

**CLIMATE CHANGE IMPACTS AND ADAPTATIONS IN THE
FORESTS OF CENTRAL NOVA SCOTIA**

by

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for the degree of Master of Environmental Studies

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ABSTRACT

Global climate change is at the forefront of issues in forest management. Forest managers are now faced with the challenge of incorporating climate change into their forest management values and objectives, as existing paradigms may be invalidated by the changing climate. The exploration of climate change impacts and formulation of potential management strategies will be necessary to reduce the vulnerability of forests. Halifax Water manages forest watersheds for the purpose of supplying clean water to much of the Halifax Regional Municipality. The purpose of this study is to characterize the future forest structure of the two principal watersheds supplying the Halifax Regional Municipality and to evaluate different adaptations incorporated into forest management using a modelling approach. The landscape disturbance model LANDIS-II and ecosystem process model PnET-II were used to simulate the forest response to climate change and adaptive measures in timber harvesting. Several impacts of climate change were examined in the study area. The most drastic effect of climate change in the watersheds was considerable change in forest composition, with a sharp decline in the abundance of boreal species, such as balsam fir and black spruce, and an aggressive increase in some temperate and pioneer species, such as red maple and aspens. Incorporating climate change adaptation into timber harvesting scenarios was found to be effective in minimizing trade-offs between timber supply and forest ecosystem integrity in the face of climate change. The watersheds managed by Halifax Water represent a situation where the principal objective is the maintenance of water quality as opposed to timber production, and therefore offer a unique opportunity to implement cutting-edge practices and adaptive forest management focused on climate change resilience and resistance while also facilitating transition to the changing climate.

LIST OF ABBREVIATIONS USED

AGB	Aboveground biomass	NSDNR	Nova Scotia Department of Natural Resources
ANPP	Aboveground net primary productivity	OGF	Old-growth forest
BSLB	Brown spruce longhorn beetle	PAR	Photosynthetically active radiation
CCCMA	Canadian Centre for Climate Modelling and Analysis	PBWP	Pockwock-Bowater Watershed Project
CFIA	Canadian Food Inspection Agency	P _{est}	Probability of establishment
CGCM	Coupled Global Climate Model	PSP	Permanent sample plot
CO ₂	Carbon dioxide	SFM	Sustainable forest management
CRCM	Canadian Regional Climate Model	SLW	Specific leaf weight
DEM	Digital Elevation Model	SRES	Special Report on Emissions Scenarios
ET	Ecotype	SWC	Soil water content
FEC	Forest ecosystem classification	WHC	Water holding capacity
FMP	Forest management plan	WUE	Water-use efficiency
FRI	Forest resource inventory		
GCM	General circulation model		
GDD	Growing degree day		
GHG	Greenhouse gas		
GIS	Geographic information system		
HB	Annually harvested biomass		
HRM	Halifax Regional Municipality		
IPCC	Intergovernmental Panel on Climate Change		
IUFRO	International Union of Forest Research Organizations		
MCE	Multi-criteria evaluation		
NDVI	Normalized Difference Vegetation Index		
NPP	Net primary productivity		

Tree Species

BF	Balsam fir
RM	Red maple
SM	Sugar maple
YB	Yellow birch
WB	White birch
BE	American beech
TL	Tamarack
WS	White spruce
BS	Black spruce
RS	Red spruce
RP	Red pine
WP	White pine
LA	Large-tooth aspen
TA	Trembling aspen
RO	Red oak
EH	Eastern hemlock

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CHAPTER 1 INTRODUCTION

1.1. Problem Statement

Global climate change is increasingly relevant in today's society and is forcing adaptation across all sectors of society and the economy (Intergovernmental Panel on Climate Change [IPCC], 2007). The forest sector is no exception, and in addition to the many changes to the sector and economic hardships experienced in the past two decades, forest managers are now faced with the necessity of addressing climate change and incorporating adaptation into forest management planning (Spittlehouse, 2005; Millar et al., 2007; Malmshheimer et al., 2008; International Union of Forest Research Organization [IUFRO], 2009; Williamson et al., 2009). The issue is no longer whether or not climate change will affect forest ecosystems, but what the regional impacts will be, and how do forest managers address them at the operational scale (Johnston et al., 2010).

There has been a recent proliferation of research and public attention about the ability of forests to mitigate the severity of climate change by capturing vast amounts of atmospheric carbon dioxide (CO₂) and storing it in forest biomass (Kurz & Apps, 1999; Kurz et al., 2009; Whalley & Walsh, 2009). However, forests are highly sensitive to even small variations in climate, and will undoubtedly be affected by global climatic change. The vulnerability and adaptive capacity of forest ecosystems and their management is a critical aspect in climate change and forest research that has received less attention than mitigation (Johnston et al., 2010). Moreover, a forest's mitigative capacity could be compromised if it is maladapted to the changes in climate (Ordóñez et al., 2010).

Climate change has the potential to directly and indirectly affect forest ecosystems through changes in natural disturbance regimes, tree physiology, forest productivity, and tree species distribution (Dale et al., 2001; Field et al., 2007; McKenney et al., 2007; Iverson et al., 2008). Furthermore, the amount of uncertainty associated with climate prediction, forest ecosystem complexity, the broad temporal and spatial scales of forest management, and the response of the forest sector to climate change pose tremendous challenges (Millar et al., 2007). The re-evaluation of forest values and the formulation of potential management tools and adaptive strategies to contend with the

existing and predicted impacts of climate change will be necessary to prepare the forest sector for uncertainty in the years to come.

1.2. Project Overview

In Halifax, Nova Scotia, Canada, Halifax Water manages its own and Crown-owned forestland for the purpose of supplying clean water to much of the Halifax Regional Municipality (HRM), the largest urban area in Atlantic Canada. To ensure high water quality, meet contractual obligations of Crown-owned land, and supplement operating costs, Halifax Water practices active forestry in the watersheds with the objective of sustaining forest resilience and resistance to pest outbreaks, fire, and extreme weather events (HRM, 2006). Halifax Water entered into a research partnership with Dalhousie University with the intent of exploring the relationships between climate change and forest ecosystems, possible impacts of climate change, and adaptive measures that might be incorporated into forest management planning. Healthy forests are best equipped for the continual provision of a healthy water supply (Neary et al., 2009), so an understanding of climate change, its effects on forests, and how best to manage these forests in an altered climate is a principal objective of Halifax Water. The purpose of this study is:

- To investigate the potential effects of climate change on the forest ecosystems within the watersheds managed by Halifax Water using a modelling approach, and to develop a conceptual framework of climate change adaptation to increase forest resilience in the face of climate change.

I attempt to answer four major research questions in this study:

- What is the potential for various climate change impacts in the Acadian Forest Region, and in Halifax Water's primary watersheds, Lake Major and Pockwock, in particular?
- What adaptive measures might help prepare the forested watersheds and their management for the changing climate?

- What must be re-evaluated in traditional modelling approaches to account for climate change?
- What is the overall level of vulnerability of the watershed forests to climate change?

There is much uncertainty surrounding climate change and its impacts on forests, and a broad understanding of the myriad possibilities is vital. Once these have been scrutinized, the formulation of adaptive measures can begin. The maintenance or enhancement of some ecosystem components may increase a forest's resilience and resistance to climate change, or even facilitate transition to the irrevocable change (Millar et al., 2007). Also, forest models are most often developed using existing and understood ecosystem processes (Kimmins et al., 2007). Many of these simulated ecosystem processes will need to be re-evaluated as climate change has the capacity to influence or alter them (Spittlehouse, 2003). A final measure of vulnerability will be informed by possible climate change impacts and adaptations (Johnston & Williamson, 2007), and will be vital in the future management of these watersheds by Halifax Water for the continual supply of pristine water.

Several specific research objectives address the research questions:

- Develop a broad working knowledge of climate change, forest ecosystems, forest management, and simulation modelling through intensive literature review and consultation with local experts in forest research and management.
- Parameterize the process-based models LANDIS-II and PnET-II to local/regional conditions, again using literature review and expert consultation.
- Select areas in the watersheds for field survey that have high levels of uncertainty in classification to reduce inaccuracy in initial conditions and to build familiarity with the study area to aid in model calibration and validation.
- Design, develop, and implement multiple modelling experiments and scenarios to investigate possible climate change impacts and adaptations.

- Formulate conclusions and recommendations based on the experimental modelling.

In the study, I assess the vulnerability of the watersheds managed by Halifax Water using multiple process-based models to investigate possible impacts of, and adaptation to, climate change. This approach of examining impacts and adaptations was developed by the IPCC (Smit & Pilifosova, 2001) and has been incorporated into forest management in Canada by provincial and federal governments (Johnston & Williamson, 2007). The primary model used for this study was LANDIS-II (Scheller et al., 2007), a spatially explicit landscape disturbance model, used to calculate forest growth, succession, mortality, disturbance, and management. The ecosystem process model PnET-II (Aber & Federer, 1992; Aber et al., 1997; Xu et al., 2009) was linked with general circulation model (GCM) data, downscaled to the study region, and used to calculate climate-sensitive tree-growth and dispersal variables to be incorporated into the LANDIS-II modelling. Two modelling experiments were designed. The first contrasted forest change in the current climate with an extreme climate change scenario, in both an intensely managed and a natural landscape, to extract possible impacts and forest responses. The second experiment simulated multiple adaptation scenarios, with forest management decisions informed by the climate change impacts observed in the first experiment and the literature, to see what aspects of timber harvesting were most important in promoting forest resilience to climate change. The combined conclusions drawn from the experimental modelling in this study were used to formulate conclusions about the overall vulnerability of the watersheds to climate change and generate recommendations for forest managers at Halifax Water to develop a climate-smart system of forest management.

The thesis is presented in the manuscript format, with five chapters. Chapter one outlines the impetus, purpose, and approach of the study, and provides in-depth review of relevant information. Chapter two describes the research methods of the entire study. Chapter three and four are free-standing manuscript-format chapters, with the former focusing on climate change impacts in the forests of the Halifax Water watersheds and the latter exploring possible climate change adaptation in forest management. The fifth

and final chapter outlines conclusions drawn from the study as a whole, with recommendations and identification of areas for future research.

1.3. Climate Change

Climate change, a global issue, is widely accepted in current forest science and management literature (Dale et al., 2001; Kurz et al., 2008; IUFRO, 2009; Williamson et al., 2009; Johnston et al., 2010). Documented evidence of climate change includes atmospheric and oceanic temperature increases, glacial melting, and sea level rises (IPCC, 2007). While the Earth's climate has changed dramatically in the past, the current warming trends indicate with a high level of confidence that the climate is changing at a rate unprecedented in over 10,000 years (IPCC, 2007). These warming trends have been linked with the large increases in atmospheric CO₂ and other anthropogenic and naturally occurring greenhouse gases (GHGs) attributed to human activity since the pre-industrial era. This rapid global increase of atmospheric CO₂ has been attributed to both fossil-fuel consumption and changes in land use.

Human activities have drastic effects on the global carbon cycle by altering the balance of geological, biological, and atmospheric carbon pools (Grace, 2004; Harmon, 2006). Forest ecosystems are a large component of the biotic carbon pool and are critical to climate change planning because they are both highly sensitive to changes in climate and drive climate by acting as carbon sinks and offsetting global emissions of CO₂ through the process of carbon sequestration and storage (Braswell & Schimel, 1997; Lauterbach, 2007; Luysaert, 2008). Changes in land use, most notably deforestation, have the potential to directly and indirectly increase atmospheric CO₂. Wildfires, timber harvesting, tree mortality, and decomposition all directly cause the release of stored carbon into the atmosphere (Harmon, 2006). Moreover, deforestation and certain other changes in land use lead to higher concentrations of atmospheric CO₂ due to the loss of carbon sequestration potential. Climate change is an impending global issue, and uncertainty and variability in the effects of climate change at the regional level are important to understand for issues in resource management.

Changes in the climate of Atlantic Canada have already been documented over recent decades (Lines et al., 2005; Vasseur & Catto, 2008). A mean increase of 0.3°C in

the region has been documented between the years 1948 and 2005, with the highest warming in the summer months (Pancura & Lines, 2005; Vasseur & Catto, 2008). Precipitation has also shown an increase of 10% since the mid-twentieth century (Vasseur & Catto, 2008). The climate of Atlantic Canada also is highly variable, as the Atlantic, Boreal, and Sub-Arctic climates are all represented. Nova Scotia's climate in particular is affected heavily by two oceanic currents, the warm Gulf Stream and the colder Labrador Current (Pancura & Lines, 2005).

Variability is an important component of climate change in the region, as the gradual increases in temperature and precipitation documented over a large temporal scale do not reflect the variability in temporal patterns and seasonality. For example, the mean temperature increases are largely explained by summer increases, and in fact in some areas there has been a mean decrease in winter temperatures (Pancura & Lines, 2005). Also, the increased precipitation is often in less-frequent events of higher volume (Field et al., 2007). An example of the implications of high variability in climatic change is an increased frequency of winter thaw-freeze events, which can cause extensive damage and mortality, termed die-back, of some tree species, as it has historically for yellow birch in eastern North America (Bourque et al., 2005).

Climate change predictions for the Maritimes and for Nova Scotia have much variation and uncertainty, as they often do not account for this regional variability (Lines et al., 2003; Pancura & Lines, 2005). Changes in climatic variables are difficult to predict at the regional scale, as GCMs generally operate with coarse resolution. However, climatic variables, such as temperature and precipitation, vary over much finer scales. One technique for predicting extremes and variability in climatic variables at the regional scale is the statistical downscaling of these global-scale GCMs (Wilby et al., 2002). Regional climate models are region-specific models that downscale coarse GCM data to a much finer spatial resolution.

A prominent example is the Canadian Regional Climate Model (CRCM), which is driven by the third-generation Coupled Global Climate Model (CGCM) and downscales data to a 46 horizontal-kilometre scale (Caya et al., 1995; Canadian Centre for Climate Modelling and Analysis [CCCMA], 2009). The CRCM climate-projection data under the Special Report on Emissions Scenarios (SRES) A2 climate scenario (IPCC, 2007) were

selected for this study. The SRES-A2 scenario is a high-emissions scenario, with atmospheric CO₂ reaching 850 ppm by the year 2100, leading to a mean temperature increase of 5.8°C and a mean total precipitation increase of 0.69 cm in the study area (CCCMA, 2009). The objective behind constraining the modelling between a current climate and extreme climate change scenario was to encompass the entire range of prediction, and thus incorporating as much uncertainty of global climate prediction as possible (Ravenscroft et al., 2010). The SRES scenarios that drive climate modelling are developed from expert narratives on possible future emissions under different demographic, technological, and economic scenarios (Nakicenovic et al., 2001), and as such they do not represent quantitative future prediction, and no scenario is more precise or accurate than another. Therefore, by encompassing the range of emission forecasts between the extreme SRES A2 scenario and current conditions, a full range of uncertainty in climate prediction can be captured.

1.4. Climate Change and Forests

Forests can regulate and drive climate change, but, as previously mentioned, are also highly sensitive to it (Johnston et al., 2010). The spatial variation of different forest regions is largely driven by climate (Norby et al., 2005). Temperature, precipitation, radiation, and atmospheric CO₂ concentrations are all aspects of climate that influence forest structure, composition, and productivity, as do nutrient availability and topography (Pickett & White, 1985). Changes in these climatic conditions that are predicted to occur over the upcoming decades and centuries will affect forest ecosystems directly, as changes in productivity and forest composition, as well as indirectly through altered fire regimes and increased frequency and magnitude of extreme weather events, insect outbreaks, and disease (Dale et al., 2001; Field et al., 2007; McKenney et al., 2007; Iverson et al., 2008).

The large variability of the climate regions across Canada has several implications for forest ecosystems and their management. The wide range of latitude and altitude in Canada and the sheer scale of the nation give rise to diverse forest regions with different species compositions, limiting factors, climatic vulnerabilities, and associated natural disturbances regimes (McKinnon & Webber, 2005; Williamson et al., 2009). In the

Acadian Forest Region, Nova Scotia in particular, the geological history of tectonic movement, volcanic activity, glaciations, and two million years of erosion of the Appalachian mountains has led to a diverse geology, topography, and soils, giving the region highly complex and wide-ranging forest ecosystems (Goldsmith, 1980; Loo & Ives, 2003). Therefore the impacts of climate change will not only be diverse in type, but also regionally variable. Forest managers will be faced with unique challenges in management due to the multitude of both complex and uncertain conditions of climatic change and associated forest response within this diverse forest region.

1.4.1. Natural Disturbance Regimes

An understanding of the dynamics of natural disturbances will also be crucial in managing forests in the face of climate change because altered regimes and increased frequency and severity of events are expected, posing a serious threat to forests and the forest sector (Peterson, 2000; Dale et al., 2001; Millar et al., 2007; Gray, 2008). Natural disturbances are a crucial component of forest-ecosystem dynamics and play a large role in determining forest composition and age structure (Pickett & White, 1985; Frelich, 2002).

Droughts are predicted to be a threat in drier areas limited by water availability (Hogg & Bernier, 2005). Water shortage is a threat to forest ecosystems as it can lead to lowered productivity, higher vulnerability to other forms of disturbance, and even tree mortality and die-back, with younger cohorts being more susceptible (Hanson & Weltzin, 2001). Friend and colleagues (2010) found in their modelling studies that drier areas such as the southwest United States and the along the Mediterranean sustained considerable losses in terrestrial ecosystem productivity due to water availability. Several studies in North America have shown that drier conditions caused by decreased precipitation in extended growing seasons have already decreased the radial growth of trees and forest production (Barber et al., 2000; Zhou et al., 2001).

Climate change is also believed to be responsible for the drought that occurred across Canada from 2001 to 2003 that was unprecedented in magnitude and duration and led to large-scale aspen die-back in the western Canadian interior (Hogg & Bernier, 2005). Furthermore, secondary impacts of drier conditions and drought include increased

vulnerabilities to other disturbances such as fire, insect outbreaks, and disease (Dale et al., 2001; Williamson et al., 2009).

Wind is a common disturbance agent in forest ecosystems across the globe, and wind disturbance, often termed windthrow, can range in aerial extent from individual tree mortality, as it does in gap disturbance regimes, to catastrophic, stand-replacing hurricanes and downbursts that flatten thousands of hectares (Mitchell, 1995; Neily et al., 2007; Rich et al., 2007). Wind disturbance has played a key role in many of the pre-settlement forest ecosystems within Nova Scotia and much of the Acadian Forest Region (Seymour, 2002; Loo & Ives, 2003), and now has a large influence on forest management practices and silviculture. Seymour and colleagues (2002) conducted an extensive analysis of Acadian forest disturbance literature and found that stand-replacing wind disturbances ranged in size from 0.2 to 3,785 ha, with a mean size ranging from 14 to 93 ha and a return interval ranging between 855 and 14,300 years. Gap disturbances were treated separately and were found to range between 4 and 1,135 m², with a mean size ranging from 24 to 126 m², and a return interval between 50 and 200 years.

The frequency and severity of windstorms and intense precipitation events are predicted to increase due to climate change, especially in the Acadian and Boreal Forests of Atlantic Canada (Peterson, 2000; Smith et al., 2001; Williamson et al., 2009). More-frequent and damaging hurricanes along coastal eastern North America are also predicted under climate change (Webster et al., 2005), and have serious implications for forest ecosystems in coastal areas (Busby et al., 2008, Steenberg & Duinker, 2010).

Changes in natural disturbance regimes are not fully understood and encompass high levels of uncertainty. For instance, the relationship between wind speeds and the subsequent scale of disturbance is highly variable across different forest types, and it is likely that disturbance severity will not simply increase linearly with wind strength (Dale et al., 2001). The full effects of altered wind regimes in forest ecosystems can therefore not be predicted with ease. As alluded to earlier, altered wind disturbance regimes have the potential not only to increase mortality and structural damage in forests, but also to alter overall forest ecosystem dynamics (Busby et al., 2008), as these ecosystems are largely defined by their natural disturbance regimes.

Managed forests such as those in the study area are more susceptible to windthrow due to the exposure of sharp forest edges, often in stands that developed in sheltered conditions (Harper et al., 2004). The on-going conversion of tolerant mixedwood forests to dense, coniferous forests in managed areas also increases the windthrow hazard (Saunders & Wagner, 2008).

Further attention must be drawn to the interrelatedness of natural disturbances. Wind-damaged stands are more susceptible to insect outbreak, particularly as blowdown areas often serve as hotspots for bark beetle population establishment, a family of forest insects that have often been linked with the changing climate (Magasi, 1995; Fleming & Candau, 1998; Neily et al., 2007). In recent years there have been several incidences of unusually large insect outbreaks, many of which are endemic species (Berg et al., 2006; Kurz et al., 2008). The mountain pine beetle is an example of an endemic species that has periodic outbreaks when conditions are favourable. However, the current outbreak in British Columbia, and more recently Alberta, has surpassed any other previous recorded outbreaks in duration and extent and is attributed to both climate change and forest vulnerability due to human impacts (Kurz et al., 2008). The pine beetle has become almost synonymous with climate change and forestry in western Canada. Moreover, with the predicted and observed warming trends, the beetle is predicted to continue its range expansion northward, eastward, and to higher elevations (Carroll, 2006). The largest recorded outbreak of the spruce beetle, another bark beetle, has also been recently documented in the Yukon (Berg et al., 2006).

The spruce budworm, an endemic defoliator in eastern Canada, has periodic outbreaks and targets balsam fir primarily, but also attacks red, black, and white spruce in times of outbreak. Gray (2008) predicted using climate change estimates that spruce budworm outbreaks in eastern Canada will be up to six years longer with 15% greater defoliation than current outbreaks. However, the spruce budworm is not as prevalent in central Nova Scotia, where the study region is situated, as it is in Cape Breton and northeast Nova Scotia (Magasi, 1995; Neily et al., 2007).

Currently in western Cape Breton, an outbreak of the spruce beetle is ravaging the white spruce population. The outbreak has been attributed to warmer than usual winters and the prevalence of even-aged mature white spruce stands that have colonized

abandoned agricultural land in the area (P. Neily, personal communication, March 30, 2010). The brown spruce longhorn beetle (BSLB) is an invasive forest insect native to Europe that was first discovered in Canada in Point Pleasant Park, Halifax, Nova Scotia (Mushrow et al., 2004). In Nova Scotian forests the BSLB attacks mainly red spruce and is now considered an invasive species (Colautti et al., 2005), with a containment area designated by the Canadian Food Inspection Agency (CFIA) that encompasses the majority of the HRM, including all of the Lake Major watershed and a portion of the Pockwock watershed (CFIA, 2007). The BSLB has been spotted by forest managers at Halifax Water in mature red spruce stands throughout the watersheds and is now considered a threat to the forests of the study area. The two bark beetles, spruce beetle and BSLB, are the most prevalent source of insect disturbance in the watersheds and subsequently are the only biological disturbance agents to be included in our modelling work, apart from the beech bark disease.

Forest disturbances in Nova Scotia are often described by five regimes: frequent stand-initiating, infrequent stand-initiating, stand-maintaining, open seral-maintaining, and gap dynamics (Frelich, 2002; Neily et al., 2007). Frequent stand-replacing disturbance regimes involve catastrophic disturbances that cause the mortality of the majority of trees in the stand, and have a return interval that is most often shorter than the longevity of the climax tree species. This results in even-aged stand dynamics, with little understory recruitment. Infrequent stand-replacing disturbance regimes also involve catastrophic disturbances causing mortality, but tend to have return intervals longer than the longevity of climax species, resulting in some uneven-aged stand characteristics. The large disturbances of these two regimes can include wind, fire, or insect events. Stand-maintaining disturbance regimes involve frequent but less severe disturbances that cause mortality in species that are not adapted to the particular disturbance, and therefore alter forest composition to favour more-tolerant species. An example of stand-maintaining disturbances is low-intensity surface fires that favour stands of fire-tolerant species such as red pine, white pine, and red oak. Open-seral-maintaining disturbance regimes most often refer to ecosystems with edaphic climax communities that maintain open-canopy conditions due to frequent and severe disturbance, such as coastal communities of wind-stunted white spruce and balsam fir. Finally, gap disturbance regimes refer to forest

ecosystems that seldom sustain stand-initiating disturbance and therefore develop an uneven-aged community where understory recruitment occurs when small gaps occur in the canopy due to small-scale insect, wind, or age-related mortality (Neily et al., 2007).

The role of fire in the Acadian Forest Region can often be a contentious issue in the literature and among forest managers in Nova Scotia. Fire has been shown historically to have largely influenced to forests of southwest Nova Scotia, and may be responsible for the barrens found in that region (Basquill et al., 2001). However, many of the recorded fires have been attributed to land clearing for agriculture during European settlement of the area (Strang, 1970). In central Nova Scotia where the study area is located, fires have played a small role in shaping the forests, as can be seen by the absence or small representation of fire-origin species such as jack pine, red pine, and red oak. Furthermore, human fire suppression further minimizes the extent of fire in the watersheds. Despite the issue of fuel-buildup and catastrophic fires resulting from fire suppression in the boreal forest (Johnson et al., 2001), fire disturbance was not considered in this study.

Given the complexity and variety of natural disturbance regimes in forest ecosystems, there is a considerable risk that altered and more-severe disturbance regimes will not only cause more tree mortality in the forest, but may alter the dynamics of the current forest ecosystems (Dale et al., 2001). Not only will this have implications for forest management and silviculture, especially the recent development of ecosystem- and natural-disturbance-based management (Harvey et al., 2002), but this could have monumental ramifications for ecological forest values such as biodiversity, wildlife habitat, and, most importantly, water supply.

1.4.2. Forest Productivity

Climate change may affect the productivity of forest ecosystems by influencing the metabolic processes of trees, mainly photosynthesis and respiration (Schimel et al., 2001). However, the response of forest productivity is predicted to vary tremendously by region and ecosystem (Pastor & Post, 1988; Schimel et al., 2001; Norby et al., 2005; Scheller & Mladenoff, 2005; McMahon et al., 2010), with the largest increases in high latitudes and altitudes (Chaplin et al., 1995), and the largest decreases in drier, moisture-

limited regions, such as the Mediterranean and southern Australia (Friend, 2010). Forest productivity is measured in several ways, including volume (or merchantable volume), carbon uptake, Normalized Difference Vegetation Index (NDVI), and biomass. However, in most studies investigating the effects of climate change on terrestrial ecosystem productivity, net primary productivity (NPP) is used, which is the rate at which plant material in an ecosystem stores chemical energy as biomass, not inclusive of that used for cellular respiration, in units of mass per unit area and time (Roy & Saugnier, 2001). In this study, aboveground net primary productivity (ANPP) and aboveground biomass (AGB), the total aboveground biomass of all tree species at a fixed point in time, were used to investigate the effects of climate change on the forest productivity of the watersheds.

