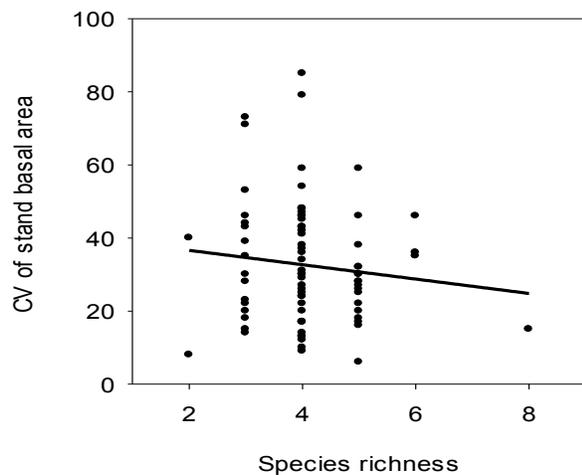


Fig. 5.1. Effect of tree species richness on coefficient of variation (CV) for stand basal area in response to spruce budworm outbreaks in the boreal forest of Canada. The fitted line is linear ($r^2 = 0.01$, $p = 0.32$).

Table 5.1 Regression results for spruce budworm outbreak ($n = 78$) in the boreal forest of Ontario, Canada.

Predictor	Estimate	P-value	R ²	AIC
Intercept	69.700000	<0.001	0.45	549
Richness	-2.634000	0.372		
Evenness	-5.876000	0.803		

<i>Abies</i>		
<i>balsamea</i>	0.483000	<0.001
<i>Picea glauca</i>	0.253600	0.305
Moist sites	-6.723000	0.087
Wet sites	0.510700	0.947
Stand age	-0.681700	0.027
Stand age ²	0.003479	0.047
Stand age ³	-0.000005	0.102

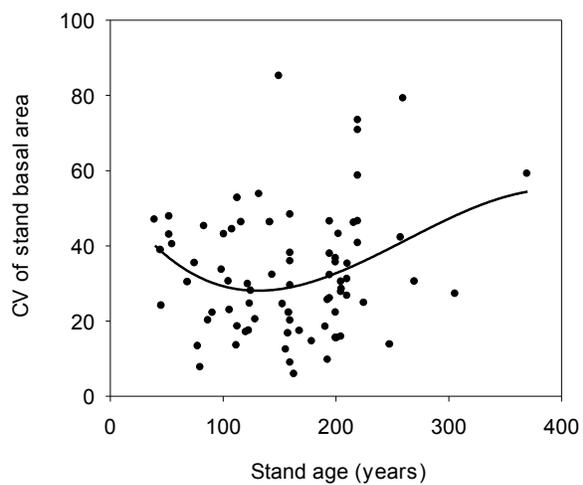


Fig. 5.2. Stand age effect on coefficient of variation (CV) for stand basal area in response to spruce budworm outbreaks in the boreal forest of Canada. The fitted line is in cubic form ($r^2 = 0.08$, $p = 0.08$).

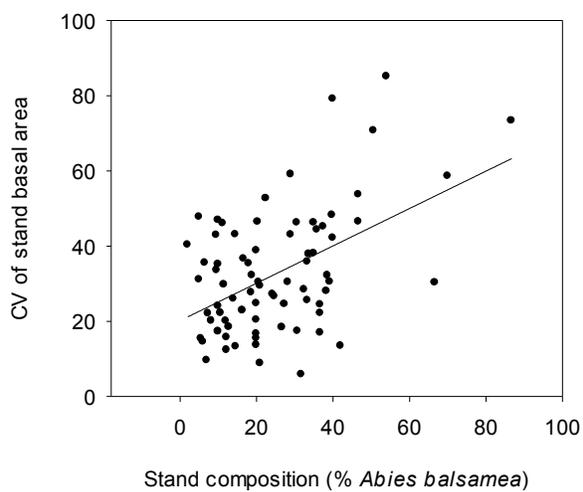


Fig. 5.3 Effects of composition of *Abies balsamea* on coefficient of variation (CV) for stand basal in response to disturbance by spruce budworm outbreak. The fitted line is linear ($r^2 = 0.24$, $p < 0.001$).

In the model for FTC, the cubic model also performed better than other models (Table 5.2; Supplementary Table S5.2). Temporal stability of stand basal area increased initially, i.e., stands age up to 100 years, decreased sharply in the older stands, i.e., stand age > 100, followed by a slight decrease in the oldest stands (Fig. 5.3). There was no significant effect of SMR on CV of stand basal area.