Global predictions of terrestrial ecosystem productivity have shown increases as high as 23% to 37%, depending upon estimated increases in atmospheric CO₂ and temperature (Norby et al., 2005; Friend, 2010). Increases in productivity in tropical and drier temperate regions are believed to be driven by CO₂, whereas increases in northern and wetter temperate regions tend to be driven by temperature (Melillo et al., 1993). The complete effect of climate change on terrestrial ecosystem productivity, including forest ecosystems, is still not fully understood, as studies often have variable or conflicting findings with high levels of uncertainty (Heimann & Reichstein, 2008; Williamson et al., 2009).

There are several possible factors that could cause a change in the growth rate of plants and ecosystem productivity, the most probable being increased atmospheric CO₂ concentrations, increased temperatures, longer growing seasons, and changes in soil moisture and nutrient regimes (McMahon et al., 2010). An increase in atmospheric CO₂ has the potential to increase NPP in a process known as carbon fertilization or enrichment (Aber et al., 2001; Xu et al., 2007; Friend et al., 2010). This refers to a plant's ability to maintain higher rates of photosynthesis due to lowered stomatal conductance caused by an enriched atmospheric CO₂ concentration. The lowered stomatal conductance of plants means lowered evapotranspiration, and therefore higher water-use efficiency (WUE), the ratio of CO₂ sequestered to water lost by stomatal conductance, the latter also called

transpiration. This increase in WUE reduces limitations to productivity due to soil water availability (Farquhar et al., 1980).

There is some debate as to the overall influence of carbon fertilization on forest productivity (Curtis & Wang, 1998; Mingkui & Woodward, 1998; Gitay et al., 2001). Temperate and boreal forest species, especially conifers, have been predicted to experience a much smaller increase in WUE in comparison with other plant species and terrestrial ecosystems, such as grasslands (Saxe et al., 2001; Xu et al., 2009; Tian et al., 2010). Still others predict that increases in productivity observed at the onset of climate change will eventually decrease as plants acclimate to the higher CO₂ concentrations (Mingkui & Woodward, 1998; Gitay et al., 2001). Due to the uncertainty surrounding the full effects of carbon fertilization on forest ecosystems, changes in stomatal conductance were not included in the PnET-II modelling for this study. This decision is supported in other studies using PnET-II and LANDIS-II (Scheller & Mladenoff, 2008; Gustafson et al., 2010), but warrants more investigation and further study. Furthermore, the wet climate of the Acadian Forest Region suggests that in the absence of edaphic moisture and nutrient limitations, temperature, rather than CO₂, is the limiting factor for forest productivity in the study area (Melillo et al., 1993).

Increasing temperatures in the changing climate can lead to longer growing seasons, as measured by growing degree days (GDDs) and first and last frosts (McMahon et al., 2010, Bourque et al., 2010). A longer growing season means that trees are metabolically active for a longer portion of the year and therefore sequester more carbon and accumulate more biomass (McMahon et al., 2010). Increases in forests of mid- to high-range latitudes have already been observed (Braswell & Schimel, 1997; Zhou et al., 2001; Bunn & Goetz, 2006). However, if soil water availability or moisture are limiting, or growing-season temperatures exceed optimal temperatures for photosynthesis of the particular tree species, then a lengthening of the growing season could have negative effects on forest productivity (Aber et al., 2001).

As previously mentioned, the possible benefits of elevated atmospheric CO₂ and temperature for forest productivity can only be realized in the absence of soil nutrient and moisture limitations, often called edaphic constraints. Changes in precipitation due to climate change can have varying effects on forest productivity. More precipitation,

especially in areas where stress due to soil water availability is a limiting factor, can increase NPP, especially if WUE is elevated due to CO₂ fertilization. However, the temporal variation of precipitation events will be crucial to the effects of precipitation on forest productivity. The amount of precipitation during the growing season is often predicted to decrease, causing droughts in some areas and limiting productivity due to stress associated with lower soil water availability (Barber et al., 2002).

Nutrient availability in the soil, nitrogen in particular, is another major limiting factor for forest productivity. Nitrogen availability in the soil may increase as a result of increased decomposition of dead organic matter in the elevated temperature (Saxe et al., 2001; Verburg, 2005). For this study, while variation in soil nutrient regimes was accounted for in the modelling, soil nutrient levels were assumed to be constant for the simulations.

The cumulative effects of climate change on terrestrial ecosystem productivity, including forest ecosystems, are still not fully understood, as studies often have variable or conflicting findings with high levels of uncertainty (Heimann & Reichstein, 2008). Moreover, the response of forest productivity is predicted to vary tremendously by region and ecosystem (Pastor & Post, 1988; Schimel et al., 2001; Norby et al., 2005; Friend, 2010). Factors such as natural disturbances, competition, growth and successional processes, and barriers to dispersal will also be crucial in predicting the effects of climate change on forest productivity (Scheller & Mladenoff, 2005).

Forest composition at the landscape scale will also likely be highly influential on forest productivity, as some tree species within an ecosystem may no longer be favoured in the altered climate, while others may migrate from southerly regions due to a northern shift in their climatic range limits (McKenney et al., 2007). This is particularly important in the study area and Acadian Forest Region as a whole, as it is a transitional forest region between the boreal forest to the north and the temperate forest to the southwest, with a mix of colder-climate boreal species and warmer-climate temperate species (Neilson, 1993; Noble, 1993; Loo & Ives, 2003). A study in a transitional forest in northern Wisconsin using methods similar to this study found that boreal species sustained a loss in overall biomass, while southern, temperate species had an increase (He et al., 1998). Changes in natural disturbance regimes will also affect overall ecosystem

productivity, as a forest ecosystem in more favourable growing conditions may still sustain decreased productivity with more-frequent and severe natural disturbances (Dale et al., 2001). Anthropogenic disturbances, both timber harvesting and fragmentation due to development and agriculture, also play a large role in the productivity of forests at the landscape scale (Ravenscroft et al., 2010). It is important to incorporate these variables in forest productivity in any study investigating forest response to climate change.

1.4.3. Tree Species Distribution

Climate is a main controlling factor in the geographic distribution of plants, and changes in climate, such as increased atmospheric CO₂ and temperature and altered precipitation rates, are predicted to affect the distribution, phenology, and physiology of trees, as well as the functioning of forest ecosystems (McKenney et al., 2007; Xu et al., 2007; Iverson et al., 2008; Bourque et al., 2010). Several geophysical variables related to climate are largely responsible for tree species distribution and abundance, which include soil water content, GDDs (a temperature-based index of growing season length), soil fertility, and photosynthetically active radiation (PAR; the proportion of incident solar radiation that can be used by plants in photosynthesis), all of which are predicted to change in the near future (IPCC, 2007; Xu et al., 2009; Bourque et al., 2010). Changes in the geographic distribution, or range, of tree species in response to climate change will likely vary widely between species depending on life cycle, biology, current range, and forest community composition (Hansen et al., 2001; Bourque & Hassan, 2008; Thomson et al., 2009). Consequently, a restructuring of many forest communities is likely to occur as range shifts will occur at the individual species level, not the community level (Webb & Bartlein, 1992). Such severe changes in forest composition could affect complex ecosystem processes such as competition and succession in unforeseen ways (Gustafson et al., 2010).

Studies of pre-historic changes in climate suggest that tree species may sustain severe changes in distribution, leading to the alteration of established forest communities (DeHayes et al., 2000). However, a major concern is that the rate of the current changes in climate far exceeds the migration rates of tree species (IPCC, 2007). Furthermore, the disturbed and fragmented state of forests today due to the intensive history of human use

may impede tree species migration in response to a warming climate (Scheller & Mladenoff, 2008).

Broad-scale modelling studies in North America and Europe have investigated the response in climatic range of many tree species and have found variable changes in range size and northward shifts up to 700 km (Sykes & Prentice, 1996; Iverson et al., 2004; Iverson et al., 2008; McKenney et al., 2007). McKenney and colleagues (2007) modelled changes in the ranges of 130 North American tree species assuming a doubling of atmospheric CO₂ in two scenarios: a full-dispersal scenario where trees can migrate throughout their existing and predicted ranges, and a no-dispersal scenario where trees can migrate only to overlapping areas in existing and predicted ranges. They predicted an average northward shift of 700 km and 330 km and average size decrease of 12% and 58% of tree species ranges for the full- and no-dispersal scenarios, respectively. Iverson and colleagues (Iverson et al., 2004; Iverson et al., 2008) conducted similar studies focused in the eastern United States, and found a northeast shifting trend in species distributions, with a general retreat of the northern spruce-fir regions and an advance of the southern oak and pine regions.

Several Nova Scotian species, such as balsam fir, black spruce, sugar maple, red oak, yellow birch, white pine, and red maple, are predicted to have extreme range shifts (McKenney et al., 2007; Bourque & Hassan, 2008; Bourque et al., 2010). The Maritimes are predicted to have a significant increase in the number of species that are climatically favoured (McKenney et al., 2007), yet the province is geographically isolated from propagules of many of these newly favoured southerly temperate species, and it is predicted that the migration rates of many tree species may lag significantly behind the rate of climate change (Scheller & Mladenoff, 2008; Ravenscroft et al., 2010). The ability of seedlings to establish is highly sensitive to climate (He et al., 1998; Ravenscroft et al., 2010), and the composition of Nova Scotian forests may be radically altered as the temperature and precipitation change, with decreased success of colder-climate boreal species such as balsam fir and black spruce, and increased success of many warmer-climate temperate species, such as red maple (Bourque & Hassan, 2008; Bourque et al., 2010).

The impacts of climate change on forest composition are likely to be most severe at transitional areas between biomes, also called ecotones, because they contain a mix of tree species near the southern and northern limits of their respective ranges (Neilson, 1993; Noble, 1993; Pitelka, 1997; Ravenscroft et al., 2010). The Acadian Forest Region of Atlantic Canada and the northeast United States is an example of a transitional forest region between the boreal and temperate forest. As such, it is characterized by a mix of species from both regions, which makes it vulnerable to widespread changes in forest composition with climate change (Loo & Ives, 2003; Mosseler et al., 2003). The forests of northern Wisconsin and northeast Minnesota are studied examples of transitional forests that have been predicted to undergo severe changes in forest composition due to climate change (Pastor & Post, 1988; Scheller & Mladenoff, 2005; Scheller & Mladenoff, 2008).

To investigate the myriad of climate change implications for tree species distribution and forest composition, it is important to differentiate between realized and fundamental niches. A fundamental niche, also called potential range, is the geographic range determined by favourable climatic conditions for establishment and growth, and is also termed a climate envelope (He et al., 1998; McKenney et al., 2007). A realized niche, also called the actual range, is the geographic range where a given species is found, and is generally smaller than the fundamental niche because it includes biological and geophysical restrictions on dispersal, such as competition, soil moisture, nutrient regimes, disturbance history, and topographic and anthropogenic barriers to dispersal (Xu et al., 2007). An altered climate may lead to a shift in the favourable climatic conditions that envelope the range of a tree species, but the actual change in distribution of that species will be highly dependent on the aforementioned biological and geophysical variables (Hampe, 2004).

The release from competition, biological control from insects, diseases, and herbivory, or even adaptive evolution may exacerbate range shifts in ways not predicted by conventional modelling techniques (Bradshaw & Holzapfel, 2006). Many studies that examine the effects of climate change on tree species distribution focus only on climatic variables and fundamental niches (McKenney et al., 2007; Iverson et al., 2008). Studies of this nature model the shifts in ranges of tree species whereby a range is defined as

anywhere the climate favours establishment and growth. This is also termed the climate envelope approach, and while potentially useful at broad scales, they exclude many regional processes that are pronounced at the landscape scale, such as the aforementioned biological and geophysical factors of competition, soil dynamics, dispersal, and disturbance (Hampe, 2004). The use of the ecosystem process model PnET-II and the landscape disturbance model LANDIS-II enables inclusion of the effects of these biological and geophysical factors that are critical at the scale of our study area.

Forest composition is both a large determinant and indicator of forest ecosystem dynamics, as it is interrelated with forest productivity, wildlife habitat, natural disturbance regimes, and water quality, as well as forest ecosystem services, such as timber production and recreational/aesthetic values. The response of forest composition to climate change will therefore be critical to analyze and understand.

1.5. Forest Management

1.5.1. Historical Practices and Recent Developments

Forest management refers to a range of human activities in and directed towards forest land for the purpose of attaining and maintaining economic (e.g. timber production and water supply), social (e.g. recreation and aesthetics), and environmental (e.g. biodiversity and wildlife habitat) goals (Davis & Johnson, 1987; Sturtevant et al., 2007). These many goals are maintained or achieved under the implementation of different management tools, such as silvicultural activities, forest inventory, simulation modelling, public consultation, conservation, and scientific studies (Sturtevant et al., 2007). It is the responsibility of forest managers to manage forest landscapes according to societal values and the ecosystem services they provide, and either to reject old or incorporate new management practices so that they are consistent with changing societal, economic, and ecological values (Kimmins, 2002). In many recent aspects of forest management these ideals have been upheld, but in others, most notably climate change, they have not, or are in a preliminary state of development.

In many respects, forest management can be compared to agriculture, but a vital divergence is that forest management operates within an ecosystem. Therefore the recognition of ecosystem complexity and maintenance of forest ecosystem integrity is

pivotal in the continual provision of forest ecosystem services (Puettmann et al., 2009). There have been many recent sustainable and ecological trends in forest management, such as the rise of concepts like sustainable forest management (SFM), complexity, and biodiversity. This development has been in part attributed to a noticeable decline of the wood supply and quality, a myriad of ecological impacts across many forest ecosystems, a variable economy, and a shift in societal values and awareness (Kimmins, 2003; Van Damme et al., 2008). The guiding principles in the development of SFM have been the expansion of the temporal scales, spatial scales, and value arrays in which forests are managed, which necessitates the inclusion of new and numerous management tools and interdisciplinary approaches to forest management planning (Van Damme et al., 2008).

Kimmins (2002) outlined the development of forest management paradigms in Canada and the United States. Early, post-settlement forestry was entirely focused on exploitation as the chief management approach, with the extraction of timber without consideration of the forests' continuing ability to provide it. Since most European settlers lacked ecological knowledge of the forests they exploited, this stage led to the depletion of the resource. The noticeable decline in timber resources led to an administrative stage of forestry, which was still centralized around the supply of timber, but was regulation-based. However, there was still a lack of recognition of non-timber forest values and the ecological functioning of forests in this stage, and as such it was not sustainable.

In pre-settlement Nova Scotia, the indigenous Mi'kmaq population also exploited the forest for several resources, but not at the scale to deplete forest resources (McGee, 1974). More-intensive and extensive forest management began with European settlement in the sixteenth and early seventeenth centuries. As is the case with most of Canada, early Nova Scotian settlers adopted European forestry practices without an understanding or consideration of local ecology, and the increasing exploitation intensity associated with population growth led to the degradation of the province's forests (Loo & Ives, 2003; Puettmann et al., 2009). Nova Scotia has the longest history of forest management in Canada, with centuries of selectively harvesting the best stock, also called high-grading, and deforestation for agriculture (Loo & Ives, 2003). More recently, the advent of the pulp and paper industry in the region has led to many more softwood plantations and intensive silviculture (Beyeler, 2002). This, in addition to the proliferation of white

spruce on abandoned agricultural land, has greatly increased the coniferous forest area in the province. Recent forest management and development has also yielded a more fragmented and younger forest, with a higher prevalence of early successional broadleaved species, such as red maple and white birch (Loo & Ives, 2003). Interestingly, balsam fir is the only major species that has not been historically targeted by a commercial industry, which in part explains its ubiquitous presence in managed forests (Forbes et al., 1998). In central Nova Scotia and the study area, these past trends in forest management are highly evident.

Ecosystem-based management began picking up steam in the last decade of the twentieth century, and represented a shift away from single-species, even-aged management to multi-species and whole-system approaches (Grumbine, 1994; Riley, 1995; Cortner & Moore, 1999). While often interpreted differently, a broad definition is managing a sustainable resource flow without compromising ecosystem integrity or functioning (Puettmann et al., 2009). Ecosystem-based management does not represent a strict regime of silvicultural practices, but rather a shift in management values and a wide array of management techniques. A prevalent technique in ecosystem-based management is the use of ecological boundary delineation for the purposes of management particular to different ecosystems, and timber harvest practices that emulate natural disturbance regimes (Harvey et al., 2002; D'Eon, 2006; Kimmins et al., 2008). A major tool in ecosystem-based management is forest ecosystem classification (FEC), which enables the organization of ecological units and processes into conceptually manageable elements (Treitz & Howarth, 2000). FEC refers to a framework or guideline of stand-level vegetation, soil, and ecosystem classification directed towards operational planning and decision support.

The Nova Scotia Department of Natural Resources (NSDNR) has also recently made strides towards ecosystem-based management on Crown lands with the implementation of uneven-aged management and natural-disturbance-based practices (NSDNR, 2008). These new developments draw heavily on the FEC of Nova Scotia, which classifies forest ecosystems based on forest cover, soil type, herb/shrub layers, and natural disturbance regimes, and outlines corresponding management recommendations (Keys et al., 2003; McGrath, 2007; 2009). This study incorporates several aspects of the

provincial FEC in the modelling framework, which will be discussed further in the following chapters.

An ecosystem approach to forest management certainly has advantages over traditional timber-oriented forest management, but is by no means a final and static solution. Ecosystem-based management often defines natural conditions as an ultimate management goal. Given that climate change has the potential to alter forest ecosystem function and reorder structure, a re-evaluation of ecosystem-based management goals will likely be necessary.

1.5.2. Forest Management in a Changing Climate

Forest managers are currently faced with a breadth of challenges, including the incorporation of the relatively newly emerged concepts of ecosystem- or natural-disturbance-based sustainable forestry, the recent economic downturn, and the threat of climate change. Furthermore, the setting for these changes is forests with a long history of timber extraction that has left many forest ecosystems in a degenerative state, and a future wrought with the impacts and uncertainty of climate change. The actions taken into account for climate change in forest management will be critical, as forests are highly sensitive to changes in climate, they have an ability to affect global climatic patterns, and forest management activities have the ability to increase or decrease the effects of climate change on forests (Franklin et al., 2001; Noss, 2001; Scheller & Mladenoff, 2005; Ravenscroft et al., 2010). The sensitivity of forest ecosystems to climate and the long temporal scale of forest response increase the vulnerability of the forest sector to climate change (Williamson et al., 2009). As forest managers acknowledge the threat of climate change to the attainment of forest management goals, they recognize the need for the development of new and appropriate management tools to minimize and manage the impacts of climate change to the forest sector.

There are two contrasting but not mutually exclusive categories of forest management strategies associated with climate change: mitigation and adaptation (Kurz & Apps, 1999; Spittlehouse, 2005; Millar et al., 2007). Mitigation refers to the ability of forests to diminish climate change by acting as carbon sinks through the processes of carbon sequestration and storage (Grace, 2004). There are considerable research efforts

and management initiatives into the sustainable maximization of carbon capture in forests to mitigate the effects of climate change (Grace, 2004; Luysaert, 2008). However, much less attention has been given to adaptation in the field of forest management and climate change (Johnston et al., 2010). Not only is this a critical area of understanding, as forest ecosystems are highly likely to be affected by the changing climate, but a lack of emphasis on adaptation in the development of climate change strategies may in fact compromise mitigation initiatives, as forest productivity, and subsequently carbon uptake, may be compromised in a degraded forest that is maladapted to the changing climate (Ordóñez et al., 2010).

Adaptation refers to the alteration of a given system either in response to or in anticipation of environmental change. Adaptation is closely linked to the vulnerability of a system, along with possible impacts, risk and uncertainty, and overall capacity for adaptation (Spittlehouse & Stewart, 2003; Johnston & Williamson, 2007; Ordóñez et al., 2010).

Adaptive measures accommodating climate change frequently refer to the necessity for flexibility and adaptive capacity of forest management and policy, but examples of specific adaptation strategies, especially at the operational scale, are relatively rare in the literature, due to both a lack of research and understanding as well as the lack of documentation by forest practitioners across Canada (Johnston et al., 2010). Millar and colleagues (2007) outline the utility of segregating adaptation measures into categories of forest resistance, resilience, and promoting forest change, in an approach that has been widely accepted (Malmshemer et al., 2008; Bolte et al., 2009; Heller & Zavaleta, 2009). The resistance and resilience options are more focused on uncertain conditions in the short term, where a forest is either managed to resist a number of climate-induced changes (Parker et al., 2000; Millar et al., 2007) or to be resilient the predicted impacts of climate change – most often natural disturbances (Dale et al., 2001; Price & Neville, 2003; Spittlehouse & Stewart, 2003). The final category of adaptation describes activities that accommodate change by actively managing forests to respond to the changing climate (Millar et al., 2007). This is by far the most risk-laden approach, but importantly is the most feasible in the long term as it accepts and accommodates inevitable change.

There is also a tremendous amount of vulnerability to climate change due to institutional barriers and a lack of flexibility in forest management and policy (Kimmins, 2002; Johnston et al., 2010). The complexity involved in managing forests sustainably in the face of climate change and the rapidly evolving nature of climate change research requires continual learning and improvement of forest management institutions (Van Damme et al., 2003). This is a concept known as adaptive management. Adaptive management is so vital to managing forests in a changing climate because it is focused on the recognition and minimization of uncertainty. This is done through a cyclical process of research and forecasting of optimal forest management strategies, implementation and monitoring, and management review and re-evaluation (Duinker & Trevisan, 2003). Adaptive management is critical to the technical implementation of SFM and relies heavily on the use of simulation modelling (Duinker & Trevisan, 2003; Van Damme et al., 2003).

Climate change adaptation was incorporated into the modelling framework of this study and was directed towards three aspects of timber harvests: canopy-opening size of harvests, the age of harvested trees, and the composition of harvested trees. This approach has connections with the three areas of climate change adaptation described by Millar and colleagues (2007), and is directed towards discovering the most critical components of timber harvesting to climate change adaptation.

1.6. Simulation Modelling

As management values change and temporal and spatial scales increase to include ecosystem and landscape dynamics in contemporary forest management and SFM, simulation modelling is becoming a more valuable decision-support tool (Messier et al., 2003; Van Damme et al., 2003; Iverson et al., 2008). This is largely evident in the increase in studies involving forest simulation models in the peer-reviewed literature (Messier et al., 2003). Ecological modelling is used for quantitative forecasting and experimental scenario simulation, and is a vital tool in forest management as it facilitates the organization of vast amounts of information on processes and relationships in natural systems (Messier et al., 2003). The use of modelling and forecasting to provide an interface with real-world systems and planning processes is also a critical aspect of

adaptive management and SFM. Scenario analysis of optimal forest management strategies sets the direction for management activities, which can subsequently be monitored and improved based on performance in the adaptive management cycle of forecasting, implementing, and monitoring (Van Damme et al., 2003).

The role and value of ecological modelling has long been recognized in the field of forestry (Duinker and Baskerville, 1986; Landsberg, 2003; Messier et al., 2003; Kimmins et al., 2007). The principles of modelling have been used in forestry as early as the eighteenth century, with the development of empirical growth and yield tables (Kimmins et al., 2007). At its broadest definition, modelling in the context of forest management is a simplification of a real-world system to understand complex processes over time. Forest modelling has seen a proliferation of model types, such as landscape disturbance models, gap models, and individual tree models (Messier et al., 2003). Recent trends in forest modelling have included accounting for the carbon that is stored in trees and forests in what is called carbon budgeting, or carbon budget models (Turner et al., 1995; Kurz et al., 2002). Tracking carbon in a forest over time to develop an intimate knowledge of sequestration and storage is gaining momentum as a topic due to its relevance to climate change mitigation (Luysaert et al., 2008; IUFRO, 2009).

Most ecological models, including forest models, tend to focus on a minimal number of interactions and processes at relatively fine spatial and temporal scales. Yet as forest management values shift towards greater understanding of entire forest ecosystems and regions, there is a need to capture a greater variety of ecological processes, many of which occur over large areas and long periods of time, such as succession, natural disturbance regimes, and seed dispersal (Scheller et al., 2007; Sturtevant et al., 2007). Conversely, ecosystem processes that occur at the stand or individual tree scale cannot be ignored. For this reason, many forest researchers advocate the use of multiple models at several spatial and temporal scales to address issues in forest management such as climate change, in what is often termed a meta-modelling approach (Seely et al., 2004; Sturtevant et al., 2007). These recent trends bring to light the issue of complexity in forest models.

Representing reality in a simplified form through the process of assumption, abstraction, and aggregation is at the conceptual core of ecological modelling, as it

enables the examination of scenarios that would be otherwise impossible or unethical (Jørgensen & Bendoricchio, 2001). Despite this imperative, the simplification of real-world systems is a primary cause of error and uncertainty in the predictive capability and utility of models (Loehle, 1987). The longstanding view in forest modelling is that parsimony should be paramount, as uncertainty enters into a model at every decision point. However, due to recent shifts in forest management values (i.e. ecosystem-based management), increases in ecological knowledge, and the advancement of computing power, there has been an increasing recognition of the value of complexity in forest models (Kimmins et al., 2007). This concept lends itself to the two major categories of forest models: empirical, predictive, growth and yield models, and process-based, mechanistic, forest dynamics models. The former is the more traditional, simplified approach that focuses entirely on one goal, forest productivity, while the latter emphasizes the role of multiple and complex forest ecosystem processes and multiple spatial and temporal scales (Jørgensen & Bendoricchio, 2001; Porté & Bartelink, 2002; Kimmins et al., 2007).

The use of multiple models to investigate all the possible climate change impacts on the forest ecosystems of central Nova Scotia at different spatial and temporal scales is important for a study of this nature. The development of the LANDIS series of models and subsequent evolution of LANDIS-II over two decades and in many diverse forest ecosystems has vastly improved the capability for complexity in representing forest succession, growth, disturbance, and management prescriptions (Scheller et al., 2007). This study simulated forest growth and succession, mortality and decomposition, wind disturbance, insect disturbance, and several timber-harvest regimes at a relatively fine spatial scale of 20 m over 300 years. PnET-II, the second model used in this study, simulates forest water and carbon dynamics at the stand level, and was linked with climate prediction data from downscaled GCM output. PnET-II output was subsequently incorporated into LANDIS-II to account for the effects of a changing climate on forest ecosystem processes. Building model complexity into this study was believed to be advantageous due to both the complex nature of the Acadian forest and the possible response of forests to climate change.

An often overlooked aspect of predictive simulation modelling, especially in a system as complex as forest ecosystems, is the nature of the data generated. It is first important to recognize that this study simulated future events that are both stochastic and exploratory in nature, and therefore traditional methods of validation and analysis are not appropriate. The extent of successional, disturbance, and management interactions in process-based models such as LANDIS-II negates the rigorous statistical approach used for traditional empirical models, yet the complexity of today's issues (i.e. climate change) necessitates use of these complex process-based models (Porté & Bartelink, 2002). Furthermore, this study in particular incorporated GCM climate prediction data for the next century based on expert narrative on possible future changes in climate, which are not a rigorous quantitative prediction of future conditions (Nakicenovic et al., 2001). For this reason, inferential statistics of model output would be superfluous and risk illuminating trends that may be irrelevant or artificial. This stresses the simple but important concept that modelling studies of this nature are experiments, not predictions.

1.7. Halifax Water and Watershed Management

Arguably one of the most critical forest ecosystem services is the provision of a sustainable water supply (Jones et al., 2009), and the most sustainable and highest quality fresh water resources come from healthy forest ecosystems (Neary et al., 2009). Source water protection and watershed management refer to a collection of multi-stakeholder activities targeted towards protection of municipal water supplies at their source – usually lakes, rivers, and forested watersheds (Ivey et al., 2004; Timmer et al., 2007). Forest management in source water protection areas by water utilities has differing objectives from traditionally managed hinterland forests – given that these watersheds are drinking water sources, often for large urban areas, the principal management goal is water quality as opposed to timber production.

Timber harvesting, especially by clear-cutting, has been shown to cause nutrient and soil loss which can affect nearby surface waters due to eutrophication, acidification, and sedimentation, and can adversely affect aquatic invertebrate communities (Swank et al., 2001; Vaidya et al., 2008). The nature and degree of forest management practices in municipal water supplies are critical to the maintenance of water quality. In a review of

several water utilities practicing some level of active forest management in their watersheds, it was found that small-scale forest management aimed at water quality as opposed to maximum sustained yield of timber had little to no effect on water quality (Herbert, 2004; Herbert, 2007). It has also often been accepted that some level of forest-management intervention is in fact important for the maintenance of water quality, usually by the reduction of natural disturbance vulnerability (Barten & Ernst, 2004). Several aspects of forest management are highly important for maintaining water quality, including maintaining old-growth reserves, minimizing road density, maximizing average stand ages, and lowering logging intensity (Harmon et al., 1987; Trombulak & Frissel, 2000; Herbert, 2007). Riparian buffers around lakes, rivers, and wetlands have also been found to be a critical element for maintaining the hydrological integrity of watersheds (Naiman et al., 2000; Swank et al., 2001).

Halifax Water developed its forest management plan (FMP) to incorporate these best management practices in source water protection. In fact, several studies within the Pockwock watershed have been carried out to ensure that forestry activities are not adversely affecting water quality (McCurdy et al., 2003; Pockwock-Bowater Project Partners, 2005; Vaidya et al., 2008). The Pockwock-Bowater Watershed Project (PBWP) included a series of studies on the effects of forestry activities on forest ecosystems, soil, and water quality, and found no significant impacts on lake water quality and minimal impacts on stream water quality (Pockwock-Bowater Project Partners, 2005). However, Vaidya and colleagues (2008) found that riparian buffers, specifically the width and level of activity (no-harvest or selection harvest) of buffer zones, were important in water quality management. Another significant finding of the PBWP was the high levels of blowdown due to windthrow in the riparian buffers (Pockwock-Bowater Project Partners, 2005). Understanding these best practices in forest management for water quality will be critical as forested water supplies are faced with climate change.

Climate change is highly likely to affect water quality and quantity in forested watersheds (Mote et al., 2003). Evidence of climate change impacts on forested water-supply watersheds have already been observed, such as reduced snowpack, earlier peak snowmelts, warmer summer temperatures, and flooding (Hodgkins et al., 2003; Dettinger et al., 2004; Payne et al., 2004; Jones et al., 2009). However, the cumulative impacts of

climate-induced forest change, timber harvests, and water supply are not fully understood.

As with the relationship between timber supply and climate change, the full range of implications of climate change and water supply/quality are not fully understood, and span from the potentially detrimental to potentially beneficial. For example, mixedwood and broadleaved forests tend to be associated with higher water quality (Puhlmann et al., 2009), and transitional forest biomes such as the Acadian Forest Region are forecasted to have a higher component of temperate broadleaved species with climate change (Neilson, 1993; Bourque et al., 2010). Furthermore, increased WUE of trees due to carbon fertilization (Friend et al., 2010) may reduce evapotranspiration and subsequently increase water supply (Jones et al., 2009). Conversely, the increased frequency and severity of insect/disease outbreak, windthrow, and forest fires have negative implications for water quality, as does the salvage logging operations they necessitate (Dale et al., 2001; Lindenmayer & Noss, 2006). There is a knowledge gap around the relationship of climate change, forests, and water quality, and the stance taken in this study is that a healthy forest that incorporates climate change adaptation in its management will yield the best results for a healthy water supply.

1.8. References

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CHAPTER 2 METHODS

2.1. Study Area

The study area is situated in central Nova Scotia, Canada, and consists of three watersheds: Pockwock Lake, Tomahawk Lake, and Lake Major (Figure 1). Just north of Sackville, Nova Scotia, in Hants County and the HRM are the Crown-owned Pockwock Lake Watershed Protected Water Area and the adjacent Halifax Water-owned Tomahawk Watershed, referred to collectively onward as Pockwock. To the east by 17 km, just north of Dartmouth in the HRM is the Crown-owned Lake Major Watershed Protected Water Area and several privately-owned small properties, referred to onward as Lake Major. The watersheds are Designated Water Supply Areas and protected under the Environment Act (1994-95, c.1., s.1.). A large portion of northeast Lake Major also lies within the provincially designated Waverley-Salmon River Long Lake Wilderness Area, where no timber harvesting occurs.

Pockwock is bounded by -63.8 and -63.9 W and 44.8 and 44.9 N with an elevation ranging between 79 and 231 m above sea level. Lake Major is bounded by -63.5 and -63.6 W and 44.7 and 44.8 N with an elevation ranging between 17 and 185 m above sea level. The total annual precipitation of this region of central Nova Scotia is approximately 1,400 mm, with a mean summer temperature of 16.3°C, mean winter temperature of -5.0°C, and mean annual temperature 5.8°C. The growing season averages around 196 days, with a total of 1,522 GDD (Neily et al., 2003).

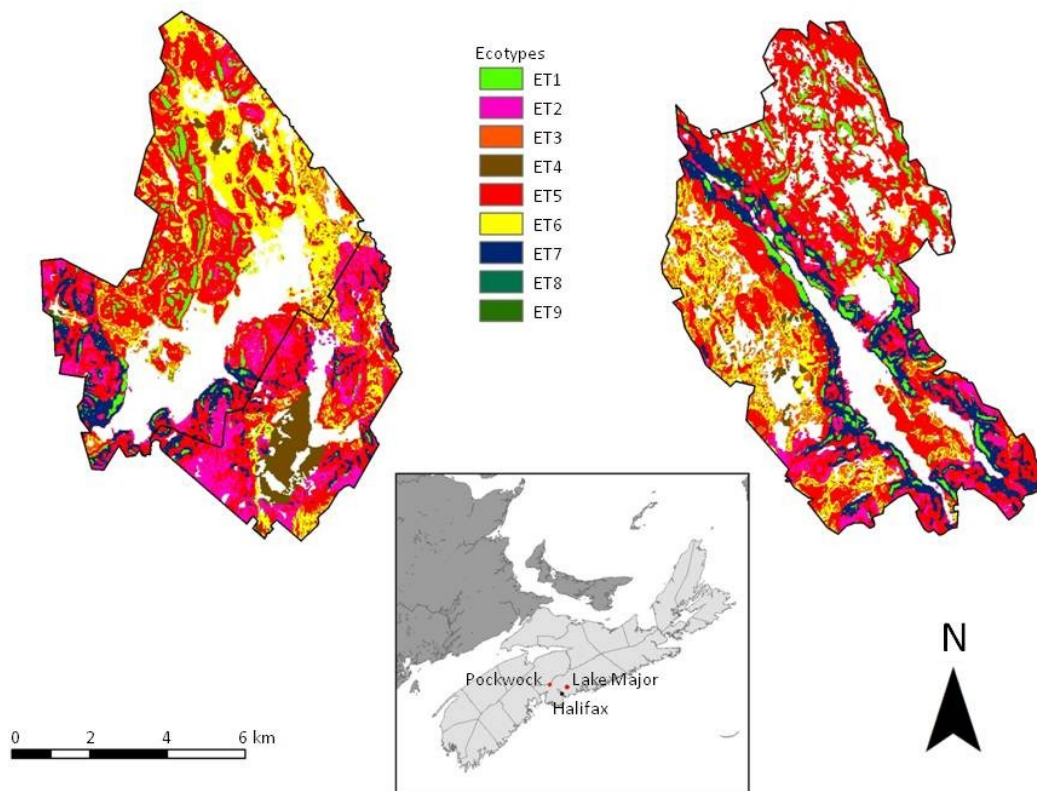


Figure 1 The Pockwock and Lake Major study areas in central Nova Scotia, Canada. The watersheds were classified using the FEC of Nova Scotia into nine different ecotypes. ET1: ecotype one, dry-poor conifer, ET2: ecotype two, fresh-poor conifer, ET3: ecotype three, moist-poor conifer, ET4: ecotype four, wet-poor conifer, ET5: ecotype five, fresh-medium conifer, ET6: ecotype six, moist-medium mixedwood, ET7: ecotype seven, fresh-rich deciduous, ET8: ecotype eight, moist-rich mixedwood, ET9: ecotype nine, wet-rich deciduous.

The regional site conditions of the study area are classified into three categories called ecodistricts in the NSDNR Ecological Land Classification (ELC; Neily et al., 2003). The first region (430-Eastern Granite Uplands) covers the northern half of Lake Major, the majority of which is contained within the protected Waverly-Salmon River Long Lake Wilderness Area, and consists of granite uplands with characteristic exposed bedrock. It is dominated by coarse-textured shallow soils. The forests of the area are mainly coniferous, with stunted black spruce and white pine on the exposed higher elevations and red spruce in the better-drained areas. The second region (440-Eastern

Interior) covers roughly the southern half of both Pockwock and Lake Major and is characterized by glacial till overlaying quartzite and slate bedrock, leading to well-drained and stoney sandy-loam soils. The forest composition of this region varies highly with soil depth from stunted intolerant broadleaved species on shallow dry soils, to red spruce, eastern hemlock, and tolerant broadleaved species in well drained deeper soils, with black spruce dominating in poorly drained areas. The final region (780-St. Margarets Bay) is the most eastern portion of the South Mountain Granite batholith, and covers the northern half of Pockwock. The typical soils of the region are well-drained shallow sandy loams over coarse and stoney glacial till, leading to forest compositions very similar to the Eastern Interior Ecodistrict, but in general with a smaller broadleaved component in well-drained areas.

Table 1 Land types (ha) in the Pockwock and Lake Major watersheds (DNR, 2010).

Land type	Pockwock	Lake Major	Study area
Total	7,134	7,000	14,134
Forested	5,511	5,115	10,626
Coniferous cover	3,836	2,387	6,223
Mixedwood cover	1,029	1,620	2,649
Non-coniferous cover	288	415	703
Inland water and wetland	1,431	1,275	2,706
Non-forested ₁	177	191	368
Barren/rock	15	417	432
Agriculture	0	2	2

1. Includes rail, road, powerline, and pipeline corridors, gravel pits, quarries, mining areas, and urban areas.

The ELC ecodistricts represent broad trends in forest composition at a relatively coarse scale. The study area is in the smaller range of those typically simulated in LANDIS-II, so it was felt that a classification system with a finer spatial resolution was necessary to capture ecosystem complexity and spatial variability at the appropriate scale. It was therefore deemed necessary to develop site data with the capability for a finer spatial resolution than that of the ELC (1:250,000). The FEC is a stand-level classification of several site, soil, and vegetation variables that is employed by forest practitioners in many regions across Canada (Sims et al., 1989; Zoladeski et al., 1995;

Keys et al., 2003). There are currently no spatial FEC data associated with the provincial FRI data, so a suitability analysis of several site variables was developed externally in a geographic information system (GIS) to define the site conditions, based on the provincial FEC, and is described in more detail shortly.

The study area is situated within the Acadian Forest Region, the forest region that occupies the majority of Nova Scotia and the Maritime provinces of Canada. The Acadian Forest Region is a transitional forest between the boreal forest to the north and the temperate forest to the south and west, and contains aspects of both. Characteristic Acadian Forest Region communities in the absence of anthropogenic disturbance are mixedwood in composition, with long-lived, shade-tolerant species such as red spruce, eastern hemlock, yellow birch, sugar maple, American beech, balsam fir, and white pine. Edaphic site conditions and disturbance favour communities of black spruce, tamarack, and shorter-lived early- to mid-successional broadleaved species such as red maple, red oak, white birch, and aspen. The main natural disturbances in the Acadian Forest Region are windthrow, insects, and diseases (Neily et al., 2007). Human impacts in the Acadian Forest Region have left a legacy of impoverished forests in the province, as the Maritimes have the longest history of forest exploitation in North America (Loo & Ives, 2003). Evidence of this includes the loss of tolerant mixedwood forests in favour of coniferous plantations and communities of intolerant broadleaved species, white spruce, and balsam fir (Saunders & Wagner, 2008).

The proximity of the study area to the major seaport of Halifax has also made it vulnerable to invasive forest insects and diseases, such as the BSLB, introduced in Halifax in the 1980s (Smith & Hurley, 2000). In Nova Scotian forests, the BSLB attacks mainly red spruce and is considered an invasive alien species (Colautti et al., 2005), with a containment area designated by CFIA that encompasses a large portion of the HRM, including all of Lake Major and a portion of Pockwock (CFIA, 2007). The beech bark disease, a combination of a scale insect and fungus, was also introduced in Halifax in late nineteenth century. The disease has virtually eliminated the role of beech as a dominant canopy species in mature Acadian forests (Loo, 2009).

2.2. Simulation Models

Two process-based, simulation models were used to explore the relationships between climate change and forest ecosystems (Figure 2). LANDIS-II (Scheller et al., 2007) is the primary model and is a spatially explicit forest landscape and disturbance model that is driven by stochastic processes. PnET-II (Aber & Federer, 1992; Aber et al., 1997; Xu et al., 2009) is a spatially dynamic deterministic ecosystem process model, used to simulate change in forest establishment and growth variables.

LANDIS-II simulates the processes of forest succession, growth, mortality, seed dispersal, and disturbance within a spatially explicit simulated landscape at a user-specified time-step. The landscape is represented in raster format, an array of cells or sites of user-specified resolution, and is stratified into areas of similar abiotic site conditions, called ecoregions. Trees are not individually represented, but rather aggregated into age cohorts of a given species, whereby any site can have multiple species-age cohorts. A series of tree-species life-history attributes included in the simulation are used to model successional processes.

Succession, biomass accumulation, dispersal, age-related mortality, and biomass decay are driven by a main succession module (Scheller & Mladenoff, 2004). The processes of biomass accumulation, mortality, and decay are modelled in terms of mass of living aboveground tree biomass per unit area for each species-age cohort (Mg/ha). Tree biomass was the only forest biomass simulated in this study. Biomass growth is measured by ANPP and is assumed to logarithmically approach a maximum ANPP value, which is calculated by PnET-II. The biomass accumulation of all age cohorts of a species cannot exceed a maximum total AGB. The actual AGB of a given species is dependent on total biomass present on a site, in order to account for the reduction in biomass accumulation as a result of inter- and intra-specific competition. Mortality of species-age cohorts occurs when longevity of that species is exceeded or the cohort is killed by disturbance, at which point the AGB of that cohort is either transferred to the dead biomass pool (as it may be for wind disturbance) or removed from the simulation (as it may be for harvest disturbance). However, the reduction of AGB of a species-age cohort due to age-related mortality begins at half of the longevity of a species and increases logistically to full biomass removal at the age of longevity. Decay is simulated using an

exponential decay equation with decay constants derived from the literature (Scheller & Mladenoff, 2004).

Seed dispersal and seedling establishment are controlled by a dispersal algorithm and stochastic establishment functions. The dispersal algorithm is Brendan Ward's Algorithm (Ward et al., 2005), a negative exponential distribution that was developed using LANDIS-II. Within the range of dispersal of an established species-age cohort, there is a probability that a seedling will become established as a new species-age cohort called the probability of establishment (P_{est}), which is both calculated from PnET-II and altered according to the literature and expert judgement. The P_{est} values are parameterized for all modelled tree species in every ecoregion, and are the main determinants of tree species distribution. A suite of optional disturbance modules is also available for LANDIS-II. This study incorporated the wind, timber harvesting, and biological disturbance modules.

LANDIS-II is a stand-alone piece of software, yet the nature of the spatial data both generated and required by the model necessitated the use of independent GIS software. Software used in this study included ArcInfo 9.3, IDRISI Kilimanjaro, and IAN 1.0.18, a raster analysis program for calculating landscape metrics (DeZonia & Mladenoff, 2004).

PnET-II simulates carbon and water dynamics of forest ecosystems based on established relationships between foliar nitrogen content and photosynthesis, which are in turn influenced by the climate variables of temperature, precipitation, PAR, and atmospheric CO_2 concentrations (Aber & Federer, 1992; Aber & Federer, 1997; Xu et al., 2009). PnET-II has been coupled with LANDIS-II and its predecessors in several studies to calculate the input parameters ANPP and P_{est} based on current and future climate, and yields valid results and meaningful implications for the relationships between forest ecosystems and climate change (Scheller & Mladenoff, 2004; Scheller & Mladenoff, 2005; Xu et al., 2007; Scheller & Mladenoff, 2008; Xu et al., 2009; Gustafson et al., 2010; Ravenscroft et al., 2010). PnET-II calculates the LANDIS-II input ANPP as the combination of wood and foliar NPP. The P_{est} values are calculated using light and water availability and optimal GDD for each tree species (Xu et al., 2009).

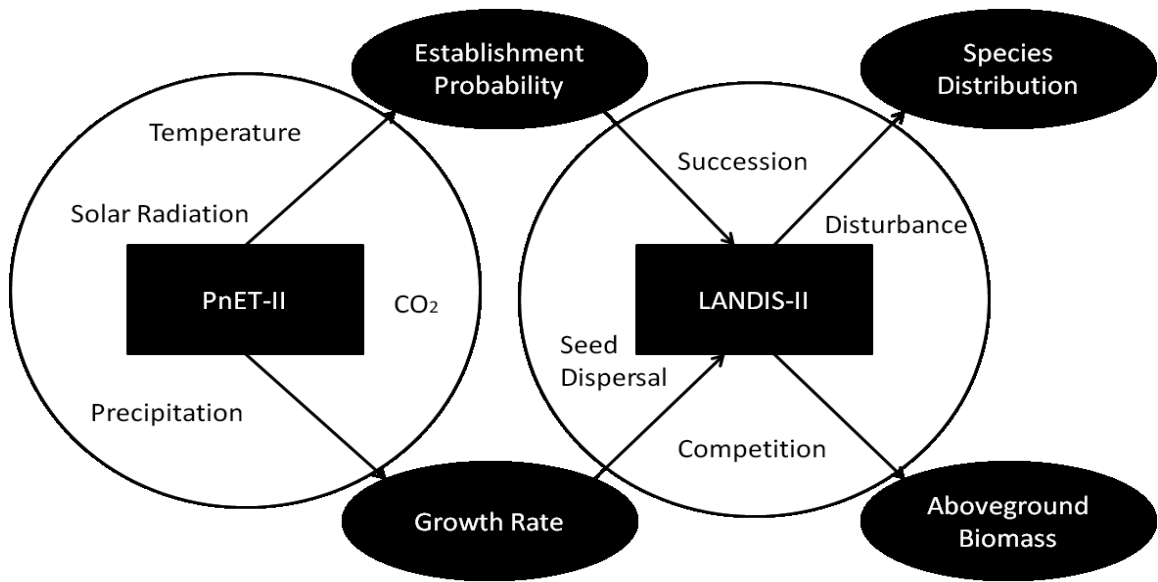


Figure 2 The modelling framework using LANDIS-II and PnET-II, adapted from Xu et al. (2009).

2.3. Model Initialization and Parameterization

The initial forest structure and composition is often less influential on simulation-model output than other forest and tree parameters, but necessitates a considerable amount of effort to construct and is often highly uncertain (Loehle, 1987; Janssen & Heuberger, 1995; Thompson et al., 2007). The initial forest structure and composition for this study were derived from both Forest Resource Inventory (FRI) data (NSDNR, 2010) and from data collected by us in a field survey of the watersheds in 2009. The forest consists of 512 stand types (communities) with a unique combination of species-age cohorts, creating 2,547 individual stands, spatially delineated by the FRI polygons, with a mean size of 4.2 ha. Areas delineated as rock barrens or wetlands in the FRI were considered non-active sites in LANDIS-II. FRI data and mapping have been found to be significantly inaccurate, and have severely limited abilities in classifying understory tree cover (Thompson et al., 2007). This uncertainty can lead to three important inaccuracies in the simulated landscape: underrepresentation of species richness and diversity, oversimplification of the stand-age structure, and a drastic underrepresentation of initial biomass. To reduce these inaccuracies, LANDIS-II was run for 500 simulation years prior to scenario analysis to try to attain steady-state or equilibrium conditions, in what is often termed a spin-up cycle (Jørgensen & Bendoricchio, 2001).

Data were collected in the field using the point-intercept method (Stumpf, 1993), and were collected in areas with the highest uncertainty in cover classification in order to supplement FRI data in the initial forest structure and composition and aid in the reduction of the uncertainty inherent in FRI data. Field data were collected in the study area from May to September 2009, using the point-intercept method to classify 1,831 ha of the 10,609 ha (17%) of forested area within the watersheds. Using the FRI database, stands were prioritized for survey by classification uncertainty (unclassified cover species or age), area (higher priority for larger stands), and accessibility (proximity to roads). A total of 24 stands were selected for data collection. The 24 surveyed stands totaled 621 ha, and the forest conditions in these stands were assigned to all communities with the same classification in the FRI database, giving the total 1,831 ha of classified area. The initial community input data and ecoregion data were in the format of 16-bit raster maps with 20-m resolution.

As mentioned, the data collected in the field and used to classify the initial conditions of the watersheds were not nearly as influential on model output as site and tree-species life-history variables. The utility of the field data in building a strong familiarity with forest conditions in the watersheds proved the most meaningful use of these data, as it assisted with model calibration and validation.

The 16 tree species included in the modelling have a wide array of parameters that define their respective life cycles, competitive abilities, biology, and climatic ranges. The parameters were obtained from a multitude of sources in the peer-reviewed literature (Baldocchi et al., 1988; Pastor & Post, 1988; Burns & Honkala, 1990; Aber et al., 1996; Aber et al., 1997; Goodale et al., 1998; Scheller & Mladenoff, 2005; Xu et al., 2009; Bourque et al., 2010) and consultation with local experts in forest ecology. Appendix A outlines all model parameters and variables used in the LANDIS-II and PnET-II simulations in detail.

Due to the uncertainty surrounding the full effects of CO₂ fertilization on forest ecosystems, changes in stomatal conductance were not included in this study, a decision that is supported in other studies using PnET-II and LANDIS-II (Scheller & Mladenoff, 2008; Gustafson et al., 2010). Furthermore, the wet climate of the Acadian Forest Region suggests that in the absence of edaphic moisture and nutrient limitations, temperature

rather than CO₂ is the limiting factor for forest productivity in the study region (Melillo et al., 1993).

A current limitation of LANDIS-II is that it does not incorporate dynamic soil-nutrient cycling. While nutrient cycles operate over a much longer timeframe than other forest processes (Johnson & Curtis, 2001), it was deemed necessary to account for soil nutrient regimes in the P_{est} values, so the establishment of some tree species was constrained to certain ecoregions depending on nutrient levels.

The climate input parameters for PnET-II were calculated from downscaled GCM projections under the SRES-A2 scenario (IPCC, 2007), discussed in a later section, and include monthly averages of mean maximum temperature (°C), mean minimum temperature (°C), total precipitation (cm), PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$), and atmospheric CO₂ (ppm). PAR was calculated as a fraction of total incident solar radiation; 0.44 from October to March and 0.48 from April to September (Byun & Cho, 2009). Atmospheric CO₂ concentration data are an estimation based on predicted future socio-economic conditions by IPCC's SRES, used in the Fourth Assessment Report (IPCC, 2007).

2.3.1. Forest Ecosystem Classification

The ecoregion data for LANDIS-II were initially developed using the provincial ELC (Neily et al., 2003), a hierarchical classification of site and climatic conditions. However, an ecoregion classification with a finer spatial resolution than was available with the ELC was desired. The FEC is a stand-level system of classification for forest ecosystems that is employed by forest practitioners in many regions across Canada (Sims et al., 1989; Zoladeski et al., 1995; Keys et al., 2003).

The FEC incorporates many biotic and abiotic forest ecosystem components such as stand composition, shrub, herb, and moss layers, soil type, geology, hydrology, slope, and topographic position (Keys et al., 2003), and was developed in the Nova Scotia model forest, which fortunately encompasses all of the study area. FEC is most often used on an individual stand basis by forest managers, yet there is increasing interest in remote sensing and GIS-based FEC of entire forest management areas and landscapes, as FEC is an integral tool for SFM (Treitz & Howarth, 2000; Colville, 2005; Günlü et al., 2009). However, because this is a stand-level system of classification, the availability of

data at the appropriate scale and accuracy is an extreme limitation in the GIS-based approach to FEC (Colville, 2005). The FEC of the study area is no exception to these challenges, yet because the goal of utilizing the FEC was more to examine changes in forest-ecosystem structure and incorporate stand-level variability in site conditions than to develop a spatially accurate classification of the study area, it was believed to be an appropriate approach.

The FEC developed for this study was carried out using the IDRISI Kilimanjaro GIS software package to conduct a multi-criteria evaluation (MCE) to assess the suitability of each site for nine different FEC ecotypes, based on soil type, surficial geology, drainage, slope, and topographic position (Figure 1; Table 2). The MCE employed weighted linear combination of raster maps derived from the previously mentioned five attributes to create a single suitability map, where one of the nine ecotypes was assigned to every site where it has the highest suitability value. In the MCE terminology, factors are quantitative continuous attributes, such as slope, where the suitability of a site for a given ecotype is dependent upon the slope value. All factors are normalized to a suitability value ranging from 0 (least suitable) to 255 (most suitable). Constraints are categorical, nominal attributes that limit the analysis to the presence of that attribute, such as soil type, whereby a site would be considered unsuitable for a given ecotype if it is not constrained by a certain soil type, while all sites that are constrained are equally suitable. Constraint data were assigned zero for not suitable and one for suitable.

This MCE utilized three factors: 1) drainage, a categorical depth-to-watertable dataset, developed by the University of New Brunswick in collaboration with the NSDNR (NSDNR, 2010), 2) slope, measured in percent rise and calculated from Digital Elevation Model (DEM) data (Geobase, 2010), and 3) and topographic position, measured with the topographic position index, a value assigned to each site based on the relative elevation of its neighbours, using DEM data. This tool was developed by Jenness (2006) and is often used in the classification of landforms (Colville, 2005; Jenness, 2006). The MCE also utilized two constraints: 1) soil type, using the soil type classification outlined by the FEC (Keys et al., 2003; Nova Forest Alliance, 2010) and 2) surficial geology, obtained from the NSDNR (NSDNR, 2009).