Table 5.2 Results of regression models for disturbance by forest tent caterpillar (n = 78) in the boreal forest of Canada.

Predictor	Estimate	Standard error	P-value	R ²	AIC
Intercept	99.760	22.940	<0.001	0.28	542
Richness	-5.170	3.857	0.185		
Evenness	8.767	20.830	0.675		
<i>Populus</i> spp.	-0.115	0.097	0.241		
<i>Betula papyrifera</i>	0.178	0.144	0.220		
Stand age	-1.630	0.543	0.004		
Stand age ²	0.012	0.005	0.019		
Stand age ³	0.000	0.000	0.059		

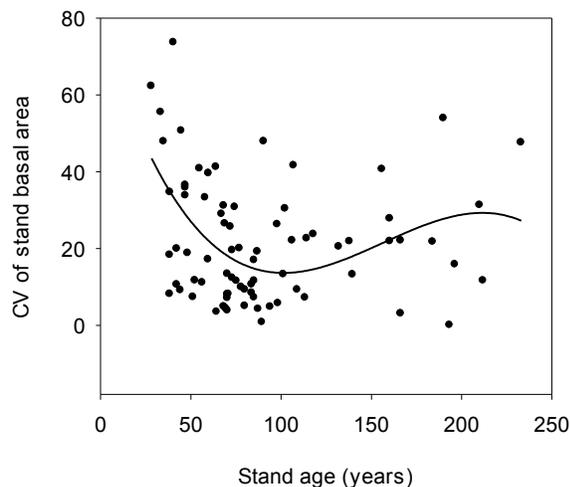


Fig. 5.3. Effects of stand age on coefficient of variation (CV) of stand basal area for the disturbance by forest tent caterpillar in the boreal forest of Canada. The fitted line is in cubic form ($r^2 = 0.21$, $p < 0.001$).

5.5 Discussion

We have shown that in forest ecosystem overstory tree species richness and species evenness are not the primary drivers of ecosystem stability, contrary to the prediction of statistical averaging (Doak et al. 1998). However, a study in grassland reported that species richness strongly stabilizes ecosystem stability (Isbell et al. 2015). Other empirical studies have also shown that temporal stability increased with species richness (Tilman 1996, Jucker et al. 2014, Morin et al. 2014). The disparity in the results is because of failing to account for effects of critical drivers of ecosystem stability such as species composition and stand age, which can override species richness effect on ecosystem stability. The stabilizing effect of diversity on ecosystem stability as reported in grasslands is often based on the assumption that species composition is flexible among years, but slower compositional change over time in structurally complex forests could lead to differences in DSR between grasslands and forests. Our observation that DSR was not affected by tree species richness complement results by other studies who showed that species richness does not necessarily influence DSR in all forests (DeClerck et al. 2006, Grossiord et al. 2014).

A major finding from our research is that composition of *Abies balsamea* strongly influences stability of stand basal area in response to SBW. Our result is consistent with previous studies that showed that ecosystem stability is dependent on how presence of plant life history traits responds to disturbance (Johnson et al. 1996, Tilman et al. 2006). For instance *Abies balsamea* often experience mortality more than *Picea glauca* during SBW outbreaks (Nealis and Regniere 2004), which explains why *Abies balsamea* increase in

percentage abundance leads to reduce stability of stand basal area. The positive linear relationship between CV for stand basal area and composition of *Abies balsamea* confirms that the life history traits are good predictors of ecosystem response to global changes including insect disturbance.

We have demonstrated that stand age plays a critical role in influencing DSR, a consistent observation regardless of the type of insect outbreak. The quadratic relationship between CV for stand basal area and stand stage support our hypothesis. SBW outbreak selectively kills host-tree species such as *Picea glauca*. and *Abies balsamea*, reducing tree growth during insect outbreak while allowing non-host tree species (e.g., *Populus* sp.) abundances to increase following the outbreak (Nealis and Regniere 2004). Our result for FTC outbreak indicates a positive effect of stand age on DSR during the initial stand development. In contrast, a negative effect of stand age on DSR was found in older communities. This result could be attributed to significant increase in growth rate of early successional species in young stands (Caspersen and Pacala 2001, Rozendaal and Kobe 2014). The trend in DSR for the older stands is probably due to selective killing of broadleaves (e.g. *Betula* sp.) by FTC (Cooke and Roland 2007), allowing dominance of competing shade-tolerant and slow-growing conifers (Moulinier et al. 2013), resulting in the decreased in stability of stand basal area in the older stands.