Only two site parameters are required for PnET-II: soil water holding capacity (WHC), calculated by estimating available water based on sand-clay-loam content and multiplying by the average rooting-depth of a given FEC ecotype (Keys et al., 2003), and latitude.

Table 2 The major species, soil WHC, and moisture, nutrient, and natural disturbance regimes for each of the nine FEC ecotypes found in the watersheds (Keys et al., 2003).

Ecotype	Moisture regime	Nutrient regime	Major species	Natural disturbance regime	WHC (cm)	Area classified (ha)
ET1 Dry-Poor Conifer	Very dry	Very poor	Black spruce	Frequent, stand-replacing	1.55	718
ET2 Fresh-Poor Conifer	Fresh to dry	Poor to very poor	White pine, black spruce, and jack pine	Frequent, stand-maintaining	5.27	989
ET3 Moist-Poor Conifer	Fresh/moist to moist	Poor to very poor	Black spruce, red pine, and white pine	Frequent, stand-maintaining	4.48	567
ET4 Wet-Poor Conifer	Moist/wet to wet	Medium to very poor	Black spruce, red spruce, and balsam fir	Frequent to infrequent, stand-replacing	8.02	309
ET5 Fresh-Medium Conifer	Fresh/moist to dry	Medium to poor	Red spruce	Infrequent, stand-replacing	6.11	5317
ET6 Moist-Medium Mixedwood	Fresh/moist to moist/wet	Medium to poor	Red spruce, eastern hemlock, and balsam fir	Infrequent, stand-replacing	4.73	1814
ET7 Fresh-Rich Deciduous	Moist/Fresh to dry	Rich to medium	Sugar maple, yellow birch, red maple, and red spruce	Gap dynamics	6.31	1182
ET8 Moist-Rich Mixedwood	Fresh/moist to moist/wet	Rich to medium	Red maple, sugar maple, red spruce, yellow birch	Infrequent, stand-replacing	5.51	61
ET9 Wet-Rich Deciduous	Moist/wet to wet	Very rich to medium	Red maple, balsam fir, yellow birch, and red spruce	Infrequent, stand-replacing	5.31	12

2.3.2. Biological Disturbances

The biological disturbance module was parameterized to simulate bark-beetle disturbance of both the native spruce bark beetle and introduced BSLB (Magasi, 1995; Smith & Hurley, 2000). Beetle outbreak was considered chronic, with low rates of mortality occurring at every time step. White spruce, black spruce, and red spruce were the simulated host species, with vulnerability to attack occurring in the mature age class and mortality beginning at the overmature age class, as defined by the NSDNR (NSDNR, 2010). The spatial pattern of bark-beetle infestation was parameterized to be synchronous in the landscape, due to the smaller size of the watersheds (Gray, 2008).

2.3.3. Wind Disturbance

The succession, wind, biological disturbance, and harvest modules operated at 10-year time-steps. The wind disturbance module generates disturbance events stochastically, with event frequency derived from wind rotation-period parameters and event sizes derived from mean, minimum, and maximum event-size parameters, all of which were determined from historical disturbance sizes and frequencies in the Acadian Forest Region (Seymour et al., 2002). Four wind-disturbance regimes were parameterized: 1) frequent stand-initiating disturbances, 2) moderate, stand-maintaining disturbances, 3) infrequent, catastrophic disturbances, and 4) gap dynamics (Neily et al., 2007). The disturbance regimes were assigned to the nine ecotypes based on site, soil, and stand conditions (Keys et al., 2003).

Each disturbance event was assigned one of five severity classes, whereby the higher the severity of the disturbance event, the younger the species-age cohort killed. In other terms, an event with a severity of five will kill all species-age cohorts older than 20% of their longevity, and a severity of one will kill all above 85% of their longevity. This process represents a limitation in the simulation of wind disturbance, in that it is insensitive to tree species composition and stand structure, so sugar maple in an uneven-aged stand would sustain the same mortality as red spruce in an even-aged stand in an event of the same severity. However, variation in wind vulnerability due to site conditions was accounted for by simulating different disturbance regimes dependent upon FEC ecotype (Table 2).

2.3.4. Harvest Disturbance

The timber harvest disturbance module was parameterized differently for the two separate modelling experiments. Firstly, a simple even-aged, clear-cutting harvest regime was established in an attempt to mimic historic harvesting in the region to be used as a control in both modelling experiments. Total biomass of every species-age cohort was removed from each site within a harvested stand, with a yearly target or annual allowable harvest area equalling 1.5% of the watersheds. An adjacency rule of 10 yr was used, but no minimum stand age was necessary to qualify for harvesting. In all scenarios simulating timber harvesting, harvest priority was assigned based on stand age, with the oldest stands receiving the highest harvest priority. In the second modelling experiment, the timber harvest disturbance module was employed to incorporate different climate change adaptations into the harvest regimes, and will be described in detail in Section 2.4.

2.4. Experimental Design

The two simulation experiments were conducted using LANDIS-II. The first experiment is the subject of Chapter 3 and focused on the impacts of climate change in the forest ecosystems of the study area. The second experiment is the subject of Chapter 4 and examined a conceptual, landscape-scale approach to climate change adaptation in the management of the forests of the watersheds. In experiment one, a two-by-two scenario construction was used, with two disturbance scenarios and two climate scenarios (Table 3). Each scenario was run for 300 yr, representing the period from 2000 to 2300. The two disturbance scenarios included a natural disturbance regime scenario, simulating wind and bark-beetle disturbances only, and a forest-management scenario, simulating historic harvest practices in addition to the natural disturbance regimes.

Table 3 Scenario construction of the first experiment in LANDIS-II. Scenarios 1A and 1B simulated the current climate and climate change in pre-settlement Acadian forest types, while scenarios 2A and 2B simulated the two climate scenarios in an actively managed forest.

	Current climate	Climate change
Natural disturbance regimes (wind and bark beetles) only	Scenario 1A	Scenario 1B
Natural disturbance regimes and timber harvests	Scenario 2A	Scenario 2B

To account for the high levels of uncertainty in GCM climate prediction, this study simulated the forest landscape under both a current climate and extreme climate change scenario to incorporate the whole range of prediction (Ravenscroft et al., 2010). The no-change scenario used climate data from current-climate conditions, an average of the 1961-2000 climate variables output from the CRCM for the study area, with total annual precipitation ranging between approximately 1,000 mm and 1,400 mm and mean annual temperature ranging between approximately 4°C and 6°C.

The climate change scenario used in both LANDIS-II experiments was the SRES-A2 climate scenario, developed by SRES and used in the IPCC Fourth Assessment Report, which predicts atmospheric CO₂ levels stabilizing at 850 ppm by the year 2100, leading to a 5.8°C increase in mean annual temperature and a smaller 6.9 mm increase in total annual precipitation in the study area (Nakicenovic, 2001; IPCC, 2007; CCCMA, 2009). The historic and climate change data were retrieved from the CCCMA (CCCMA, 2009). Monthly data from the CRCM4.2.3 time-slice for the 1961-2100 period were used for both the current climate scenario and the climate change scenario. It may have been beneficial to contrast the SRES-A2 scenario with a more moderate IPCC climate change scenario, but the downscaled data for the study area were not available, and as such the current climate scenario was used.

The CRCM is a downscaling tool for GCM data that functions at a regional scale of 46 horizontal kilometres in North America. It is driven by the CGCM3 for the baseline years of 1960-2000 and the SRES-A2 scenario for the years of 2001-2100 (IPCC, 2007; CCCMA, 2009). Monthly means of maximum temperature, minimum temperature, total precipitation, PAR, and atmospheric CO₂ were input in PnET-II to model ANPP and P_{est} for subsequent input into LANDIS-II.

In the climate change scenarios within both experiments, the climate-driven changes in the ANPP and P_{est} variables were quantified every 10 yr from 2001 to 2100 for input into LANDIS-II. The climate change scenarios in LANDIS-II simulated the

PnET-II-derived variables for the first century of simulation, while maintaining the 2091-2100 ANPP and P_{est} variables for the remaining two centuries of simulation. The 500 yr spin-up cycles were simulated under the 1961-2000 climate, using the same ANPP and P_{est} values simulated in the current climate scenarios. In experiment one, historic timber harvesting was simulated in the spin-up cycle for scenarios 2A and 2B, but not scenarios 1A and 1B, which simulated natural disturbance regimes only in order to return the initial forest communities to typical pre-settlement Acadian forest. In experiment two, the spin-up cycles for all scenarios simulated historic timber harvesting.

In the second experiment, climate change adaptation was incorporated into timber harvesting (Figure 3). Three experimental harvest treatments for the timber harvesting module in LANDIS-II were developed in consultation with local forest researchers and forest managers at Halifax Water based on management goals and objectives, and the capacity of the modelling framework. The focus was directed towards three components of timber harvests: canopy-opening size of cuts, age of the trees removed from a harvested stand, and composition of trees removed from a harvested stand.

The size treatment targeted different spatial orientations and sizes of canopy openings within harvests. It is possible to have multiple prescriptions within a harvest treatment in LANDIS-II, and the size treatment was the one where this feature was employed. Three prescriptions were simulated in this treatment based on the composition and natural disturbance regimes of the forest ecosystems, called ecotypes in the FEC of Nova Scotia (Keys et al., 2003; McGrath, 2007; 2009). Clear-cutting was prescribed in coniferous ecotypes with frequent stand-replacing disturbances, with harvest size targeted between 1 ha and 10 ha. Group selection was prescribed in tolerant coniferous and mixedwood ecotypes with infrequent stand-replacing or stand-maintaining disturbances, with opening sizes of 0.1 ha. Finally, individual tree selection was prescribed in tolerant broadleaved ecotypes with gap dynamics, with opening sizes set as small as possible, 0.04 ha (i.e. input map resolution). Total biomass of all species-age cohorts in openings of all three prescriptions was removed on all harvested sites, and stands required a minimum cover age of 50 yr to qualify for harvesting.

The age treatment was the least complex, and focused on the age of sexual maturity and seed production of harvested trees. All species-age cohorts in a harvested

stand at or below the age of sexual maturity were exempt from harvesting, in order to promote rapid succession to climax communities. Harvest size was targeted between 1 ha and 10 ha and total biomass of all species-age cohorts at least one time-step (10 yr) older than the age of sexual maturity was removed. A minimum cover age of 50 yr was again required for harvesting.

The third and final composition treatment constrained which tree species were harvested in a stand and was the only species-specific treatment. The 16 tree species included in the modelling were aggregated into three groups based on the change in their distribution in response to climate change in the first experiment. The tree species were either harvested or retained depending on their simulated response to climate change and on management values at Halifax Water. The first group consisted of colder-climate boreal species that experienced a decrease in landscape presence and abundance due to climate change, and included balsam fir, black spruce, white birch, white spruce, red pine, and tamarack. These were termed priority-removal species and were harvested. The second group consisted of more temperate species and pioneer species that were highly favoured in the warmer climate and/or exhibited considerable increases in landscape presence, which were red maple, white pine, large-tooth aspen, and trembling aspen. These were termed opportunistic-removal species and were harvested. The third group consisted of a combination of species that were either favoured in the warmer climate (American beech and red oak), late-successional species that were robust to the climatic changes (eastern hemlock and sugar maple), or species with a variable response depending on management activities (red spruce and yellow birch). The unifying attribute of all these species was that they were considered ecologically important and conservation priorities by managers at Halifax Water. These species were termed conservation targets, and were excluded from harvesting in all stands. Harvest size was again targeted between 1 ha and 10 ha and required a cover age greater than 50 yr. Despite the species-oriented nature of this treatment, the composition of a stand did not influence the harvesting priority.

Stands with a cover age greater than 50 yr that met the necessary conditions of a given timber harvest treatment were prioritized by age at each time-step, whereby the oldest qualifying stand was most likely to be harvested. An adjacency rule of 10 yr was

also used. The annual allowable harvest area in all scenarios save the control was maintained at 1% in accordance with the current Halifax Water forest management plan. Importantly, less than 1% could be harvested if defined conditions for harvesting were not met at a given time-step.

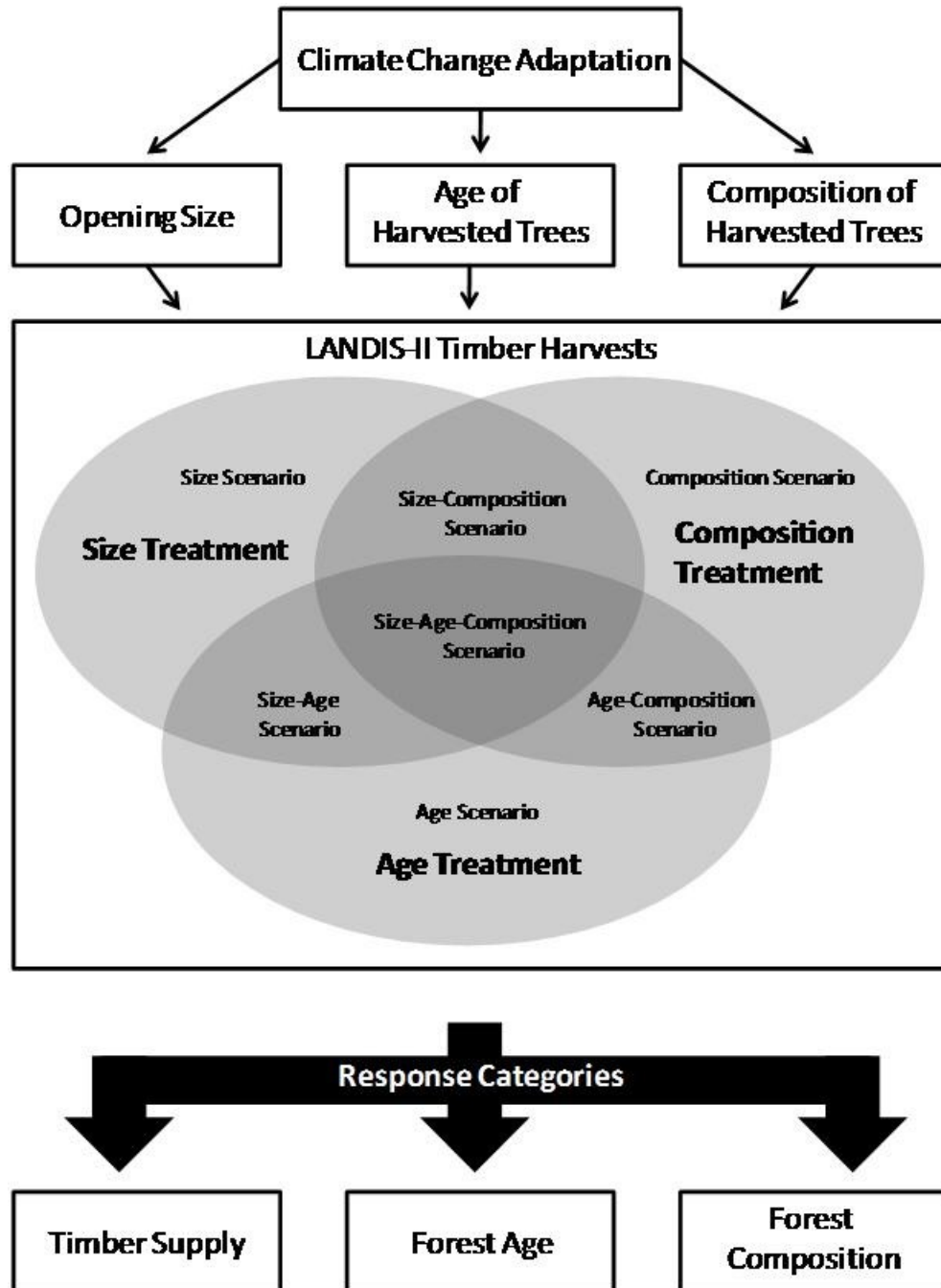


Figure 3 Conceptual framework for the implementation of climate change adaptation into this study. The opening size, age of harvested trees, and composition of harvested trees were manipulated in response to anticipated and simulated climate change impacts in the watersheds to create the three size, age, and composition experimental adaptation treatments. The treatments were simulated in seven different climate change scenarios in LANDIS-II. Forest change in the scenarios was evaluated in three different response categories: timber supply, forest age, and forest composition.

Eight scenarios were simulated in this study: one control and seven experimental (Table 4). The control scenario was identical to scenario-simulated even-aged timber harvesting calibrated to historical practices in central Nova Scotia used in experiment one. Each of the three adaptation treatments were simulated individually in the first three scenarios. The treatments were then simulated in all possible combinations with each other in the final four scenarios. Each scenario was again simulated for 300 yr, representing 2000 to 2300.

Table 4 Scenario construction of the climate change adaptation experiment in LANDIS-II. The different adaptation treatments simulated in the seven experimental scenarios are marked by an X.

Adaptation	Size treatment	Age treatment	Composition treatment
Control scenario			
Size scenario	X		
Age scenario		X	
Composition scenario			X
Size-age scenario	X	X	
Size-composition scenario	X		X
Age-composition scenario		X	X
Size-age-composition scenario	X	X	X

2.5. Data Analysis

Each LANDIS-II scenario in both experiments was replicated five times to account for the stochasticity of seed dispersal, seedling establishment, and disturbance events (Ravenscroft et al., 2010). Because the variance of the response variables between replications was so low (typically between 1-2%), significance testing between scenarios

would be irrelevant and one replication was therefore selected at random for further analysis among ecotypes at simulation year 2300.

A rigorous quantitative validation of a modelling study of this nature is essentially impossible (Jørgensen & Bendoricchio, 2001). This is because an external validation dataset of the appropriate scale is not accessible, and more importantly, at a conceptual level, projections of future conditions, such as climate change, cannot be validated (Rastetter, 1996). This illustrates the fundamental concept that the use of simulation models is a valuable tool for experimental exploration and forecasting of future scenarios, rather than a precision tool for predicting future conditions, which also invalidates the use of inferential statistics to test between scenarios. For simulations of undisturbed forest conditions such as scenario 1A, the necessary historical data of forest conditions are rarely available. For this reason, forest models with broad spatial and temporal scales, such as LANDIS-II, use a combination of the literature, expert consultation, and field sampling, when available, to assess model reliability and validity (Vanclay & Skovsgaard, 1997). In this study, model output of the no-harvest simulations was compared to the literature of historical conditions (Goldsmith, 1980; Loo & Ives, 2003) and old-growth (Mosseler et al., 2003; Stewart et al., 2003) in the Acadian Forest Region, and assessed by local forest researchers and practitioners, including the forest manager at Halifax Water. For the harvest scenarios, model reliability and validity were assessed using permanent sample plot (PSP) data of current forest conditions from the NSDNR (Townsend, 2003).

In the first experiment, the effects of the changing climate on forests were gauged in terms of forest composition, productivity, and age structure, at both watershed and ecotype scales. Forest composition was indicated by the landscape presence (%) of each tree species at simulation year 2300, calculated simply as the percent of active cells where a given species had at least one age cohort present. The biomass variable was total living AGB of all tree species, expressed in Mg/ha. Biomass was graphed as a time series for the entire 300 yr simulation at the watershed scale to observe any temporal patterns. The AGB variable was also calculated for year 2300 at the ecotype scale. The age variable was the area covered by five seral stages for the entire watersheds, similar to

Gustafson et al. (2010). The five seral stages were establishment (0–40 yr), early-seral (41–100 yr), mid-seral (101–140 yr), late-seral (140–200 yr), and old-growth (> 200 yr).

To assess a coarse measure of forest resilience, biodiversity and structural complexity indicators were used. The biodiversity indicator was species richness and the structural complexity indicator was the evenness of age-class distributions, calculated using Shannon-Weaver evenness, a measure of evenness based on Shannon's index of diversity (Shannon & Weaver, 1963; DeZonia & Mladenoff, 2004). Species richness was simply the number of species present on a site (raster cell), averaged at the watershed and ecotype scale. Evenness was the measured diversity of all age cohorts on a site, calculated with Shannon's diversity index, divided by the maximum possible diversity on that site. The indicator ranges between 0 and 1, where a value of 1 represents a completely even distribution of age cohorts on a site. External software used for analysis included ArcInfo 9.3, IDRISI Kilimanjaro, and IAN 1.0.18 (DeZonia & Mladenoff, 2004).

In the second experiment, a more detailed analysis of the timber harvesting was necessary. A time-series graph of average watershed AGB (Mg/ha) and total annual biomass removed in timber harvesting (HB; Mg/yr) for the entire 300 yr simulation was used to analyse the effect of each scenario on a coarse measure of harvest yield, as well as the combined effect of climate change and climate change adaptation on landscape-level forest productivity.

To examine the effects of climate change on forest age, average cover age (yr) was calculated at simulation-year 2300. Also, average patch size (ha) and total area (ha) of old-growth forest (OGF) were calculated at simulation-year 2300. In this study, OGF patches were calculated using eight nearest neighbours of sites with a maximum cohort-age equalling or greater than 125 yr (Stewart & Neily, 2008). Average OGF patch size was calculated from maximum cover-age raster maps output from LANDIS-II in the IAN 1.0.23 software package (DeZonia & Mladenoff, 2004).

In light of the more conceptual and landscape-scale approach to climate change adaptation in forest management introduced in this study, it was felt that an alternative spatial representation of the forest would better illuminate the effects of the different adaptation treatments. Rather than define and map climate-driven changes in existing

forest communities as is often done (Iverson & Prasad, 2001; Ravenscroft et al., 2010), tree species were aggregated and mapped according to their response to climate change in the first experiment, rather than their community associations. This was believed to be a useful approach, as climate change may lead to a restructuring of forest communities and ecosystems because tree species distribution will be affected at the individual species level, not community level (Webb & Bartlein, 1992; Hansen et al., 2001; Bourque & Hassan, 2008; Thomson et al., 2009). These mapped species groupings (Table 5) corresponded to the three groups of species defined in the composition treatment.

Table 5 Tree species grouped according to their response to climate change in the composition treatment, and mapped for all scenarios.

Species grouping	Explanation	Species
Priority removal	Species with a decrease in landscape presence due to climate change	Balsam fir, white birch, tamarack, white spruce, black spruce, and red pine
Opportunistic removal	Species with a large increase in landscape presence due to climate change	Red maple, white pine, large-tooth aspen, and trembling aspen
Conservation target	Species with a variable response or little change in distribution due to climate change and deemed a conservation priority in the study area.	Sugar maple, yellow birch, American beech, red spruce, red oak, and eastern hemlock

The spatial distribution of these three categories was mapped according to age, whereby a site was classified as a response category based on the oldest species-age cohort present on that site. These raster images were generated directly in LANDIS-II for each scenario at simulation year 2300, and at year 2000 for the control only (as maps would be virtually identical between scenarios at this point) to illustrate the initial conditions. The Pockwock watershed was selected for mapping. Time-series graphs of the change in landscape presence (%) of these response categories were also included. Finally, to provide some insight into the species-level effects of climate change adaptation, the change in species landscape presence (%) between simulation year 2000 and 2300 was tabulated.

To assess the efficacy of each adaptation strategy and organize the data presented in this study, forest response categories were delineated that reflected the management

values and objectives in the watersheds. Given the nature of LANDIS-II for simulating forest dynamics of larger areas and timeframes and the conceptual approach to climate change adaptation in this study, these were conceived as values-based categories applied at the landscape-scale. The three response categories in which adaptation was evaluated were timber supply, forest age, and forest composition. The timber supply category examined the AGB and HB data, the forest age category examined the average cover age and OGF variables, and the forest composition category examined the landscape presence data for the groupings of tree species, as well as the change in landscape presence over the course of the simulation for each species.

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CHAPTER 3 MODELLING THE EFFECTS OF CLIMATE CHANGE, TIMBER HARVEST, AND NATURAL DISTURBANCE ON THE FORESTS OF A WATER SUPPLY IN CENTRAL NOVA SCOTIA, CANADA

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3.1. Introduction

Climate change poses numerous threats to forests around the globe due to changes in forest productivity, shifting ranges of tree species, and changes in natural disturbance regimes (Dale et al., 2001; Field et al., 2007; McKenney et al., 2007; Iverson et al., 2008). However, the future brings with it a great level of uncertainty, as the extent of climate change will greatly depend on our actions today and will vary tremendously across biomes and regions (Norby et al., 2005; Intergovernmental Panel on Climate Change [IPCC], 2007). Forests store vast amounts of carbon in the biomass of trees, and have the potential to mitigate climate change by acting as sinks for atmospheric carbon dioxide (CO₂). Forest management may have a role to play in the mitigation of global climatic change, but forests are also highly vulnerable to changes in climate (Williamson et al., 2009). Understanding the range of possible impacts on forest ecosystems will be critical in ensuring their future functioning and the continuing provision of the services upon which society has become dependent. In central Nova Scotia, Canada, one such ecosystem service is the provision of clean drinking water to the major urban core of Atlantic Canada. As such, the impacts of climate change on the forests of these watersheds and subsequent mitigative forest management activities will be important in the sustainability of the water source.

The productivity of forests, as indicated by net primary productivity (NPP) and aboveground biomass (AGB), may be affected in varying ways by climate change. The metabolic processes of trees, mainly photosynthesis and respiration, may benefit from the changes in climate, leading to increases in forest productivity (Schimel et al., 2001;

Norby et al., 2005). A rise in temperature often means a lengthening of the growing season when trees are metabolically active, meaning a longer portion of the year for trees to sequester carbon and accumulate biomass (McMahon et al., 2010). This has already been observed in forests at high latitudes (Braswell & Schimel, 1997; Zhou et al., 2001; Bunn & Goetz, 2006).

However, if soil water or nutrients are limiting, or growing season temperatures exceed optimal temperatures for photosynthesis, then a lengthening of the growing season could have negative effects on forest productivity (Aber et al., 2001). Changes in soil moisture and nutrient regimes may also result from climate change (McMahon et al., 2010). More precipitation, especially in areas where stress due to soil water availability is a limiting factor, can increase NPP. However, the temporal variation of precipitation events will be critical, as the amount of precipitation during the growing season is often predicted to decrease, causing droughts in some areas and limiting productivity due to stress associated with lower soil water availability (Barber et al., 2002).

Nutrient availability in the soil, nitrogen in particular, may also increase as a result of increased decomposition of dead organic matter under elevated temperatures (Saxe et al., 2001; Körner et al., 2005; Verburg, 2005). Yet another possible benefit to forest productivity is the increased atmospheric CO₂ itself, in a process known as CO₂ fertilization or enrichment (Aber et al., 2001; Xu et al., 2007; Friend et al., 2010). This refers to a plant's ability to maintain higher rates of photosynthesis due to lowered stomatal conductance caused by an enriched atmospheric CO₂ concentration (Field et al., 1995; Medlyn et al., 2001; Friend, 2010). The lowered stomatal conductance means lowered evapotranspiration, and therefore higher water-use efficiency (WUE), which is the ratio of CO₂ sequestered to water lost by stomatal conductance, leading to higher NPP (Farquhar et al., 1980). There is debate as to the overall influence of CO₂ fertilization on forest productivity (Curtis & Wang, 1998; Mingkui & Woodward, 1998; Gitay et al., 2001). Temperate and boreal forest species, especially conifers, have been predicted to experience a much smaller increase in WUE in comparison with other plant species and terrestrial ecosystems, such as grasslands (Saxe et al., 2001; Xu et al., 2009; Tian et al., 2010). Still others predict that increases in productivity observed at the onset of climate

change will eventually decrease as plants acclimate to the higher CO₂ concentrations (Mingui & Woodward, 1998; Gitay et al., 2001).

The cumulative effects of climate change on terrestrial ecosystem productivity, including forest ecosystems, are still not fully understood, as studies often have variable or conflicting findings with high levels of uncertainty (Heimann & Reichstein, 2008). Moreover, the response of forest productivity is predicted to vary tremendously by region and ecosystem (Pastor & Post, 1988; Schimel et al., 2001; Norby et al., 2005; Friend, 2010). Factors such as natural disturbances, growth and successional processes, and barriers to dispersal will also be crucial in predicting the effects of climate change on forest productivity (Scheller & Mladenoff, 2005). Forest composition at the landscape scale will likely be highly influential on forest productivity, as some tree species within an ecosystem may no longer be favoured to establish in the altered climate, while others may migrate from southerly regions due to a northern shift in their climatic range limits.

Climate is a main controlling factor in the geographic distribution of plants (Forman, 1964), and changes in climate, such as increased atmospheric CO₂ and temperature and altered precipitation, are predicted to affect the distribution, phenology, and physiology of trees as well as the functioning of forest ecosystems (McKenney et al., 2007; Xu et al., 2007; Iverson et al., 2008; Bourque et al., 2010). Several geophysical variables related to climate are largely responsible for tree species distribution and abundance, which include soil water content, growing degree days (GDD; a temperature-based index of growing season length), soil fertility, and photosynthetically active radiation (PAR; the proportion of incident solar radiation that can be used by plants in photosynthesis), all of which are predicted to change in the near future (IPCC, 2007; Xu et al., 2009; Bourque et al., 2010). Changes in the geographic distribution, or range, of tree species in response to climate change will likely vary widely among species depending on life cycle, biology, current range, and forest community composition (Hansen et al., 2001; Bourque & Hassan, 2008; Thomson et al., 2009). Consequently, a restructuring of many forest communities is likely to occur as range shifts will occur at the individual species level, not the community level (Webb & Bartlein, 1992). Such severe changes in forest composition could affect complex ecosystem processes such as competition and succession in unforeseen ways (Gustafson et al., 2010).

Broad-scale modelling studies in North America and Europe have investigated the response in climatic range of many tree species and have found variable changes in range size and northward shifts up to 700 km (Sykes & Prentice, 1996; Iversen et al., 2004; Iversen et al., 2008; McKenney et al., 2007). The impacts of climate change on forest composition are likely to be most severe at transitional areas between biomes, also called ecotones, because they contain a mix of tree species near the southern and northern limits of their respective ranges (Neilson, 1993; Noble, 1993; Pitelka, 1997; Ravenscroft et al., 2010). The Acadian Forest Region of Atlantic Canada and the northeast United States is an example of a transitional forest region between the boreal forest to the north and the temperate forest to the south. As such, it is characterized by a mix of species from both regions, which makes it vulnerable to widespread changes in forest composition with climate change (Loo & Ives, 2003; Mosseler et al., 2003). The forests of northern Wisconsin and northeast Minnesota are studied examples of transitional forests that have been predicted to undergo severe changes in forest composition due to climate change (Pastor & Post, 1988; Scheller & Mladenoff, 2005; Scheller & Mladenoff, 2008).

In Nova Scotia, boreal species such as balsam fir, black spruce, and white birch, are predicted to have smaller potential ranges or even suffer provincial extirpation, while warmer-climate temperate species such as sugar maple, red oak, white pine, and red maple are predicted to have an increase in their potential range (McKenney et al., 2007; Bourque & Hassan, 2008; Bourque et al., 2010). To investigate the myriad of implications of climate change for tree species distribution and forest composition, it is important to differentiate between realized and fundamental niches. A fundamental niche, also called potential range, is the geographic range determined by favourable climatic conditions for establishment and growth, and is also termed a climate envelope (He et al., 1999; McKenney et al., 2007). A realized niche, also called the actual range, is the geographic range where a given species is found, and is generally smaller than the fundamental niche because it includes biological and geophysical restrictions on dispersal, such as competition, soil moisture, nutrient regimes, disturbance history, and topographic and anthropogenic barriers to dispersal (Xu et al., 2007). An altered climate may lead to a shift in the favourable climatic conditions that envelope the range of a tree species, but the actual change in distribution of that species will be highly dependent on

the aforementioned biological and geophysical variables (Hampe, 2004). Exploring which tree species can grow and are favoured in a given landscape is a vital aspect of sustainable forest management, so any changes in the possible distribution of these tree species should be studied.

An understanding of the dynamics of natural disturbance will also be crucial in managing forests in the face of climate change because altered regimes and increased frequency and severity of events are expected, posing a serious threat to forests and the forest sector (Peterson, 2000; Dale et al., 2001; Millar et al., 2007; Gray, 2008). Natural disturbances are a crucial component of forest-ecosystem dynamics and play a large role in determining forest composition and age structure (Pickett & White, 1985; Frelich, 2002). Examples of recent severe natural disturbances in Canada that have in part been attributed to climate change include the mountain pine beetle outbreak in British Columbia and Alberta (Kurz et al., 2008), the 2001-2003 drought causing large-scale die-back in the western Canadian interior (Hogg & Bernier, 2006), and the largest recorded outbreak of spruce bark beetle in the Yukon (Berg et al., 2006).

In central Nova Scotia and the majority of the Acadian Forest Region, wind and insects are the most frequent natural disturbances (Loo & Ives, 2003). Recent examples of these disturbances that may have been exacerbated by climate change include spruce-bark-beetle outbreaks in the Cape Breton Highlands and Hurricane Juan, which in 2003 caused widespread tree mortality in central Nova Scotia (Neily et al., 2007; Steenberg & Duinker, 2010). The forest management history of Nova Scotia has left a legacy of forest landscapes that are much more vulnerable to natural disturbance due to prevalence of intensive and extensive even-aged forest management, and the widespread loss of tolerant mixedwood communities in favour of young communities of conifers and intolerant broadleaved species (Goldsmith, 1980; Mosseler et al., 2003). A change in natural disturbance regimes, especially an increase in the magnitude and severity of wind events and insect outbreaks, is also an important issue in source-water protection, as an increase in forest disturbances has negative implications for water quality (Dunne et al., 2001).

The ability to model the intricate and numerous processes involved in forest ecosystems and their management is severely limited by uncertainty and lack of knowledge, insufficient or unobtainable data, and the sheer computational magnitude of

what such a study would involve (Sturtevant et al., 2007). Studies that investigate the effects of climate change on forests at the national and continental scale are highly important in understanding broad patterns of change. However, studies that model forest response to climate change at the landscape or watershed scale are critical because they allow for inclusion of intricate biological, geophysical, and climatic processes into the modelling framework. The modelling framework provided by LANDIS-II and PnET-II can be linked with general circulation model (GCM) output data and are proven tools in examining detailed effects of climate change on forest ecosystems at an operational landscape scale (He et al., 1999; Scheller & Mladenoff, 2005; Scheller et al., 2008; Scheller & Mladenoff, 2008; Xu et al., 2009; Gustafson et al., 2010; Ravenscroft et al., 2010). We believe that this approach will allow for an assessment of the threats of climate change to the forests of the Acadian Forest Region within a critical management area. Such an approach has not yet been taken in this unique forest region.

The purpose of this study is to investigate the effects of climate change on the forests of two watersheds in central Nova Scotia that provide potable water in the Halifax Regional Municipality. The Pockwock and Lake Major watersheds are managed by Halifax Water, a utility that practices active forest management within the watersheds. The study is one of several approaches to be used to incorporate climate change into its forest-management planning. There may also be some serious implications of climate change for future water quality and source water protection, but the intricate dynamics of forests and water quality and what changes in those dynamics might imply are not the focus of this project. Study objectives include: 1) assessing the effects of a severe climate change scenario on the composition, structure, and productivity of the forests of central Nova Scotia, 2) examining the influence of intensive forest management on the response of the forests to the changing climate, and 3) observing how climate change may restructure forest ecosystems using the Nova Scotia Forest Ecosystem Classification framework (Keys et al., 2003).

3.2. Methods

3.2.1. Study Area

The study area consisted of the Pockwock Lake, Tomahawk Lake, and Lake Major watersheds located in central Nova Scotia, Canada (Figure 4). The watersheds are in two discrete areas approximately 17 km apart - to the west is the Crown-owned Pockwock Lake Watershed Protected Water Area and the adjacent Halifax-Water-owned Tomahawk Watershed, referred to collectively as Pockwock, and to the east is the Crown- and privately-owned Lake Major Watershed Protected Water Area, referred to as Lake Major. The watersheds are bounded by -63.9 W, -63.5 W, 44.7 N, and 44.9 N, with an elevation ranging between 17 m and 231 m above sea level. The total annual precipitation of this region of central Nova Scotia is approximately 1,400 mm, with a mean summer temperature of 16.3°C, mean winter temperature of -5.0°C, and mean annual temperature 5.8°C. The growing season averages around 196 days, with a total of 1,522 GDD (Neily et al., 2003).

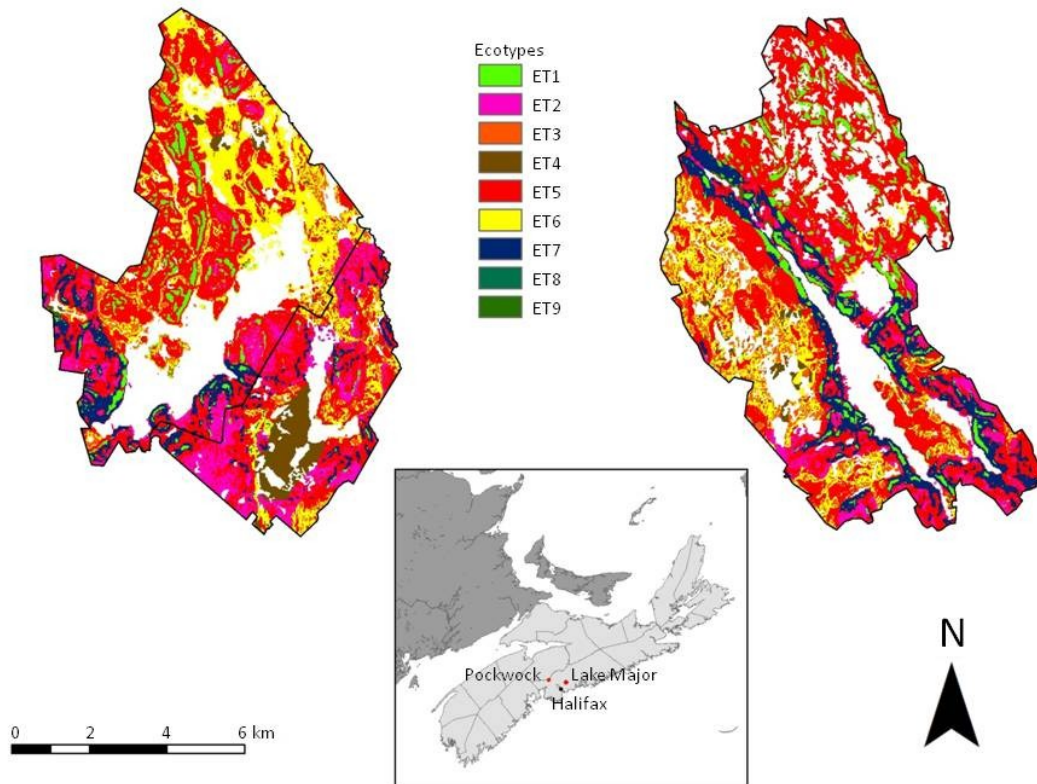


Figure 4 The Pockwock and Lake Major study areas in central Nova Scotia, Canada. The watersheds were classified using the FEC of Nova Scotia into nine different ecotypes. ET1: ecotype one, dry-poor conifer, ET2: ecotype two, fresh-poor conifer, ET3: ecotype three, moist-poor conifer, ET4: ecotype four, wet-poor conifer, ET5: ecotype five, fresh-medium conifer, ET6: ecotype six, moist-medium mixedwood, ET7: ecotype seven, fresh-rich deciduous, ET8: ecotype eight, moist-rich mixedwood, ET9: ecotype nine, wet-rich deciduous.

The site conditions of the study area can be divided into three broad regions, defined as ecodistricts in the Nova Scotia Department of Natural Resources' (NSDNR) Ecological Land Classification (ELC; Neily et al., 2003). The three ecodistricts are: (a) the Eastern Granite Uplands, an area of coarse granitic soils characterized by frequently exposed bedrock with black-spruce—white-pine communities that cover the northern half of Lake Major; (b) the Eastern Interior, characterized by well-drained sandy loams over glacial till with highly variable coniferous and mixedwood forests and covering roughly the southern half of both Pockwock and Lake Major; and (c) St. Margarets Bay, part of the South Mountain granite batholith with well-drained sandy loams and a wide range of forest cover similar to the Eastern Interior, covering the northern half of Pockwock.

The three ELC ecodistricts illustrate broad trends in forest composition, yet the study area is at the small end of the spectrum of those typically modelled using LANDIS-II. Therefore, a fine spatial resolution (20 m) was used to capture a finer level of ecosystem complexity and spatial variability. It was subsequently deemed necessary to develop a site classification with the capability for a higher spatial resolution than that of the ELC (1:250,000). Forest ecosystem classification (FEC) is a stand-level classification of site, soil, and vegetation that is employed by forest practitioners in many regions across Canada (Sims et al., 1989; Zoladeski et al., 1995; Keys et al., 2003). It was used to define the site conditions of the study area using a suitability analysis within a geographic information system (GIS).

The FEC is most often used on an individual-stand basis by forest managers. However, there is increasing interest in remote sensing and GIS-based FEC of entire forest management areas and landscapes, as FEC is an integral tool for ecosystem-based components of sustainable forest management (Treitz & Howarth, 2000; Colville, 2005; Günlü et al., 2009). Because the FEC is a stand-level system of classification, the

availability of data at the appropriate scale and accuracy is an extreme limitation in the GIS-based approach to FEC (Colville, 2005). The FEC of the study area is no exception to these challenges, yet because the goal of utilizing the FEC was more to examine changes in forest-ecosystem structure and incorporate stand-level variability in site conditions than to develop a spatially accurate classification of the study area, we felt it was an appropriate approach to take.

The FEC developed for the study (Table 6; Figure 4) was carried out using the IDRISI GIS software package to conduct a weighted linear combination approach of assessing the suitability of each site for nine FEC ecotypes described by Keys et al. (2003), based on soil type, surficial geology, drainage, slope, and topographic position data from multiple sources (Keys et al., 2003; Jenness, 2006; Nova Forest Alliance, 2010; NSDNR, 2010).

Table 6 The major species, soil water-holding capacity (WHC), and moisture, nutrient, and natural disturbance regimes for each of the nine FEC ecotypes found in the watersheds (Keys et al., 2003).

Ecotype	Moisture regime	Nutrient regime	Major species	Natural disturbance regime	WHC (cm)	Area classified (ha)
ET1 Dry-Poor Conifer	Very dry	Very poor	Black spruce	Frequent, stand-replacing	1.55	718
ET2 Fresh-Poor Conifer	Fresh to dry	Poor to very poor	White pine, black spruce, and jack pine	Frequent, stand-maintaining	5.27	989
ET3 Moist-Poor Conifer	Fresh/moist to moist	Poor to very poor	Black spruce, red pine, and white pine	Frequent, stand-maintaining	4.48	567
ET4 Wet-Poor Conifer	Moist/wet to wet	Medium to very poor	Black spruce, red spruce, and balsam fir	Frequent to infrequent, stand-replacing	8.02	309
ET5 Fresh-Medium Conifer	Fresh/moist to dry	Medium to poor	Red spruce	Infrequent, stand-replacing	6.11	5317
ET6 Moist-Medium Mixedwood	Fresh/moist to moist/wet	Medium to poor	Red spruce, eastern hemlock, and balsam fir	Infrequent, stand-replacing	4.73	1814
ET7 Fresh-Rich Deciduous	Moist/Fresh to dry	Rich to medium	Sugar maple, yellow birch, red maple, and red spruce	Gap dynamics	6.31	1182

Ecotype	Moisture regime	Nutrient regime	Major species	Natural disturbance regime	WHC (cm)	Area classified (ha)
ET8 Moist-Rich Mixedwood	Fresh/moist to moist/wet	Rich to medium	Red maple, sugar maple, red spruce, yellow birch	Infrequent, stand-replacing	5.51	61
ET9 Wet-Rich Deciduous	Moist/wet to wet	Very rich to medium	Red maple, balsam fir, yellow birch, and red spruce	Infrequent, stand-replacing	5.31	12

The study area is situated within the Acadian Forest Region, the forest region that occupies the majority of Nova Scotia and the Maritime provinces of Canada. The Acadian Forest Region is a transitional forest between the boreal forest to the north and the temperate forest to the south and west, and contains aspects of both. Characteristic Acadian Forest Region communities in the absence of anthropogenic disturbance are mixedwood in composition, with long-lived, shade-tolerant species such as red spruce, eastern hemlock, yellow birch, sugar maple, beech, balsam fir, and white pine. Edaphic site conditions and disturbance favour communities of black spruce, tamarack, and shorter-lived early- to mid-successional broadleaved species such as red maple, red oak, white birch, and aspen. The main natural disturbances in the Acadian Forest Region are windthrow, insects, and diseases (Loo & Ives, 2003; Mosseler et al., 2003). Human impacts in the Acadian Forest Region have left a legacy of impoverished forests in the province, as the Maritimes have the longest history of forest exploitation in North America (Loo & Ives, 2003). Evidence of this includes the loss of tolerant mixedwood forests in favour of coniferous plantations and communities of intolerant broadleaved species, white spruce, and balsam fir (Saunders & Wagner, 2008).

The proximity of the study area to the major seaport of Halifax has also made the study area vulnerable to invasive forest insects and diseases, such as the beech bark disease, a combination of a scale insect and a fungus, introduced in Halifax in late nineteenth century, which has virtually eliminated the role of beech as a dominant canopy species in mature Acadian forests, and the brown spruce longhorn beetle (BSLB), also introduced in Halifax in the 1980s (Smith & Hurley, 2000; Loo, 2009). In Nova Scotian forests, the BSLB attacks mainly red spruce and is considered an invasive alien species (Colautti et al., 2005), with a containment area designated by the Canadian Food

Inspection Agency (CFIA) that encompasses a large portion of the Halifax Regional Municipality, including all of Lake Major and a portion of Pockwock (CFIA, 2007).

3.2.2. Simulation Models

Our study employed two simulation models: a spatially explicit forest landscape and disturbance model, LANDIS-II (Scheller et al., 2007), and a spatially dynamic ecosystem process model, PnET-II (Aber & Federer, 1992; Aber et al., 1997; Xu et al., 2009). LANDIS-II is a stochastic model that simulates the processes of forest succession, growth, mortality, seed dispersal, and disturbance within a spatially explicit simulated landscape at a user-specified time-step. The landscape is represented in raster format, an array of cells or sites of user-specified resolution, and is stratified into areas of similar abiotic conditions, called ecoregions. Trees are not individually represented, but rather aggregated into age cohorts of a given species, whereby any site can have multiple species-age cohorts. A series of tree-species life-history attributes included in the simulation are used to model successional processes. Succession, biomass accumulation, dispersal, age-related mortality, and biomass decay are driven by a central succession module (Scheller & Mladenoff, 2004). Seed dispersal and seedling establishment are controlled by Ward's algorithm (Ward et al., 2005) and the stochastic probability of establishment (P_{est}) parameter, respectively. The aboveground net primary productivity (ANPP) and P_{est} values were derived from PnET-II output for each tree species in each ecoregion, which in this study were the nine FEC ecotypes. A suite of optional disturbance modules is also available for LANDIS-II. This study incorporated the wind, timber harvesting, and biological disturbance modules.

PnET-II simulates carbon and water dynamics of forest ecosystems based on established relationships between foliar nitrogen content and photosynthesis, which are in turn influenced by the climate variables of temperature, precipitation, PAR, and atmospheric CO_2 concentrations (Aber & Federer, 1992; Aber & Federer, 1997; Xu et al., 2009). PnET-II has been coupled with LANDIS-II and its predecessors in several studies to calculate the input parameters ANPP and P_{est} based on current and future climates, and have yielded valid results and meaningful implications for the relationships between forest ecosystems and climate change (Scheller & Mladenoff, 2004; Scheller &

Mladenoff, 2005; Xu et al., 2007; Scheller & Mladenoff, 2008; Xu et al., 2009; Gustafson et al., 2010; Ravenscroft et al., 2010). PnET-II calculates the LANDIS-II input ANPP as the combination of wood and foliar NPP. The P_{est} values are calculated using light and water availability and optimal GDD for each tree species (Xu et al., 2009).

3.2.3. Model Initialization and Parameterization

The initial forest structure and composition are a tremendous source of uncertainty in forest modelling and represent a challenge in all forest modelling studies (Loehle, 1987; Janssen & Heuberger, 1995; Thompson et al., 2007). The initial forest structure and composition for this study were derived from both forest resource inventory (FRI) data (NSDNR, 2010) and from data collected by us in a field survey of the watersheds in 2009. The forest consists of 512 stand types (communities) with a unique combination of species-age cohorts, creating 2,547 individual stands, spatially delineated by the FRI polygons, with a mean size of 4.2 ha. Areas delineated as rock barrens or wetlands in the FRI were considered non-active sites in LANDIS-II. FRI data and mapping have been found to be significantly inaccurate, and have severely limited abilities in classifying understory tree cover (Thompson et al., 2007). This uncertainty can lead to three important inaccuracies in the simulated landscape: underrepresentation of species richness and diversity, oversimplification of the stand-age structure, and a drastic underrepresentation of initial biomass. To reduce these inaccuracies, LANDIS-II was run for 500 simulation years prior to scenario analysis to try to attain steady-state or equilibrium conditions, in what is often termed a spin-up cycle (Jørgensen & Bendricchio, 2001).

The 16 tree species (Table 7) included in the modelling have an array of parameters that define their respective life cycles, competitive abilities, biology, and climatic ranges. The parameters were obtained from a multitude of sources in the peer-reviewed literature (Burns & Honkala, 1990; Aber et al., 1996; Aber et al., 1997; Goodale et al., 1998; Scheller & Mladenoff, 2005; Xu et al., 2009; Bourque et al., 2010) and consultation with local experts in forest ecology. Due to the uncertainty surrounding the full effects of CO₂ fertilization on forest ecosystems, changes in stomatal conductance were not included in this study, a decision that is supported in other studies using PnET-II

and LANDIS-II (Scheller & Mladenoff, 2008; Gustafson et al., 2010). Furthermore, the wet climate of the Acadian Forest Region suggests that in the absence of edaphic moisture and nutrient limitations, temperature rather than CO₂ is the limiting factor for forest productivity in the study region (Melillo et al., 1993). A current limitation of LANDIS-II is that it does not incorporate dynamic soil-nutrient cycling. While nutrient cycles operate over a much longer timeframe than other forest processes (Johnson & Curtis, 2001), it was deemed necessary to account for soil nutrient regimes in the P_{est} values, so the establishment of some tree species was constrained to certain ecotypes depending on nutrient levels.

Table 7 List of tree species and the change in P_{est} and ANPP between simulation year 2000 and 2300 due to climate change.

Species	P _{est}	ANPP
Balsam fir	-0.39	-152
Red maple	0.63	36
Sugar maple	-0.04	18
Yellow birch	-0.32	28
White birch	-0.44	-85
American beech	0.17	11
Tamarack	-0.46	0
White spruce	-0.10	-258
Black spruce	-0.33	-342
Red spruce	-0.37	-87
Red pine	-0.13	-10
White pine	0.14	-134
Large-tooth aspen	-0.02	-46
Trembling aspen	-0.04	-46
Red oak	0.16	11
Eastern hemlock	0.24	26

The succession, wind, biological disturbance, and harvest modules operated at 10 yr time-steps. The wind disturbance module generates disturbance events stochastically, with event frequency derived from wind rotation-period parameters and event sizes derived from mean, minimum, and maximum event-size parameters, all of which were determined from historical disturbance sizes and frequencies in the Acadian Forest Region (Seymour et al., 2002). Four wind-disturbance regimes were parameterized: 1) frequent stand-initiating disturbances, 2) moderate, stand-maintaining disturbances, 3)

infrequent, catastrophic disturbances, and 4) gap dynamics (Neily et al., 2007). The different disturbance regimes were assigned to the nine ecotypes based on site, soil, and stand conditions (Keys et al., 2003).

The biological disturbance module was parameterized to simulate bark-beetle disturbance of both the native spruce bark beetle and introduced BSLB (Magasi, 1995; Smith & Hurley, 2000). Beetle outbreak was considered chronic, with low rates of mortality occurring at every time-step. White spruce, black spruce, and red spruce were the simulated host species, with vulnerability to attack occurring in the mature age class and mortality beginning at the overmature age class, as defined by the NSDNR (NSDNR, 2010). The spatial pattern of bark-beetle infestation was parameterized to be synchronous in the landscape, due to the small size of the watersheds (Gray, 2008). The harvest-disturbance module was parameterized in a simple manner in an attempt to mimic historical, even-aged clear-cutting. Harvest priority was assigned based on stand age, with the oldest stands receiving the highest harvest priority. Total biomass of every species-age cohort was removed from each site within a harvested stand, with a yearly target or annual allowable harvest area equalling 1.5% of the watersheds.

3.2.4. Experimental Design

For this study, a two-by-two scenario construction was used, with two disturbance scenarios and two climate scenarios (Table 8). Each scenario was run for 300 yr, representing the period of 2000 to 2300. The two disturbance scenarios included a natural disturbance regime scenario, simulating wind and bark-beetle disturbances only, and a forest management scenario, simulating historic harvest practices in addition to the natural disturbance regimes.

Table 8 Scenario construction of the first experiment in LANDIS-II. Scenarios 1A and 1B simulated the current climate and climate change in pre-settlement Acadian forest communities, while scenarios 2A and 2B simulated the two climate scenarios in an actively managed forest.