The result for FTC outbreak also showed that stability of stand basal area decreased slightly in the oldest stands. We speculate that in the oldest stands, especially in the old growth stage of stand development, tree mortality usually intensifies due to ageing and insect outbreaks which takes time before eventually killing heavily defoliated broadleaf trees (Chen and Popadiouk 2002, Moulinier et al. 2013). As a result, small gaps develops in the forest

canopy which improves light availability that favors release and recruitment of advance regeneration of coniferous from subcanopy into the overstory canopy (Kneeshaw and Bergeron 1998, Moulinier et al. 2011), leading to a marginal decrease in temporal stability of stand level basal area in the oldest stands.

Disturbance regimes are being modified by global climate change with expected changes in incidence of insect outbreaks (Percy et al. 2002), together with human domination of Earth's ecosystems lead to drastic changes with profound losses in biodiversity, potentially affecting services that human derive from ecosystems (Vitousek et al. 1997, Chapin et al. 2000). The result for SBW is much needed for long-term forest management planning purposes due to ongoing range expansion and increases in SBW outbreaks in Canadian forests (Pureswaran et al. 2015).

5.6 Conclusion

In summary, our findings showed that temporal stability of stand level basal area was not directly related to overstory tree species diversity. Species composition and stand stage were the most important factors influencing variation in stand level basal area in response to SBW. Additionally, stand age influenced variation in stand level basal area in response to FTC. Our findings suggest that temporal stability of ecosystem functions in boreal forest is influenced by stand development and species composition depending on the type of insect outbreak.

CHAPTER 6: GENERAL CONCLUSION

This study provides evidence that there is a strong interactive effect between frequency of disturbance and disturbance intensity, suggesting that the relationship between species richness and disturbance frequency depends on disturbance intensity. Tree species richness peaked at intermediate frequency of disturbance following both high and intermediate disturbance intensity. These findings indicate that the IDH is a universal hypothesis that can be applied as a predictive model for the protection and conservation of plant species diversity when disturbance frequency with intermediate intensity of disturbance is manipulated in forest management practices in tropical and temperate biomes.

Nonetheless, the IDH was not supported in the natural boreal forest landscape, in that both positive and negative patterns of diversity were observed for overstory trees species following time since fire. Time since fire and local site conditions were rather the two greatest drivers of tree species diversity, implying that both are essential for maintaining biodiversity in the North American boreal forest. The result also revealed that through time since fire, local site conditions indirectly influenced tree species diversity. This evidence reflects the critical role of local site condition in influencing plant coexistence which cannot be overlooked in predictive models because forest managers are likely to deal with a wide range of site conditions, especially in the boreal forest which is associated with heterogeneous landscape. Although the analysis adequately explain patterns of diversity and disturbance relationships for tree species alone, it is likely that other plant types such as understory layer would respond differently. Therefore, future research into diversity patterns should focus on the understory layer.

The study highlighted that complex interacting mechanisms could drive patterns of diversity and disturbance relationships in the natural forest. For instance, local site conditions and mean annual temperature had strong direct effect on TSF, while through TSF; mean annual temperature indirectly influenced species richness and evenness. This result is useful for explaining why simplistic theories of species coexistence (e.g., IDH), seem to fail empirically, because multiple environmental factors often act simultaneously in maintaining plant species coexistence, especially in natural forest ecosystems.

Furthermore, changes in mean annual temperature and precipitation were the two principal regulators of fire frequency in the studied boreal forest, despite controlling for several local environmental factors. Implying that climate control on fire regimes overrides effects of local site factors. Fire cycle increased substantially over the 1883-2011 time period, attributed to the influences of climatic factors in the large natural boreal forest.

My research also revealed that in the boreal forest of North America, temporal stability of stand basal area was unaffected by tree species diversity. The composition of *Abies balsamea* strongly influenced temporal stability of stand basal area in response to SBW. As a result, future increase in basal area proportion of *Abies balsamea* would lead to extensive damage of forest stands during SBW outbreaks; therefore, these stands should be identified and selected for early preventative harvesting.