	Current climate	Climate change
Natural disturbance regimes (wind and bark beetles)	Scenario 1A	Scenario 1B
Natural disturbance regimes and timber harvests	Scenario 2A	Scenario 2B

To account for the high levels of uncertainty in GCM climate modelling, this study simulated the forest landscape under both a current climate and extreme climate change scenario to incorporate the whole range of prediction (Ravenscroft et al., 2010). The no-change scenario used the current-climate conditions, an average of the 1961-2000 climate variables output from the Canadian Regional Climate Model (CRCM) for the study area, with total annual precipitation ranging between approximately 1,000 mm and 1,400 mm and mean annual temperature ranging between approximately 4°C and 6°C.

The climate change scenario used was the SRES-A2 climate scenario, used in the IPCC Fourth Assessment Report, which predicts atmospheric CO₂ levels stabilizing at 850 ppm by the year 2100, leading to a 5.8°C increase in mean annual temperature and a smaller 6.9 mm increase in total annual precipitation in the study area (Nakicenovic, 2001; IPCC, 2007; CCCMA, 2009). The historic and climate change data were retrieved from the Canadian Centre for Climate Modelling and Analysis (CCCMA; CCCMA, 2009). Monthly data from the CRCM4.2.3 time-slice for the 1961-2100 period were used for both the current climate scenario and the climate change scenario. The CRCM is a downscaling tool for GCM data that functions at a regional scale of 46 horizontal kilometres in North America. It is driven by the Coupled Global Climate Model (CGCM3) for the baseline years of 1960-2000 and the SRES-A2 scenario for the years of 2001-2100 (IPCC, 2007; CCCMA, 2009). Monthly means of maximum temperature, minimum temperature, total precipitation, PAR, and atmospheric CO₂ were input in PnET-II to model ANPP and P_{est} for subsequent input into LANDIS-II.

In the scenarios 1B and 2B, the climate-driven changes in the ANPP and P_{est} variables were quantified every 10 yr in PnET-II from 2001 to 2100 for input into LANDIS-II. The climate change scenarios in LANDIS-II simulated the PnET-II-derived variables for the first century of simulation, while maintaining the 2091-2100 ANPP and P_{est} variables for the remaining two centuries of simulation. The 500 yr spin-up cycles were simulated under the 1961-2000 climate, using the same ANPP and P_{est} values

simulated in the current climate scenarios 1A and 2A. Timber harvesting was simulated in the spin-up cycle for scenarios 2A and 2B, but not scenarios 1A and 1B.

3.2.5. Data Analysis

Each LANDIS-II scenario was replicated five times to account for the stochasticity of seed dispersal, seedling establishment, and disturbance events (Ravenscroft et al., 2010). Because the variance of the response variables between replications was so low (typically between 1-2%), significance testing between scenarios would be irrelevant and one replication was therefore selected at random for further analysis among ecotypes at simulation year 2300.

The effects of the changing climate on forests were gauged in terms of forest composition, productivity, and age structure, at both watershed and ecotype scales. Forest composition was indicated by the landscape presence (%) of each tree species at simulation year 2300, calculated simply as the percent of active cells where a given species had at least one age cohort present. The biomass variable was total living AGB of all tree species, expressed in Mg/ha. Biomass was graphed as a time series for the entire 300 yr simulation at the watershed scale to observe any temporal patterns. The AGB variable was also calculated for year 2300 at the ecotype scale. The age variable was the area covered by five seral stages for the entire watersheds, similar to Gustafson et al. (2010). The five seral stages were establishment (0–40 yr), early-seral (41–100 yr), mid-seral (101–140 yr), late-seral (140–200 yr), and old-growth (> 200 yr).

To assess a coarse measure of forest resilience, biodiversity and structural complexity indicators were used. The biodiversity indicator was species richness and the structural complexity indicator was the evenness of age-class distributions, calculated using Shannon-Weaver evenness, a measure of evenness based on Shannon's index of diversity (Shannon & Weaver, 1963; DeZonia & Mladenoff, 2004). Species richness was simply the number of species present on a site (raster cell), averaged at the watershed and ecotype scale. Evenness was the measured diversity of all age cohorts on a site, calculated with Shannon's diversity index, divided by the maximum possible diversity on that site. The indicator ranges between 0 and 1, where a value of 1 represents a completely even distribution of age cohorts on a site. External software used for analysis

included ArcInfo 9.3, IDRISI Kilimanjaro, and IAN 1.0.18, a raster analysis program for calculating landscape metrics (DeZonia & Mladenoff, 2004).

A rigorous quantitative validation of a modelling study of this nature is essentially impossible (Jørgensen & Bendoricchio, 2001). This is because an external validation dataset of the appropriate scale is not accessible, and more importantly, at a conceptual level, projections of future conditions, such as climate change, cannot be validated (Rastetter, 1996). This illustrates the fundamental concept that the use of simulation models is a valuable tool for experimental exploration and forecasting of future scenarios, rather than a precision tool for predicting future conditions, which also invalidates the use of inferential statistics between scenarios. For simulations of undisturbed forest conditions such as scenario 1A, the necessary historical data of forest conditions are rarely available. For this reason, forest models with broad spatial and temporal scales, such as LANDIS-II, use a combination of the literature, expert consultation, and field sampling, when available, to assess model reliability and validity (Vanclay & Skovsgaard, 1997). In this study, model output of the no-harvest simulations was compared to the literature of historical conditions (Goldsmith, 1980; Loo & Ives, 2003) and old-growth (Mosseler et al., 2003; Stewart et al., 2003) in the Acadian Forest Region, and assessed by local forest researchers and practitioners, including the forest manager for Halifax Water. For the harvest scenarios, model reliability and validity were assessed using permanent sample plot data of current forest conditions from the NSDNR (Townsend, 2003).

3.3. Results

3.3.1. Forest Composition

Scenario 1A was a valuable tool in assessing model validity and obtaining a control treatment to gauge the influence of timber harvest and climate change on the study region. The model results of scenario 1A compared well with pre-settlement conditions of the Acadian Forest Region from the literature and expert consultation, with a dominance of shade-tolerant, longer-lived species typical of climax communities, including red spruce, eastern hemlock, beech, sugar maple, and balsam fir, all of which were present on greater than 65% of the landscape (Figure 5). Harvest disturbance in

scenario 2A led to a much higher distribution of the early- to mid-successional species, such as yellow birch, white pine, red oak, red maple, white birch, large-tooth aspen, and trembling aspen.

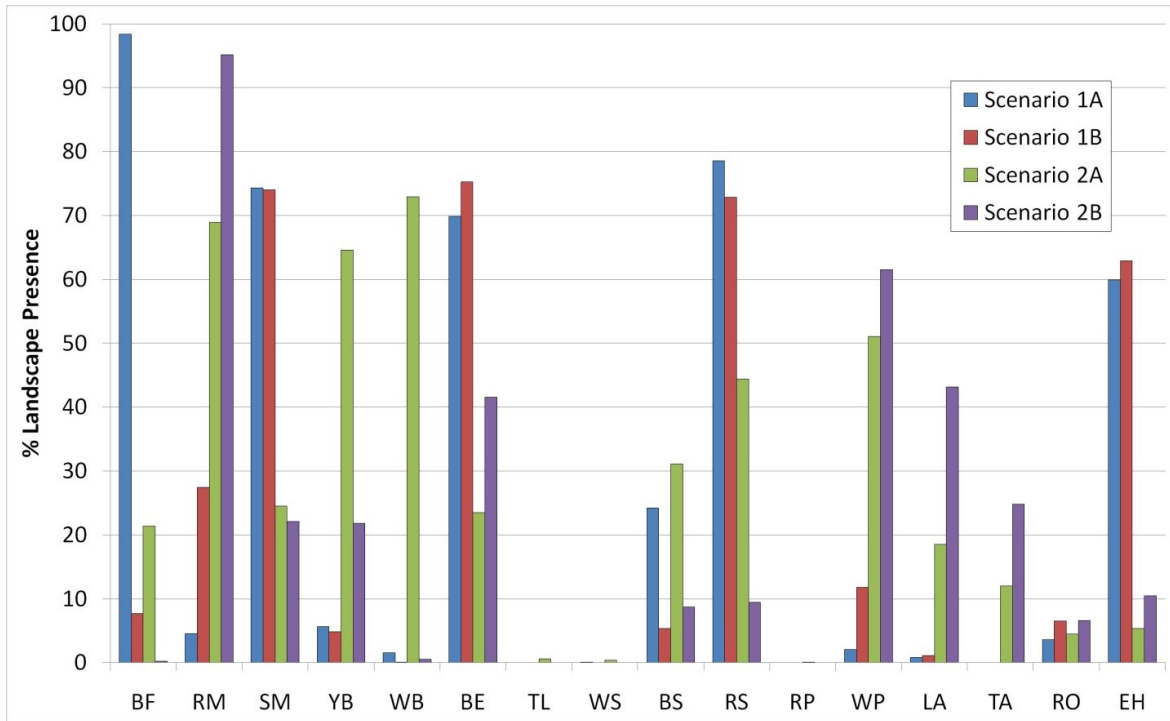


Figure 5 Landscape presence of the 16 tree species in the entire study area at simulation year 2300 for all four scenarios. BF: balsam fir, RM: red maple, SM: sugar maple, YB: yellow birch, WB: white birch, BE: American beech, TL: tamarack, WS: white spruce, BS: black spruce, RS: red spruce, RP: red pine, WP: white pine, LA: large-tooth aspen, TA: trembling aspen, RO: red oak, EH: eastern hemlock.

Forest composition was altered in the climate change scenarios in both the presence and absence of timber harvest. In scenario 1B, balsam fir sustained by far the largest drop in landscape presence in comparison to the current climate conditions, with a decrease of 91%. Black spruce experienced the second greatest drop, at 19%. Red spruce, white birch, yellow birch, and sugar maple also had small declines. The largest increase in landscape presence was red maple, with 23%, followed by white pine with 10%. Beech, red oak, and eastern hemlock had smaller increases. Tamarack, white

spruce, red pine, large-tooth aspen, and trembling aspen were either absent or sparsely distributed in scenarios 1A and 1B, and had negligible changes in distribution.

Timber harvest in scenario 2B had the effect of exaggerating both negative and positive responses of landscape presence due to climate change. In scenario 2B, yellow birch had a decrease of 43% compared to 1% and red spruce had a loss of 35% compared to 6%. Balsam fir, black spruce, and white birch sustained a decrease in landscape presence as they did in scenario 2B, though the decrease of white birch was much larger as it was much more widely dispersed due to timber harvesting. Red maple, white pine, red oak, and eastern hemlock all had increases similar to those of scenario 2B. The aspen species had much larger increases, again likely due to the effects of timber harvesting.

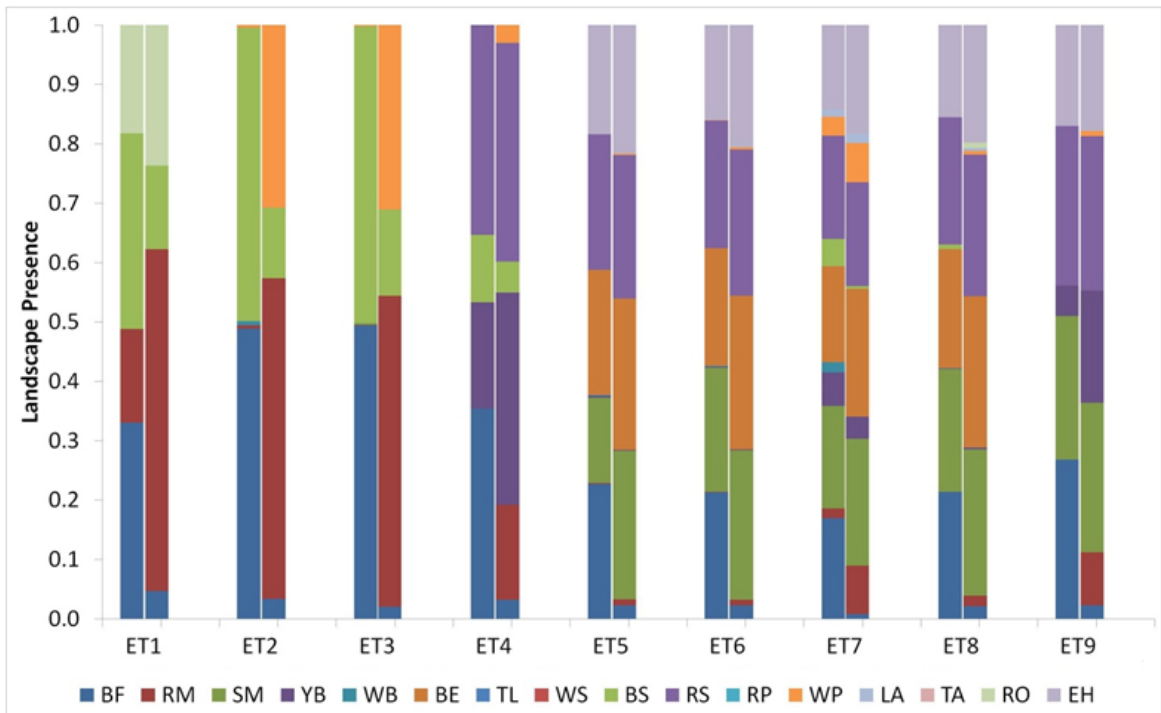


Figure 6 A comparison of the landscape presence of the 16 tree species in each ecotype between scenarios 1A and 1B, with landscape presence proportionally represented for comparative purposes. BF: balsam fir, RM: red maple, SM: sugar maple, YB: yellow birch, WB: white birch, BE: American beech, TL: tamarack, WS: white spruce, BS: black spruce, RS: red spruce, RP: red pine, WP: white pine, LA: large-tooth aspen, TA: trembling aspen, RO: red oak, EH: eastern hemlock. ET1: ecotype one, dry-poor conifer, ET2: ecotype two, fresh-poor conifer, ET3: ecotype three, moist-poor conifer, ET4: ecotype four, wet-poor conifer, ET5:

ecotype five, fresh-medium conifer, ET6: ecotype six, moist-medium mixedwood, ET7: ecotype seven, fresh-rich deciduous, ET8: ecotype eight, moist-rich mixedwood, ET9: ecotype nine, wet-rich deciduous.

The coniferous, nutrient-poor ecotypes ET1, ET2, and ET3 all experienced severe changes in composition in scenario 1B in comparison to 1A, with the recession of balsam fir and black spruce and advancement of red maple and white pine (Figure 6). ET4 had a much smaller increase of red maple and white pine, likely due to the presence of red spruce. The remaining ecotypes had greater diversity and abundance of late-successional species, and had much less severe changes in forest composition, with the most noticeable change being the recession of balsam fir.

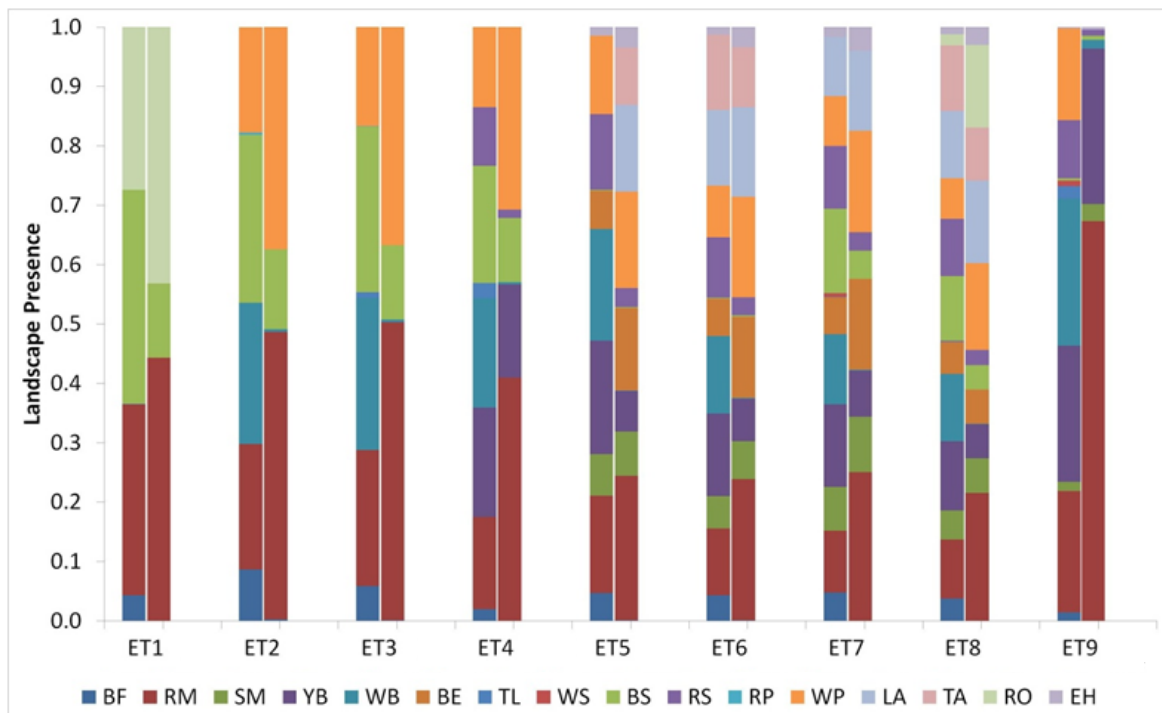


Figure 7 A comparison of the landscape presence of the 16 tree species in each ecotype between scenarios 2A and 2B, with landscape presence proportionally represented for comparative purposes. BF: balsam fir, RM: red maple, SM: sugar maple, YB: yellow birch, WB: white birch, BE: American beech, TL: tamarack, WS: white spruce, BS: black spruce, RS: red spruce, RP: red pine, WP: white pine, LA: large-tooth aspen, TA: trembling aspen, RO: red oak, EH: eastern hemlock. ET1: ecotype one, dry-poor conifer, ET2: ecotype two, fresh-poor conifer, ET3: ecotype three, moist-poor conifer, ET4: ecotype four, wet-poor conifer, ET5:

ecotype five, fresh-medium conifer, ET6: ecotype six, moist-medium mixedwood, ET7: ecotype seven, fresh-rich deciduous, ET8: ecotype eight, moist-rich mixedwood, ET9: ecotype nine, wet-rich deciduous.

Early- and mid-successional species were much more abundant in scenarios 2A and 2B due to both timber harvesting and favoured establishment in the changing climate (Figure 7). Most notably, red maple was the dominant species in every ecotype in scenario 2B. The degree of change in forest composition was much greater with timber harvests. In the coniferous nutrient-poor ecotypes ET1, ET2, ET3, and ET4, there was an increase in the landscape presence of red maple and white pine as there was in scenario 1B, but their dispersal was initially much greater due to timber harvest. Timber harvesting also led to the complete removal of balsam fir and white birch in these ecotypes. In ET5, the most common ecotype in the watersheds, there was a much greater increase in landscape presence of the aspen species in comparison to other ecotypes. Eastern hemlock, beech, and sugar maple remained relatively robust to large changes in landscape presence, as they did in scenario 1B, yet their distribution was much smaller due to timber harvesting. There was high degree of change in composition in ET9, with red maple becoming highly dominant.

3.3.2. Biomass

The AGB of the simulated forest was altered in the climate change scenarios, yet not nearly as severely as with forest composition. Timber harvesting had a far greater impact on AGB, with mean AGB in scenario 2A being approximately 67% (85 Mg/ha) lower than in scenario 1A at year 2300. There was also a divergent response of forest biomass to climate change with and without timber harvest (Figure 8). In scenarios 1A and 1B, mean AGB of the entire landscape at year 2300 decreased from 258 to 240 Mg/ha with climate change. In scenarios 2A and 2B, mean AGB increased from 172 to 186 Mg/ha at year 2300. The temporal pattern of the response in forest productivity to climate change was also notable. The AGB in both climate change scenarios increased with the onset of climate change at year 2000, reaching a peak in the second half of the first century of simulation, and declining thereafter. The difference was that in scenario 1B, AGB reached an equilibrium approximately 19 Mg/ha lower than that of scenario

1A, and scenario 2B reached an equilibrium approximately 15 Mg/ha higher than that of scenario 2A. Balsam fir and red maple were the species that were most negatively and positively affected by climate change, respectively (Figure 9).

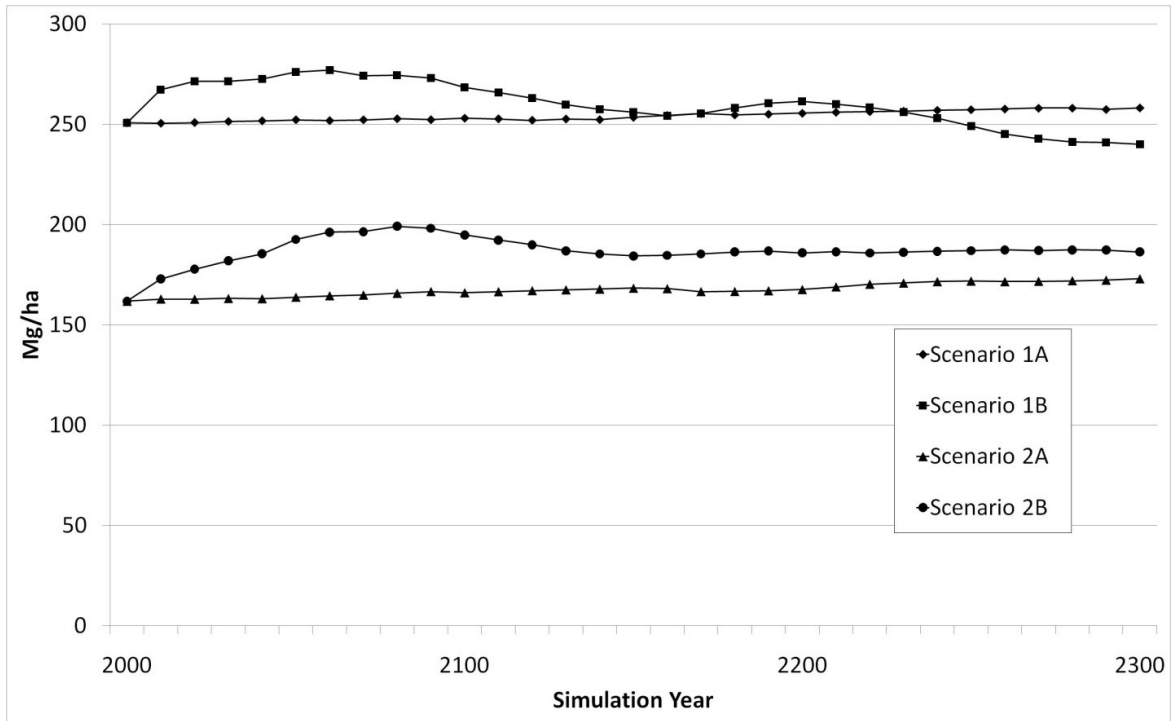


Figure 8 Time-series graph of mean AGB (Mg/ha) in the four scenarios for the entire study area over the 300 yr simulations.

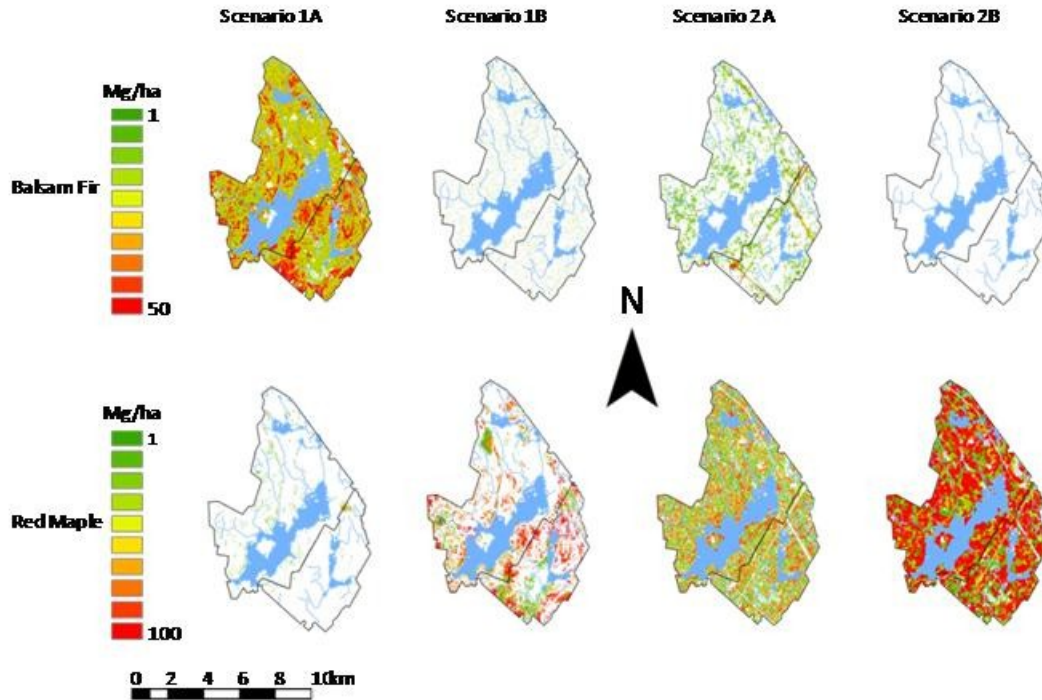


Figure 9 Red-maple and balsam-fir distribution and AGB (Mg/ha) mapped in the Pockwock watershed in the four scenarios at year 2300 to illustrate the effects of climate change on the landscape presence and biomass of the two most impacted tree species.

The AGB of the nine ecotypes varied in their responses to climate change. In comparing scenarios 1A and 1B (Figure 10), ET1 experienced the largest increase in AGB with 59 Mg/ha. Other ecotypes that increased in productivity were ET3, ET6, and ET9. The largest decrease in AGB was ET4 with a loss of 67 Mg/ha. Other ecotypes that decreased in AGB were ET2, ET5, ET7, and ET8.

In comparing scenarios 2A and 2B, the degree of climate-driven change in AGB was much less. The largest decrease was ET9, with a loss of 9 Mg/ha, which had been found to increase in productivity in the absence of timber harvesting. The other ecotypes that sustained a loss in AGB were ET4 and ET7. The largest increase in AGB again was ET1 with 52 Mg/ha, which is more than twice the increase than any other ecotype. The other ecotypes with increases in AGB were ET2, ET3, ET5, ET6, and ET8. Of those, ET2, ET5, and ET8 were found to have a decrease in AGB in the absence of timber harvesting.

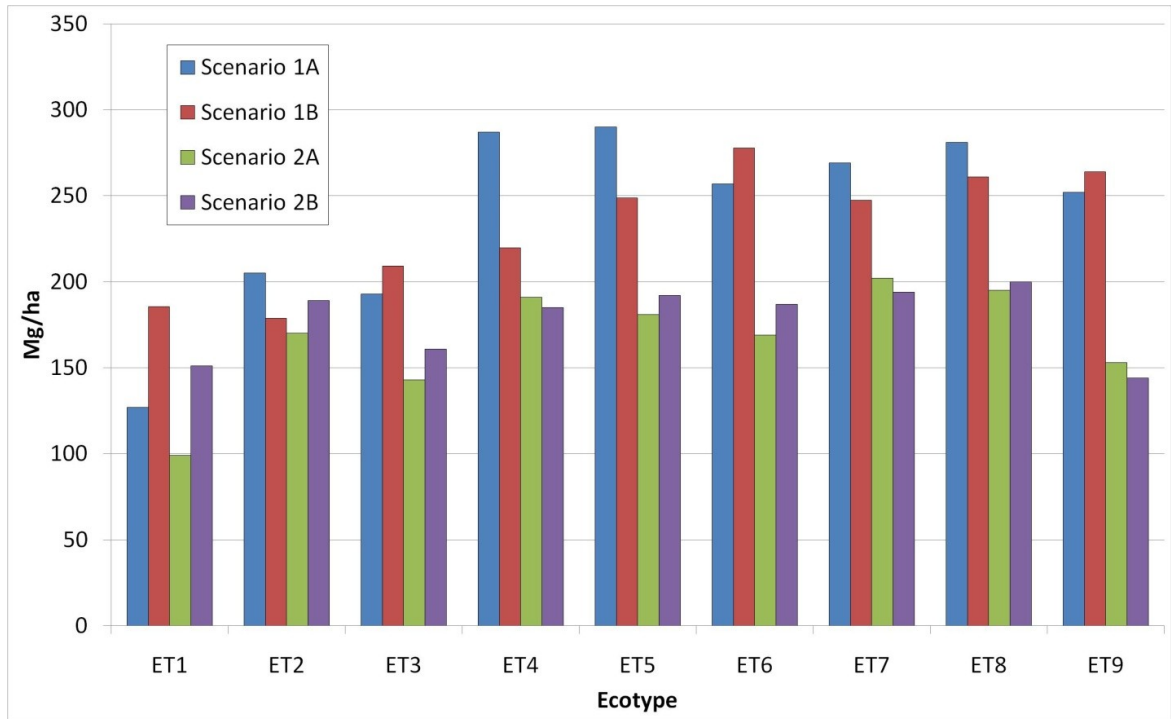


Figure 10 Average aboveground biomass (Mg/ha) of each ecotype in the four scenarios at simulation year 2300. ET1: ecotype one, dry-poor conifer, ET2: ecotype two, fresh-poor conifer, ET3: ecotype three, moist-poor conifer, ET4: ecotype four, wet-poor conifer, ET5: ecotype five, fresh-medium conifer, ET6: ecotype six, moist-medium mixedwood, ET7: ecotype seven, fresh-rich deciduous, ET8: ecotype eight, moist-rich mixedwood, ET9: ecotype nine, wet-rich deciduous.

3.3.3. Age Structure

There were no major changes in the average cover-age of the watersheds due to climate change, as indicated by the area covered by each seral stage (Figure 11). Timber harvesting had a severe impact on forest age in scenarios 2A and 2B, leading to a much younger forest, primarily in the establishment and early-seral stages. Conversely, the vast majority of the study area was in the old-growth stage in scenarios 1A and 1B.

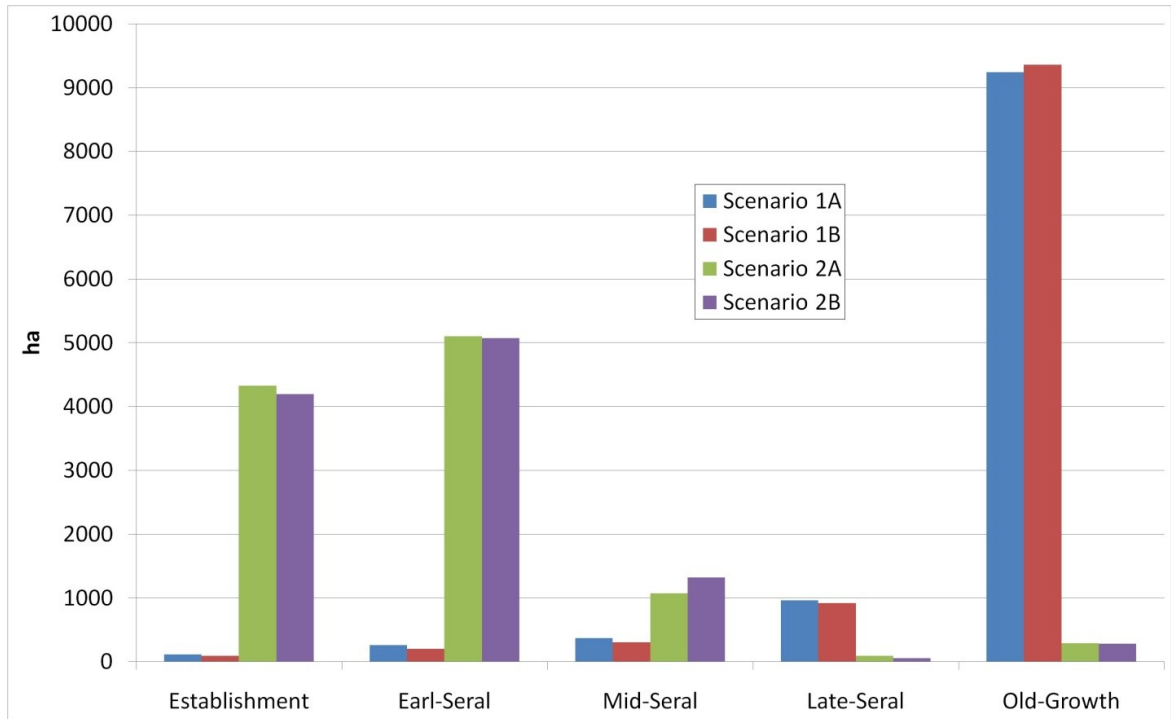


Figure 11 Seral-stage representation of the study area in the four scenarios at simulation year 2300.

3.3.4. Biodiversity and Structural Complexity

Species richness was negatively affected by climate change with and without timber harvesting at the watershed and ecotype scales (Table 9). Also, while species richness was lower in the absence of timber harvesting due to shade exclusion by late-successional species, species richness in both scenarios 1B and 2B declined to similar values. Climate change also caused a small increase in age-class diversity as indicated by Shannon-Weaver evenness between scenarios 1A and 1B, while causing a small decrease between scenarios 2A and 2B. At the ecotype scale, decreases in age-class diversity and species richness tended to be more severe in the mixedwood and deciduous ecotypes ET5, ET6, ET7, ET8, and ET9 than in the coniferous, nutrient-poor ecotypes ET1, ET2, ET3, and ET4, though response between ecotypes of these indicators was highly variable.

Table 9 Average species richness and Shannon-Weaver evenness of each site at the watershed and ecotypes scale for all four scenarios at simulation year 2300.

	Scenario 1A	Scenario 1B	Scenario 2A	Scenario 2B
Species richness				
Watersheds	4.24	3.49	4.47	3.47
ET1	3.00	2.30	2.45	2.21
ET2	2.02	1.84	3.26	2.03
ET3	2.00	1.66	3.12	1.95
ET4	2.83	2.46	4.58	2.35
ET5	4.72	3.91	4.33	3.88
ET6	4.64	3.84	5.56	3.95
ET7	5.50	4.40	5.97	3.78
ET8	4.67	3.91	6.34	4.64
ET9	3.72	3.52	3.76	2.14
Shannon-Weaver evenness				
Watersheds	0.93	0.95	0.73	0.70
ET1	0.77	0.79	0.79	0.80
ET2	0.78	0.75	0.82	0.81
ET3	0.80	0.74	0.80	0.84
ET4	0.86	0.89	0.88	0.88
ET5	0.87	0.91	0.74	0.71
ET6	0.87	0.92	0.77	0.73
ET7	0.92	0.92	0.81	0.75
ET8	0.92	0.93	0.80	0.83
ET9	0.96	0.95	0.92	0.91

3.4. Discussion

The species composition of the forest ecosystems within the study watersheds were noticeably altered by the change in climate. The warmer and wetter climate affected the probability of establishment and subsequent canopy recruitment of many tree species (McKenney et al., 2007; Xu et al., 2009), and therefore altered the forest composition of the watersheds. Studies of pre-historic changes in climate suggest that tree species may sustain drastic changes in distribution, leading to the alteration of established forest communities (DeHayes et al., 2000). However, a major concern is that the rate of current climate change far exceeds the migration rates and genetic adaptability of tree species (IPCC, 2007; Scheller & Mladenoff, 2008). Furthermore, the disturbed and fragmented state of forests today due to the intensive history of human use may impede tree-species migration in response to a warming climate (Scheller & Mladenoff, 2005). In the study area, some species experienced considerable increases in landscape presence, while others suffered extreme declines in their abundance or even extirpation from the study area. Most notable responses of those tree species whose range was negatively affected by climate change was the almost complete disappearance of balsam

fir and white birch. Black spruce, red spruce, and yellow birch also experienced considerable decreases in landscape presence. White spruce, red pine, and tamarack were also negatively affected by climate change, yet they were so sparsely distributed in the study area that there was little effect on overall forest composition. The establishment probabilities of several species were favoured in the warmer climate, and they experienced a resulting increase in their landscape presence and abundance. The most apparent of these increases was red maple, which became a highly dominant species in the watersheds, especially where timber harvest occurred. White pine, American beech, eastern hemlock, red oak, large-tooth aspen, and trembling aspen were also more widely distributed.

The changes in distribution of tree species are consistent with recent national- and continental-scale studies modelling range shifts of most North American tree species (Iverson et al., 2004; McKenney et al., 2007; Iverson et al., 2008) as well as many LANDIS-II studies on the impacts of climate change on tree-species distribution in transitional boreal-temperate forests in the northern Minnesota and Wisconsin (He et al., 1999; Sheller & Mladenoff, 2005; Scheller & Mladenoff, 2008; Ravenscroft et al., 2010). The Acadian Forest Region is also a transitional forest region, or ecotone, between the boreal forest to the north and temperate forest to the south (Loo & Ives, 2003). As expected, a decrease in the abundance of colder-climate boreal species and an increase in warmer-climate temperate species were observed, and due to the mix of boreal and temperate species in the Acadian Forest Region and study area near both the southern and northern limits of their ranges, this meant a significant change in forest composition.

Gustafson and colleagues (2010) conducted a study in the Siberian boreal forest using similar methods, and found that forest pests had a greater effect on species and age-class composition than did the direct effects of climate. This further implicates the vulnerability of transitional forests such as the Acadian Forest Region to climate change, especially in comparison to less diverse forest regions like the boreal forest. Bourque and colleagues (2010) have conducted multiple modelling studies investigating the impacts of climate change on selected tree-species distributions in Nova Scotia (Bourque & Hassan, 2008; Bourque et al., 2010). In these studies, boreal species such as black spruce and balsam fir were restricted to high elevations and colder areas in the altered climate, while

temperate species such as red oak and American beech were favoured by the increased growing season. Also of note in the Bourque et al. (2010) study was that some species that had an increase in their distribution in this study, such as white pine and trembling aspen, responded positively to climate change in the first several decades but eventually saw a decrease in their potential range in Nova Scotia. It is likely that this discrepancy can be attributed landscape processes such as competitive release and existing seed sources not included in the other study. This is supported by the PnET-II output establishment probabilities for the aspen species, which exhibited a small decrease in P_{est} , while the aspens still had an overall increase in abundance, especially when timber harvesting was simulated. This is a highly relevant issue as it influences what climate-driven changes in tree species distribution will be seen on the ground. In support of the role of landscape processes as well as climate conditions in changes to forest composition, Landhäusser and colleagues (2010) found that the current advancement of aspen to higher altitudes in the upper foothills region of Alberta can likely be attributed to both climate change and forest management practices.

The national-scale studies use what is called a climate envelope approach, where a species' potential range is determined entirely by climatic conditions, also called a fundamental niche (Hampe, 2005; McKenney et al., 2007; Iversen et al., 2008). The study done in Nova Scotia was also restricted to climatic ranges, yet did include soil moisture in the modelling framework (Bourque et al., 2010). To date, ours is the only study within the Acadian Forest Region that modelled the effects of climate change on forest ecosystems while incorporating biological and geophysical landscape processes, such as natural and anthropogenic disturbance, competition and succession, seed dispersal, and fragmentation. In the aforementioned studies, the Acadian Forest Region in Atlantic Canada and New England is predicted to have favourable conditions for more tree species than most other regions in North America in the changed climate, based on climatic variables alone (McKenney et al., 2007). However, Nova Scotia is geographically isolated from the propagules of the majority species predicted to migrate northward, and without the introduction of previously absent temperate species, there could be serious declines in species and ecosystem diversity, increased abundance of

pioneer tree species, and the dominance of a few existing native Nova Scotia tree species such as red maple.

Red maple and other pioneer tree species present a serious existing threat to the biodiversity of the watersheds due to the long and intensive history of forest management in the area. Red maple, white birch, and aspen species have all become more abundant in the province in the past several decades, and red maple is already the dominant broadleaved species in the study area and the province (Townsend, 2003). Now, as these degraded forest ecosystems are faced with a changing climate, there is a further threat to forest-ecosystem functioning and biodiversity as climate change is often found to favour shade-intolerant, early-successional tree species (Ravenscroft et al., 2010). Late-successional species appeared to be much less elastic in the response to climate change. It will therefore be critical to maintain climax species such as sugar maple, eastern hemlock, and red spruce to slow the migration of newly favoured pioneer species and prevent the homogenization of forest ecosystems (Scheller & Mladenoff, 2005). Active management to restrict red-maple dominance in conifer-dominated ecosystems has been previously suggested in similar studies (Ravenscroft et al., 2010), and may be pertinent to management initiatives in the watersheds. This issue is illustrated in scenarios 1A and 1B, where in the absence of timber harvest, the abundance of late-successional species in ecotypes without edaphic constraints restricted the abundance of red maple and aspen species due to shade exclusion. These ecotypes saw a reduced climate-induced advancement of pioneer species, and a smaller loss of late-successional species such as red spruce and yellow birch.

The sharp decline in the abundance of boreal species can likely be attributed entirely to climate change, while the increase of other species may be due to the altered climate as well as competitive release from species that are no longer favoured. This point is exemplified by the aspen species, which experienced very little change in their establishment probabilities in response to climate change, but have considerable increases in landscape presence. Competition also has implications for forest productivity and migration of newly favoured species. In previous studies, interspecific competition is believed to have slowed species migration and range expansion of species favoured by a warmer climate or of climax species that are more climate-neutral (Scheller & Mladenoff,

2005; Scheller & Mladenoff, 2008). This may have negative implications for forest productivity, as the presence of these boreal species that are no longer favoured in the changing climate could impede colonization of by other species due to light and nutrient competition, leaving an abundance of forests communities in a depauperate state.

Forest productivity is both an important measure of ecosystem functioning and of high interest to forest managers (Lambert et al., 2005). It is widely speculated in the literature that climate change will lead to an increase in NPP of terrestrial ecosystems, including forests (Schimel et al., 2001; Norby et al., 2005; Xu et al., 2007; Friend et al., 2010). However, it is also mentioned in several studies how critical non-climatic factors such as species composition, competition, and natural disturbances will be to overall ecosystem productivity (Hampe, 2005; Scheller & Mladenoff, 2008). The productivity and AGB of forest ecosystems in the watersheds was affected by climate change, yet this study illustrates that the response of ANPP will vary tremendously among ecosystems, and more specifically, will be highly dependent on species composition. Ecosystems that are currently limited by water availability or that favour broadleaved temperate species may experience increases in productivity, while conifer-dominated ecosystems with species more typical of the boreal forest, especially moist and nutrient poor ecotypes, will likely experience decreases in productivity (McMahon et al., 2010). In this study it is difficult to determine the direct effects of climate change on forest productivity, as the changes in forest composition appeared to be much more influential on AGB. In forest regions such as the Acadian Forest Region, with a mix of boreal and temperate species, changes in forest composition may be the most important factor in the response of forest productivity to climate change. Furthermore, the complete restructuring of some forest ecosystems in this study led to small or variable changes in forest productivity. This appears to be a highly incidental result of the modelling approach, and the implications of a complete change in tree species composition for ecosystem functioning and water quality warrant further study.

The effects of disturbance may also be as or more important than the effects of climate change on forest productivity and composition (Schimel et al., 2001). The increase in AGB in the majority of ecotypes and in the entire study area in scenario 2B was most likely due to the fact that timber harvest greatly increased the abundance of

early- and mid-successional species in the watersheds. Many of these species experienced climate-induced increases in growth rates, so a managed forest with a greater abundance of these species will subsequently have a more rapid response in productivity than old forests. Red maple in particular experienced much higher productivity and alarmingly comprised almost two thirds of the total AGB in the watersheds. The previously described lag in response time of forest composition in the absence of intensive timber-harvest disturbance may also explain the decrease in tree biomass observed in scenario 1B. More of the climatically unfavoured boreal species were present on the landscape in scenario 1B and likely slowed the increase in landscape presence and abundance of fast-growing pioneer species. Therefore, the observed drop in AGB in unmanaged forests due to climate change may be followed by a slow increase and greater total biomass of the forests, over a longer timeframe. Conversely, the divergent response of AGB with and without timber harvesting may support the existing theory that the change in climate accelerates forest productivity, but has no beneficial effects and may be detrimental to the total AGB capacity of forests (Körner et al., 2005; Williamson et al., 2009). In effect, forests in a warmer, wetter climate may have no change, or even a decrease, in their maximum biomass potential, but may arrive at that potential faster.

A limitation of this study was that only one group of forest insects was simulated, representing the spruce bark beetle and the introduced BSLB. An increased prevalence of forest insects and disease is expected to occur in the warmer climate (Gray, 2008; Dukes et al., 2009), which may have implications for forest productivity that are not included in this study. Other studies have found that predicted increases in forest productivity have been negated by increased frequency and severity of natural disturbances (Kurz et al., 2008; Gustafson et al., 2010). The frequency and severity of wind disturbances are also expected to increase (Peterson, 2000), yet changes in wind patterns and the relationship between increased wind events and forest disturbances are highly uncertain and difficult to predict (Dale et al., 2001). In the initial modelling of this study, the response variables were found to be highly insensitive to a doubling of wind event frequency and size. However, there are many limitations to the wind disturbance module of LANDIS-II, the most crucial being the lack of species differentiation in wind

disturbances and the inability to incorporate the vulnerability of timber-harvest edges, which are highly important in the wind vulnerability of a managed forest (Harper et al., 2004). Changes in forest composition were the most influential impact of climate change in this study, but it will be critical to further study the role of altered natural disturbance regimes in the watersheds.

While the dynamic simulation of natural disturbances in this study was limited, it was possible to examine changes in resistance and resilience of the forests to natural disturbances. Two important indicators of resistance and resilience to both natural and anthropogenic disturbances are forest biodiversity and structural complexity (Rich et al., 2007). In this study these elements were indicated by species richness and the evenness of the distribution of age classes. At the ecotype scale, coniferous nutrient-poor ecotypes experienced the biggest alterations in composition. Mixedwood and deciduous ecotypes have a higher broadleaf component, as well as more long-lived, late-successional species, and were subsequently more resistant to climate-induced changes in composition. However, these ecotypes tended to experience greater losses to structural complexity and biodiversity. This suggests that while coniferous and nutrient-poor ecotypes with frequent natural disturbances are more likely to experience greater and more rapid changes in forest composition, the late-successional tolerant mixedwood ecotypes will experience a decrease in ecosystem resistance and resilience to future disturbance.

Disturbance due to timber harvest had varying effects on the response of different components of forest ecosystems to climate change. Widespread, stand-replacing disturbances such as timber harvests have the capability of altering the effects of climate change on forest composition (He et al., 1999; Scheller & Mladenoff, 2005). Without question, timber harvest had drastic effects on forest ecosystems due to a prevalence of open canopy conditions, leading to a much wider dispersal of short-lived, shade-intolerant, early-successional species, such as red maple, white birch, large-tooth aspen, and trembling aspen, and higher abundance of mid-successional species such as yellow birch and white pine. Landscape-scale timber harvesting also led to a much younger and more even age distribution and lower AGB. Given the complexity and interrelatedness of forest ecosystem processes (Kimmins et al., 2008), the possibility for forest management

to alter the response of forest ecosystems to climate change in major and unexpected ways needs to be explored.

Red spruce is one of the most commercially and ecologically important tree species in the Acadian Forest Region (Stewart et al., 2003). While it may have a smaller potential range due to climate change, it is more resilient to the warming climate than black and white spruce, which have a more northerly range (Farrar, 1995). In the absence of timber harvesting, red spruce suffered a minimal retreat with climate change and maintained its dominance in the forests of the study area. However, when forest management was simulated, the decrease in distribution of red spruce was greatly amplified. A similar trend was seen with yellow birch, an important mid- to late-successional broadleaf species in the watersheds. The sensitivity of these species to timber harvesting as the climate changes, and the importance of other more climatically robust, late-successional species such as eastern hemlock and sugar maple, stress the importance of incorporating specific silvicultural activities in management plans that address ecosystem- and species-specific impacts of climate change at the operational scale. Also, many early-successional species were favoured in a warmer climate and can disperse over the study area much faster in an intensively managed forest. The intensity of forest management may dictate the level of dispersal of these newly favoured species and the dominance of red maple.

FEC is a highly valuable tool for forest managers to practice ecosystem-based sustainable forest management (Kimmins, 2003). The FEC in Nova Scotia is still under development by the provincial government, and the results of this study have many implications for future FEC frameworks and forest management recommendations. Climate change may lead to a reordering of forest ecosystem composition and structure, so the classification of a given ecosystem unit may need to be re-addressed within an established FEC. Furthermore, FECs are usually associated with ecosystem-specific management recommendations. The inclusion of ecosystem-specific climate change vulnerability or even specific adaptation recommendations could be a tremendous asset in the FEC of Nova Scotia.

The forest ecosystems in this study are also representative of some of the largest ecological regions in the province, as classified by the province's current land

classification system (Neily et al., 2003), so conclusions from this study may be relevant to many of the managed forests in Nova Scotia. This study also stresses the vulnerability of the Acadian Forest Region of the Canadian Maritime provinces and America's New England states to predicted changes in climate in the coming decades and centuries. The ability of Halifax Water to incorporate climate change into its forest management planning will hopefully benefit from the results of this study, which is an important step in source water protection and continuing provision of clean drinking water in Nova Scotia.

3.5. Conclusion

In our simulation-based study, changes in forest composition were the most obvious impact of climate change in the watersheds managed by Halifax Water, with colder-climate boreal species retreating in the region, and warmer-climate temperate species and climate neutral, late-successional species experiencing an increase in landscape presence or little change in distribution, respectively. These changes were most severe at the ecotype scale in conifer-dominated and nutrient-poor ecotypes. More-diverse and nutrient-rich mixedwood and broadleaved ecotypes were less affected by changes in composition, but experienced a decrease in their resistance and resilience to disturbance, as indicated by forest biodiversity and structural complexity. The prominence of climate-driven changes in forest composition within the findings of this study is certainly influenced by the choice of simulation models and the experimental design. However, the magnitude of these impacts is still a valid concern, and should be incorporated into future research. The full effects of climate change on natural disturbances in the watersheds and the Acadian Forest Region is one area that will need further study.

The response of forest AGB was overshadowed by changes in forest composition at the ecotype scale, but over the entire watersheds, forests were more productive in the changing climate when timber was harvested. Conversely, there was a decrease in total biomass of the watersheds in the absence of timber harvesting, supporting the theory that climate change may benefit the productivity of younger managed forests with an

abundance of early-successional broadleaved species, but there will be no change or even a decrease in the total biomass potential of old-growth forests.

Forest management will have an important role to play in the coming decades and centuries, and in many instances may expedite the acclimation of forest ecosystems to the changing climate. There is a time lag in the response of boreal species to climate change, as the warmer climate does not cause mortality, but limits the ability of new seedlings to establish. In forest ecosystems dominated by boreal conifers and northern broadleaved species, there may be a period where the forests remain in a depauperate state because colonization of newly favoured temperate species is slowed by nutrient and light competition. The response of forest biomass and species distribution to climate change was also sensitive to forest management activities, and intensive timber harvesting may exacerbate negative impacts of climate change. Furthermore, climate change favoured many mid- to early-successional tree species, especially red maple, and timber harvesting may increase the risk of losing tree species and ecosystem diversity due to the homogenization of forest composition in many areas. This has implications for the forests of Nova Scotia and the Acadian Forest Region, and may contribute to future development of climate-smart FEC and management in the watersheds managed by Halifax Water. The continual supply of clean water is a vital ecosystem service that is directly related to forest health, and as such forest response to climate change will be critical in the future management of these watersheds.

3.6. References

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CHAPTER 4 EXPLORING ADAPTATION TO CLIMATE CHANGE IN FOREST MANAGEMENT IN A NOVA SCOTIAN WATER SUPPLY

James Steenberg was responsible for the research and writing of this manuscript. Peter Duinker was the thesis supervisor and Peter Bush was a thesis committee member. Both provided guidance, revision, and feedback. This paper will be submitted to the journal *Forest Ecology and Management*.

4.1 Introduction

The threat of climate change is now recognized as a legitimate and imminent issue at the forefront of the forest sector (Intergovernmental Panel on Climate Change [IPCC], 2007; International Union of Forest Research Organizations [IUFRO], 2009; Williamson et al., 2009). Research on climate change and forests has greatly developed in recent years (Spittlehouse, 2005; Millar et al., 2007; Malmshheimer et al., 2008; Johnston et al., 2010), while current impacts on forests are becoming evident and widespread (Berg et al., 2006; Hogg & Bernier, 2006; Kurz et al., 2008;).

Direct effects of the changing climate include changes in the metabolic processes and growth rates of trees, due to increased temperatures, carbon fertilization, and climate-induced changes in soil and moisture regimes, leading to changes in forest productivity (Schimel et al., 2001; Norby et al., 2005; McMahon et al., 2010). Increases in forest productivity attributed to elevated temperatures and longer growing seasons have already been observed in high-latitude areas (Braswell & Schimel, 1997; Zhou et al., 2001; Bunn & Goetz, 2006). Much study has also been dedicated to changes in tree-species distribution due to shifting ranges (McKenney et al., 2007; Iverson et al., 2008; Bourque et al., 2010), possibly leading to the restructuring of existing forest communities (Webb & Bartlein, 1992; Scheller & Mladenoff, 2005).

Indirect effects of climate change on forest ecosystems result from changes in natural disturbance regimes (Peterson, 2000; Dale et al., 2001; Gray, 2008). The predicted increase in frequency and severity of disturbance events, such as windstorms, hurricanes, and insect and disease outbreaks may have adverse effects on forest ecosystems, as disturbance regimes are an integral component of forest-ecosystem dynamics (Frelich, 2002).