Finally, temporal stability of stand basal area was strongly influenced by stand development in response to SBW and FTC outbreaks. The evidence also showed that stand age up to about 100 years generally provides greater ecosystem stability in response insect outbreaks than older forest stands. Therefore, the shift towards older forest stands from longer fire cycle poses threat to the boreal forest of North America during insect outbreaks, except

where younger forest stands predominate the landscape. During such outbreaks, management interventions should aim at selecting older stands for salvage logging to reduce the vulnerability of stands to the insect outbreaks, which could also serve as source of revenue generation for forest landowners.

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APPENDIX I. SUPPLEMENTAL INFORMATION FOR CHAPTER 2

Table S2.1 Original source of data used in the meta-analysis.

Author	Title	Source
Aweto 1981	Secondary succession and soil fertility restoration in south-western Nigeria: I. succession	Journal of Ecology
Berry et al 2008	Impacts of selective logging on tree diversity across a rainforest landscape: the importance of spatial scale	Landscape Ecology Proceedings of the National Academy of Sciences of the United States of America
Brown and Gurevitch 2004	Long-term impacts of logging on forest diversity in Madagascar	Forest Ecology and Management
Capitanio and Carcailler 2008	Post-fire Mediterranean vegetation dynamics and diversity: a discussion of succession models	Journal of Ecology
Carreno-Rocabado et al 2012	Effects of disturbance intensity on species and functional diversity in a tropical forest	ProQuest and Information and Learning Company
Dickson 2009	Secondary diversity: ecological and spectral dimensions of secondary succession following smallholder cultivation in the southern Yucatan	Biological Conservation
Ding et al 2012	Recovery of woody plant diversity in tropical rain forests in southern China after logging and shifting cultivation	Forest Ecology and Management
Dolanc et al 2003	The effects of silvicultural thinning on trees regenerating in strip clear-cuts in the Peruvian Amazon	Applied Vegetation Science
Ehrensperger et al 2013	Fire impact on the woody plant components of dry deciduous forest in Central Menabe, Madagascar	Biodiversity and Conservation
Gemerden 2003	Recovery of conservation values in Central African rain forest after logging and shifting cultivation	Biodiversity and Conservation
Howorth and Pendry 2006	Post-cultivation secondary succession in a Venezuelan lower montane rain forest	Plant Ecology
Imai et al 2012	Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales	Plant Ecology
Ito 1997	Diversity of forest tree species in Yanbaru, the northern part of Okinawa island	Forest Ecology and Management
Jenkins and	Composition and diversity of woody	

Parker 1998	vegetation in silvicultural openings of southern Indiana forests	Management
Kapelle et al 1995	Changes in diversity along a successional gradient in a Costa Rican upper montane quercus forest	Biodiversity and Conservation
Kapelle et al 1996	Successional age and forest structure in a Costa Rican upper montane quercus forest	Journal of Tropical Ecology
Klanderud et al 2010	Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar	Biodiversity and Conservation
Makana and Thomas 2006	Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo	Biodiversity and Conservation
Mandle 2012	Balancing biodiversity and human land use: effects of fire, grazing and harvest on plant individuals, populations and communities in the western Ghats, India	ProQuest and Information and Learning Company
Mo et al 2011	Traditional forest management has limited impact on plant diversity and composition in a tropical seasonal rainforest in SW China	Biological Conservation
Pascarella et al 2000	Short-term response of secondary forests to hurricane disturbance in Puerto Rico, USA	Ecosystems
Peet 1981	Forest vegetation of the Colorado front range	Vegetatio
Rivera et al 2000	Forest recovery in abandoned agricultural lands in a Karst region of the Dominican Republic	Plant Ecology
Saldarriaga 1988	Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela	Journal of Ecology
Schnitzer and Carson 2001	Treefall gaps and the maintenance of species diversity in a tropical forest	Ecology
Shono et al 2006	Regeneration of native plant species in restored forests on degraded lands in Singapore	Forest Ecology and Management
Slik et al 2002	Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in east Kalimantan, Indonesia	Biodiversity and Conservation
Tang et al 2013	Plant diversity patterns in subtropical evergreen broad-leaved forests of Yunnan and Taiwan	Ecological Research
Toniato and Oliveira-Filho 2004	Variations in tree community composition and structure in a fragment of tropical semi deciduous forest in southeastern Brazil related	Forest Ecology and Management

	to different human disturbance histories	
	Indigenous livelihood systems in industrial tree-plantation areas in west Kalimantan, Indonesia: Economics and plant-species richness	Agroforest Systems
Tyynela et al 2003		
Uhl and Jordan 1984	Succession and nutrient dynamics following forest cutting and burning in Amazonia	Ecology
Uhl et al. 1988	Abandoned pastures in eastern Amazonia. i. patterns of plant succession	Journal of Ecology
Uriate et al 2004	Effects of land use history on hurricane damage and recovery in a neotropical forest	Plant Ecology
Villela et al 2005	Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic forest	Journal of Biogeography
Wardle et al 2008	The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences	Oikos
Weimin Xi 2005	Forest response to natural disturbance: changes in structure and diversity on a North Carolina piedmont forest in response to catastrophic wind events	ProQuest and Information and Learning Company
Whitfeld 2011	Phylogenetic diversity, functional traits, and tropical forest succession	ProQuest and Information and Learning Company
Woods 1989	Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia	Biotropica
Wu et al 2013	Early response of stand structure and species diversity to strip-clearcut in a subtropical evergreen broad-leaved forest in Okinawa Island, Japan	Annals of Forest Science
Zhang and Zang 2011	Relationship between species richness of plant functional groups and landscape patterns in a tropical forest of Hainan Island, China	Journal of Tropical Forest Science
Zhu et al 2009	Changes in plant species diversity along a chronosequence of vegetation restoration in the humid evergreen broad-leaved forest in the rainy zone of west China	Ecological Research

APPENDIX II. SUPPLEMENTAL INFORMATION FOR CHAPTER 3

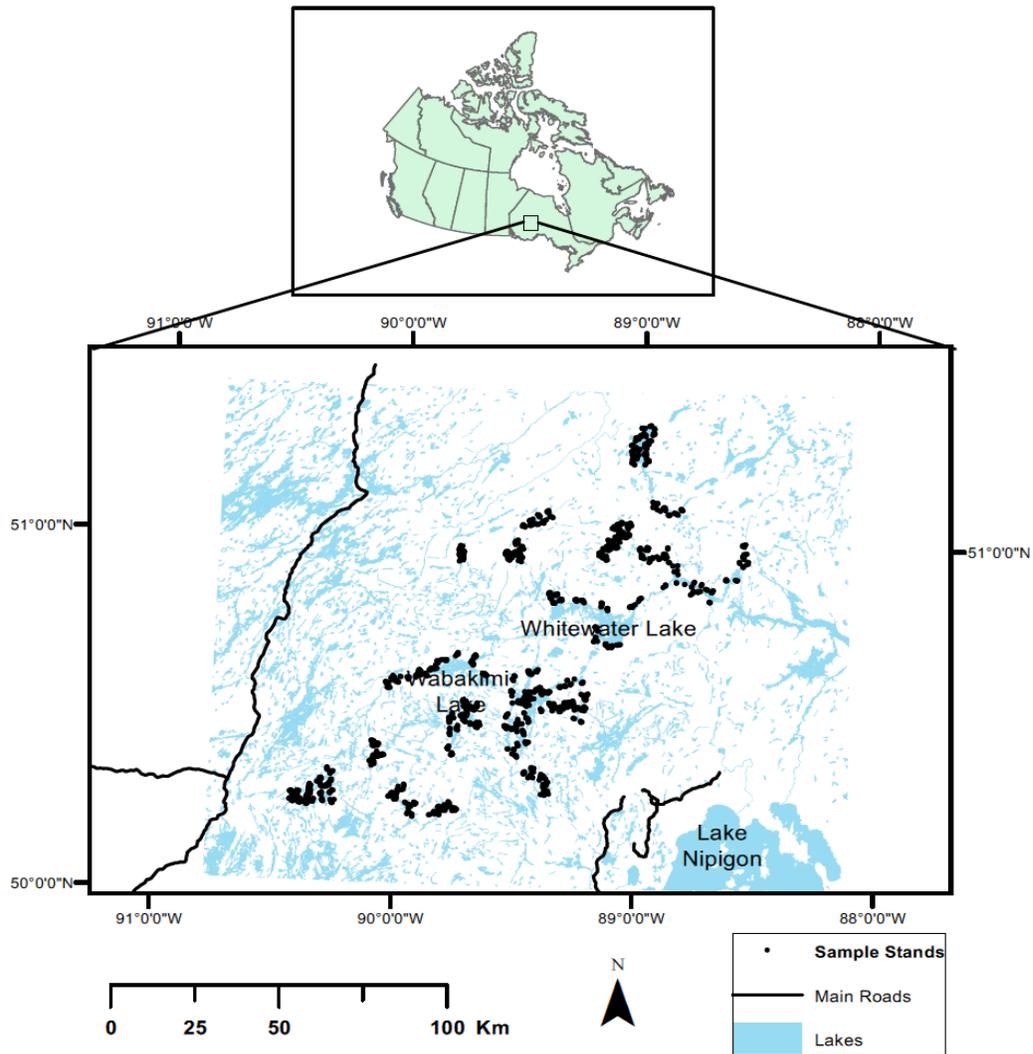


Fig. S3.1. The study plots ($n = 1018$) located in northwestern Ontario, Canada.

Table S3.1 Characteristics of study plots sampled ($n = 1018$) in the Wabakimi Provincial Park of Canada.

Characteristic	Mean	Minimum	Maximum
Species richness	3.14	2	8
Shannon's index	0.66	0.05	1.80
Species evenness	0.61	0.20	0.99
TSF*	89.00	20	209
MAT	-0.29	-0.83	0.42
MAP	711.40	701.0	724.8
SDC	1	0	9

*TSF, time since fire (years); MAT, mean annual temperature (°C); SDC, soil drainage class (median is reported instead of mean), MAP, mean annual precipitation (mm).

APPENDIX III. SUPPLEMENTAL INFORMATION FOR CHAPTER 4

Table S4.1 Characteristics of different variables used for the survival analyses.

Climate	MAT		Broad scale	Continous (°C)	
	MAP		Broad scale	Continous (mm)	
	CMI		Broad scale	Continous (cm per year)	
Georgraphy	Latitude		Broad scale	(decimal degrees)	
	Longitude		Broad scale	(decimal degrees)	
Physiography and topography	Surficial deposit	Ground moraine	Broad scale	Nominal	
		End moraine	Broad scale		
		Outwash deposit	Broad scale		
		Beach and aerolian deposit	Broad scale		
	Soil	Texture (Sandy to loamy soils)	Local scale	Nominal	
		Soil drainage class	Scale, from 0 (dry soil) to 9 (very wet soil)		Local scale
	Slope aspect	West-east axis	(x)	Local scale	Continous (x, y)
			South-north axis (y)	Local scale	
		Mean waterbreak distance	Intermediate	Continous (m)	
		Elevation	Local scale	Continous (m)	

MAT, mean annual temperature; MAP, mean annual precipitation; CMI, climate moisture

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APPENDIX IV. SUPPLEMENTAL INFORMATION FOR CHAPTER 5

Table S5.1 Comparison of different models for spruce budworm.

Model	R ²	AIC
Intercept+R	0.005	662
Intercept+R+E	0.031	661
Intercept+R+E+Bf	0.246	627
Intercept+R+E+Bf+Sw	0.296	555
Intercept+R+E+Bf +Sw+MR	0.349	554
Intercept+R+E+Bf+Sw+MR+stand age	0.350	555
Intercept+R+E+Bf+Sw+MR+stand age+stand age ²	0.419	550
Intercept+R+E+Bf+Sw+MR+stand age+stand age ² +stand age ³	0.448	549
Intercept+R+E+Bf+Sw+MR+stand age+stand age ² +stand age ³ +stand age ⁴	0.457	550

R, species richness, E, evenness, Bf, *Abies balsamea*, Sw, *Picea glauca*, MR, soil moisture regime.

Table S5.2 Comparison of different models for FTC.

Model	R ²	AIC
Intercept+R		658
Intercept+R+E	0.01	660
Intercept+R+E+P	0.01	661
Intercept+R+E+P+B	0.07	552
Intercept+R+E+P+B+stand age	0.09	553
Intercept+R+E+P+B+stand age+stand age ²	0.24	544
Intercept+R+E+P+B+stand age+stand age ² +stand age ³	0.28	542
Intercept+R+E+P+B+MR+stand age+stand age ² +stand age ³ +stand age ⁴	0.31	543

R, species richness, E, evenness, P, *Populus* spp., B, *Betula papyrifera*, MR, soil moisture.