Forest managers are currently faced with a breadth of challenges, including keeping pace with changing societal values and needs for forest ecosystem services (Kimmins, 2002), the recent economic downturn, and the threat of climate change. The multitude and regional variability of potential impacts, complexity of forest ecosystems, and uncertainty associated with climate change and subsequent forest response make this an incredibly difficult issue to tackle (Webster et al., 2003; Vasseur & Catto, 2008).

The operational forests of Canada are frequently in a fragmented and degraded state due to the history of unsustainable forestry practices (Puettmann et al., 2009), which may compromise their ability to adapt to the changing climate (Noss, 2001). The past several decades have seen the development of ecological and sustainable trends in forest management with the rise of concepts like sustainable forest management, ecosystem- and natural-disturbance-based management, complexity, and biodiversity (Grumbine, 1994; Kimmins, 2003; Puettmann, 2009). However, ecosystem-based management often defines natural conditions as an ultimate management goal, and given that climate change has the potential to alter forest ecosystem function and reorder structure, a re-evaluation of ecosystem-based management goals will likely be necessary.

Climate change is likely to hinder the ability of forest managers to reach many of their management goals and objectives (Mote et al., 2003; Ogden & Innes, 2007). This is primarily due to the fact that forest management objectives have traditionally been developed based on historical forest conditions and ecological sustainability (Lakey, 1995; Landres et al., 1999), and the assumption that if we maintain these conditions, forest ecosystems will continue to provide goods and service like timber and water (Millar et al., 2007). Changes in global climate invalidate these assumptions and we now need to incorporate climate change into forest management paradigms. While it can be argued that forests may eventually adapt to the new climate on their own, it is because we have so many societal demands on forest ecosystems that we want to facilitate this adaptation in a timely manner and in a way that our management goals and objectives are not impeded (Spittlehouse, 2005; Stephens et al., 2010). There is a further concern that inflexible policies and institutions will seriously hinder adaptation and be unable to operate under the uncertainty of climate change (Haley & Nelson, 2007). This highlights the importance of incorporating dynamic management strategies that recognize the inherit

uncertainty of future conditions, such as adaptive management (Duinker & Trevisan, 2003; Van Damme et al., 2003).

Effects of climate change on timber supply may vary and be positive or negative depending on the region, management activities, and temporal scale (Johnston & Williamson, 2005). Many regions are predicted to experience an increase in forest productivity due to climate-related changes, such as longer growing seasons, altered soil moisture and nutrient regimes, and carbon fertilization (Schimel et al., 2001; Norby et al., 2005; McMahon et al., 2010). However, predictions of the effects of climate change on forest productivity are uncertain and variable (Heimann & Reichstein, 2008), and external factors, such as management actions and natural disturbances, may be the controlling factor in the overall net change in forest productivity with climate change (Scheller & Mladenoff, 2005). Impacts on forest-based public goods/non-timber forest products, such as the supply of clean water, are also a predicted result of climate change, but are far less well understood (Mote et al., 2003; Jones et al., 2009).

In central Nova Scotia, Canada, Halifax Water manages the water supply and forests of the 14,000 ha Pockwock and Lake Major watersheds (Figure 12). Halifax Water entered into a research partnership with Dalhousie University with the intent of exploring the relationships between climate change and forest ecosystems, possible impacts of climate change, and adaptive measures that might be incorporated into forest management planning. Healthy forests are best equipped for the continual provision of a healthy water supply (Neary et al., 2009), so an understanding of climate change, its effects on forests, and how best to manage these forests in an altered climate is a principal objective of Halifax Water. The purpose of this study is to investigate climate change adaptation in forest management by building upon the research of Steenberg (2010) who studied climate change impacts in these two watersheds, and incorporate adaptive measures into an experimental modelling framework.

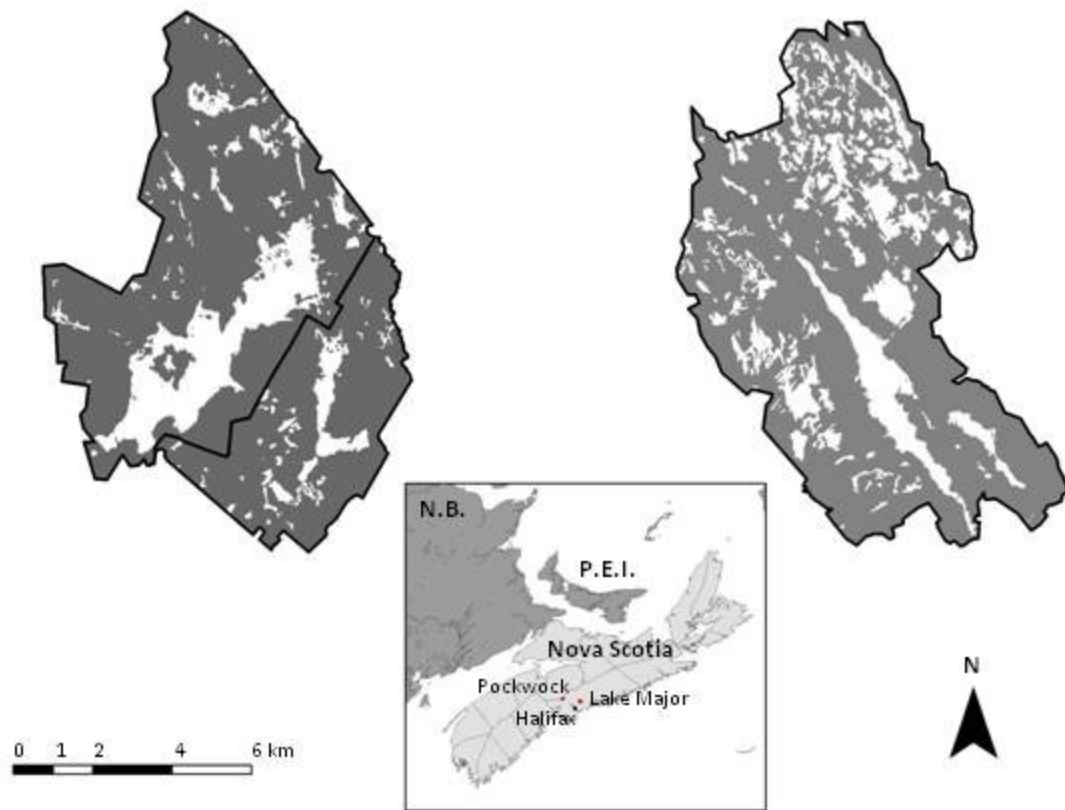


Figure 12 The Pockwock (left) and Lake Major (right) watersheds in central Nova Scotia, Canada are the principal watersheds supplying the Halifax Regional Municipality.

There is a growing recognition that forest-sector vulnerability to climate change is rarely addressed at the scale necessary for forest management decision-making (Nitschke & Innes, 2008; Johnston et al., 2010). To fully understand forest vulnerability to climate change, it is critical to explore and recognize all of the biophysical processes involved at the appropriate scales, including predicted regional impacts of climate change and the adaptive capacity of forest ecosystems and management systems (Duinker, 1990; Turner et al., 2003; Steenberg, 2010). This study, in concert with Steenberg (2010), assesses the vulnerability of the watersheds through examination of climate change impacts and adaptations (Smit & Pilifosova, 2001; Johnston & Williamson, 2007). Here we take a landscape-ecology approach to incorporating adaptation into timber harvesting using the landscape disturbance model LANDIS-II (Scheller et al., 2007), capable of simulating spatially explicit landscape succession and disturbance processes. In this manner, we

hope to research the effectiveness of different adaptation themes in timber harvesting at a fine enough spatial scale to inform management decisions of Halifax Water, but broad enough to examine forest-landscape response to adaptation in an approach that is valid within the design, scope, and temporal-spatial scales of LANDIS-II.

In consultation with managers from Halifax Water and local forest experts and researchers, we developed an experimental management framework to model a range of adaptive measures in forest management. The experimental treatments are focused on three different components of timber harvesting: 1) opening size, referring to the size of canopy openings in harvesting, 2) age of harvested trees, referring to the age cohorts targeted for harvest among those present within a stand, and 3) composition of harvested trees, referring to which species were targeted within a stand. The efficacy of these adaptive measures was evaluated in a values-based assessment of their ability to achieve forest management goals and objectives. By understanding which elements of timber harvesting are most receptive to and effective in incorporating climate change adaptation, we may begin to bridge the gap that exists between landscape ecology and resource management (Liu & Taylor, 2002) and between the theoretical and the operationally feasible.

Each of these three areas of adaptation was developed under two guiding principles: what are the predicted impacts of climate change in the study area, and what is feasible and valid within the LANDIS-II modelling framework. The forest ecosystems of the watersheds are predicted to sustain a loss in diversity and complexity due to climate change, especially in tolerant mixedwood and broadleaved ecosystems (Steenberg, 2010). By incorporating ecosystem-based management recommendations from the forest ecosystem classification (FEC) management guidelines of Nova Scotia, we significantly altered canopy-opening sizes in timber harvests, thereby promoting compositional and structural complexity within the watersheds (Keys et al., 2003; McGrath, 2007; 2009). This yields a greater span of age structures and communities, fostering forest resilience to climate change (Bradford & Kastendick, 2010). The adaptation of the age of the trees harvested from a stand was less linked to specific climate change impacts in the Steenberg (2010) study than the other adaptive measures. It targeted building forest resistance to possible impacts of climate change. By promoting more-rapid regeneration

and succession to climax Acadian forest communities, the forest ecosystems of the study area may be more resistant to climate-driven forest change (Parker et al., 2000). The final area of adaptation targets which species were removed from a harvested stand and was the most linked with the climate change impacts described in Steenberg (2010). Species no longer climatically favoured in the study area were targeted for removal, as were highly competitive species favoured by the changing climate, while some ecologically significant and climatically sensitive species were exempt from timber harvests. In this manner we strived to facilitate a progressive forest transition to an inevitable change in climate (Millar et al., 2007).

4.2. Methods

4.2.1. The Modelling Approach to Climate Change Adaptation

Forest succession, growth, mortality, seed dispersal, and disturbance in the Pockwock and Lake Major watersheds were simulated using LANDIS-II, a stochastic landscape disturbance model that operates in a spatially explicit rasterized landscape, which is stratified into areas of similar abiotic conditions, called ecoregions. Tree species are represented by species-age cohorts that are aggregated by user-defined successional time-steps, whereby any raster cell of user-defined resolution can have a unique combination of tree species-age cohorts. Wind, bark beetle, and timber harvest disturbances were simulated using optional disturbance modules. Tree species growth rates and establishment probabilities, represented by the aboveground net primary productivity (ANPP) and probability of establishment (P_{est}) variables, were derived from the ecosystem process model PnET-II (Aber & Federer, 1992; Aber et al., 1997; Xu et al., 2009), which can be linked to downscaled general circulation model (GCM) output data and thereby incorporate the effects of climate change into the modelling framework.

The multitude of necessary disturbance, site, and tree-species parameters for the models were derived from the peer-reviewed literature (Baldocchi et al., 1988; Pastor & Post, 1988; Burns & Honkala, 1990; Aber et al., 1996; Aber et al., 1997; Goodale et al., 1998; Scheller & Mladenoff, 2005; Xu et al., 2009; Bourque et al., 2010), survey data we collected in the field, and consultation with local experts in forest ecology, and were validated with provincial inventory data, existing studies, and expert opinion (Townsend,

2003). Climate change data used in the modelling were downscaled data from the Third Generation Coupled Global Climate Model (CGCM3) under the SRES-A2 climate scenario, where atmospheric carbon dioxide (CO₂) reaches 850 ppm by 2100, leading to a mean annual temperature increase of 5.8°C and a 6.9 mm increase in total precipitation in the study area (Nakicenovic, 2001; IPCC, 2007; Canadian Centre for Climate Modelling and Analysis [CCCMA], 2009). This study is a continuation of the research by Steenberg (2010), and a more detailed description of the modelling methods can be found there.

In the modelling experiment of this study, we incorporated climate change adaptation into timber harvests (Figure 13). Three experimental harvest treatments for the timber harvesting module in LANDIS-II were developed in consultation with local forest researchers and forest managers at Halifax Water based on management goals and objectives and the capacity of the modelling framework. The focus was directed towards three components of timber harvests: canopy-opening size of cuts, age of the trees removed from a harvested stand, and composition of trees removed from a harvested stand.

The size treatment targeted different spatial orientations and sizes of canopy openings within harvests. It is possible to have multiple prescriptions within a harvest treatment in LANDIS-II, and the size treatment was the only one where this feature was employed. Three prescriptions were simulated in this treatment based on the composition and natural disturbance regimes of the forest ecosystems, called ecotypes in the FEC of Nova Scotia (Keys et al., 2003; McGrath, 2007; 2009). Clear-cutting was prescribed in coniferous ecotypes with frequent stand-replacing disturbances, with harvest size targeted between 1 ha and 10 ha. Group selection was prescribed in tolerant coniferous and mixedwood ecotypes with infrequent stand-replacing or stand-maintaining disturbances, with opening sizes of 0.1 ha. Finally, individual tree selection was prescribed in tolerant broadleaved ecotypes with gap dynamics, with opening sizes set as small as possible, 0.04 ha (i.e. input map resolution). Total aboveground biomass (AGB) of all species-age cohorts in openings of all three prescriptions was removed on all harvested sites, and stands required a minimum cover age of 50 yr to qualify for harvesting.

The age treatment was the least complex, and focused on the age of sexual maturity and seed production of harvested trees. All species-age cohorts in a harvested

stand at or below the age of sexual maturity were exempt from harvesting, in order to promote rapid succession to climax forest communities. Harvest size was targeted between 1 ha and 10 ha and total AGB of all species-age cohorts at least one time-step (10 yr) older than the age of sexual maturity was removed. A minimum cover age of 50 yr was again required for harvesting.

The third and final composition treatment constrained which tree species were harvested in a stand and was the only species-specific treatment. The 16 tree species included in the modelling were aggregated into three groups based on the change in their distribution in response to climate change (Steenberg, 2010). The tree species were either harvested or retained depending on their simulated response to climate change and on management values at Halifax Water. The first group consisted of colder-climate boreal species that experienced a decrease in landscape presence and abundance due to climate change, and included balsam fir, black spruce, white birch, white spruce, red pine, and tamarack. These were termed priority-removal species and were harvested. The second group consisted of more temperate species and pioneer species that were highly favoured in the warmer climate and/or exhibited considerable increases in landscape presence, which were red maple, white pine, large-tooth aspen, and trembling aspen. These were termed opportunistic-removal species and were harvested. The third group consisted of a combination of species that were either favoured in the warmer climate (American beech and red oak), late-successional species that were robust to the climatic changes (eastern hemlock and sugar maple), or species with a variable response depending on management activities (red spruce and yellow birch). The unifying attribute of all these species was that they were considered ecologically important and conservation priorities by managers at Halifax Water. These species were termed conservation targets, and were excluded from harvesting in all stands. Harvest size was again targeted between 1 ha and 10 ha and required a cover age greater than 50 yr. Despite the species-oriented nature of this treatment, the composition of a stand did not influence the harvesting priority.

Stands with a cover age greater than 50 yr that met the necessary conditions of a given timber harvest treatment were prioritized by age at each time-step, whereby the oldest qualifying stand was most likely to be harvested. An adjacency rule of 10 yr was

also used. The annual allowable harvest area in all scenarios save the control was maintained at 1% in accordance with the current Halifax Water forest management plan. Importantly, less than 1% could be harvested if defined conditions for harvesting were not met at a given time-step.

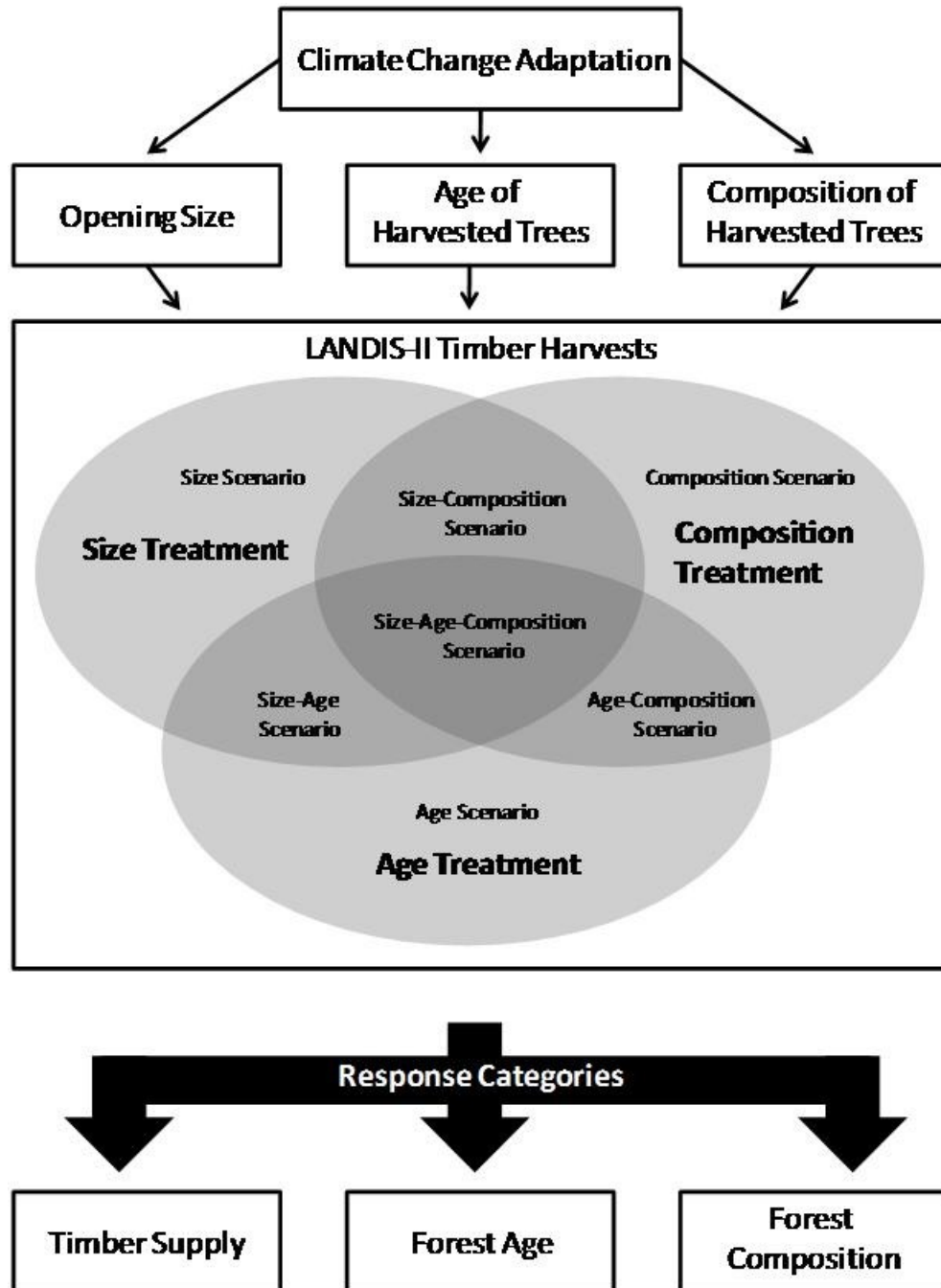


Figure 13 Conceptual framework for the implementation of climate change adaptation into this study. The opening size, age of harvested trees, and composition of harvested trees were manipulated in response to anticipated and simulated climate change impacts in the watersheds to create the three size, age, and composition experimental adaptation treatments. The treatments were simulated in seven scenarios in LANDIS-II. Forest change in the scenarios was evaluated in three different response categories: timber supply, forest age, and forest composition.

Eight scenarios were simulated in this study: one control and seven experimental (Table 10). The control scenario was identical to scenario-simulated even-aged timber harvesting calibrated to historical practices in central Nova Scotia used in Steenberg (2010). Each of the three adaptation treatments were simulated individually in the size, age, and composition scenarios. The treatments were then simulated in all possible combinations with each other in the size-age, size-composition, age-composition, and size-age-composition scenarios. Each scenario was simulated for 300 yr, representing the period from 2000 to 2300. A 500 yr spin-up was also simulated for each scenario using the control-scenario parameters. To simulate climate change in all eight scenarios, the PnET-II-derived ANPP and P_{est} variables were incorporated at every 10 yr LANDIS-II time-step from 2000 to 2100, and the 2091 to 2100 ANPP and P_{est} variables were maintained throughout the remaining two centuries of simulation.

Table 10 Scenario construction of the climate change adaptation experiment in LANDIS-II. The different adaptation treatments simulated in the seven experimental scenarios are marked by an X.

Adaptation	Size treatment	Age treatment	Composition treatment
Control scenario			
Size scenario	X		
Age scenario		X	
Composition scenario			X
Size-age scenario	X	X	
Size-composition scenario	X		X
Age-composition scenario		X	X
Size-age-composition scenario	X	X	X

4.2.2. Data Analysis and Response Categories

LANDIS-II, with its suite of disturbance parameters, is a relatively complex model that generates a broad spectrum of output (Scheller et al., 2007; Sturtevant et al., 2007). Critical thought was given to the most informative method of data presentation within the scope of this study. A time-series graph of average watershed AGB (Mg/ha) and total annual harvested biomass (HB; Mg/yr) for the entire 300 yr simulation was used to analyse the effect of each scenario on a coarse measure of harvest yield, as well as the combined effect of climate change and climate change adaptation on landscape-level forest productivity. In this study, tree biomass was the only forest biomass simulated.

To examine the effects of climate change on forest age, average cover age (yr) was calculated at simulation-year 2300 in all scenarios. Also, average patch size (ha) and total area (ha) of old-growth forest (OGF) were calculated at simulation-year 2300. In this study, OGF patches were calculated using eight nearest neighbours of sites where the oldest cohort-age had to equal or be greater than 125 yr (Stewart & Neily, 2008). Average OGF patch size was calculated from maximum cover-age raster maps output from LANDIS-II in the IAN 1.0.23 software package (DeZonia & Mladenoff, 2004).

In light of the more conceptual and landscape-scale approach to climate change adaptation in forest management introduced in this study, we felt that an alternative spatial representation of the forest would better illuminate the effects of the different adaptation treatments. Rather than define and map climate-driven changes in existing forest communities as is often done (Iverson & Prasad, 2001; Ravenscroft et al., 2010), tree species were aggregated and mapped according to their response to climate change (Steenberg, 2010), rather than their community associations. We felt this was the best approach, as climate change may lead to a restructuring of forest communities and ecosystems because tree-species distribution will be affected at the individual species level, not community level (Webb & Bartlein, 1992; Hansen et al., 2001; Bourque & Hassan, 2008; Thomson et al., 2009). These mapped species groupings corresponded to the three groups of species defined in the composition treatment (Table 11).

Table 11 Tree species grouped according to their response to climate change in the composition treatment, and mapped for all scenarios.

Species grouping	Explanation	Species
Priority removal	Species with a decrease in landscape presence due to climate change	Balsam fir, white birch, tamarack, white spruce, black spruce, and red pine
Opportunistic removal	Species with a large increase in landscape presence due to climate change	Red maple, white pine, large-tooth aspen, and trembling aspen
Conservation target	Species with a variable response or little change in distribution due to climate change and deemed a conservation priority in the study area.	Sugar maple, yellow birch, American beech, red spruce, red oak, and eastern hemlock

The spatial distribution of these three categories was mapped according to age, whereby a site was classified as a given grouping based on the oldest species-age cohort present on that site. These raster images were generated directly in LANDIS-II for each scenario at simulation year 2300, and at year 2000 for the control only (as maps would be virtually identical between scenarios at this point) to illustrate the initial conditions. Time-series graphs of the change in landscape presence (%) over the 300 yr simulation of these response categories were also included. Finally, to provide some insight into the species-level effects of climate change adaptation, we tabulated the change in landscape presence (%) of the major tree species between simulation year 2000 and 2300.

To assess the efficacy of the each adaptation strategy and organize the data presented in this study, we delineated categories of forest response to adaptation that reflected some management values and objectives in the watersheds. Given the nature of LANDIS-II for simulating forest dynamics of larger areas and timeframes and the conceptual, landscape-scale approach to climate change adaptation in this study, we felt these should be values-based categories assessed at the landscape scale. The three response categories in which adaptation was evaluated were timber supply, forest age, and forest composition. The timber supply category examined the AGB and HB data, the forest age category examined the average cover age and OGF variables, and the forest composition category examined the landscape presence data for the groupings of tree species, as well as the change in landscape presence over the course of the simulation for each species.

4.3. Results

4.3.1. Timber Supply Response Category

There was a noticeable change in both HB and AGB with each adaptation treatment (Figure 14). However, it is first important to understand the control scenario, as it represents a no-adaptation situation. Conditions for timber harvesting appeared favourable with climate change, as HB increased from just over 14,000 Mg/yr to just over 25,000 Mg/yr by the second century of simulation. There was also a sharp rise in AGB in the first century of the simulation that appeared to be driven by the change in climate, which eventually decreased due to the increased timber harvesting.

The size scenario resulted in a drastic decrease in HB at less than half that of the control scenario, at just under 8,000 Mg/yr. This was to be expected given the nature of the selection harvesting recommended in the FEC management guidelines for Nova Scotia. With the lowered harvest intensity, there was also an overall increase in AGB in addition to that attributed to climate change. The age scenario resulted in by far the highest timber harvest productivity of the adaptation scenarios, levelling off at approximately 25,000 Mg/yr, as in the control scenario. The AGB in the age scenario also reached a similar value as the control scenario, at approximately 185 Mg/ha, though there was a smaller climate-induced rise in the first century of the simulation. The composition scenario was an extreme adaptation treatment in terms of timber harvesting, and this was evident in the drop of HB to less than 1,000 Mg/yr after the first century. The non-intensive harvesting also appeared to lead to the climate-driven rise in forest productivity to be drawn out over the first two centuries of the simulation, unlike the previous scenarios.

In the size-age scenario, the first of the combinational scenarios, AGB and HB were almost identical to the size scenario, suggesting that the size treatment was the limiting factor for HB in these scenarios. In the size-composition scenario, HB was sustained at a much lower level than in the size and size-age scenarios, but was still greater than in the composition scenario, with the composition treatment alone. The AGB in the size-composition scenario was slightly higher than the size-age scenario, where the size treatment was combined with the age treatment. The age-composition scenario had a high HB of 23,000 Mg/yr and subsequently had the lowest AGB of all

scenarios, both of which were a considerable change to the composition treatment alone in the composition scenario, illustrating the influence of the higher removal rates in the age treatment on the composition treatment. In the final size-age-composition scenario, the temporal patterns of HB and AGB were very similar to all scenarios that incorporated the size treatment, further implicating this adaptive treatment as a limiting factor for timber harvesting. The exception was when the size treatment was combined with the composition treatment and a further reduction in HB was seen.

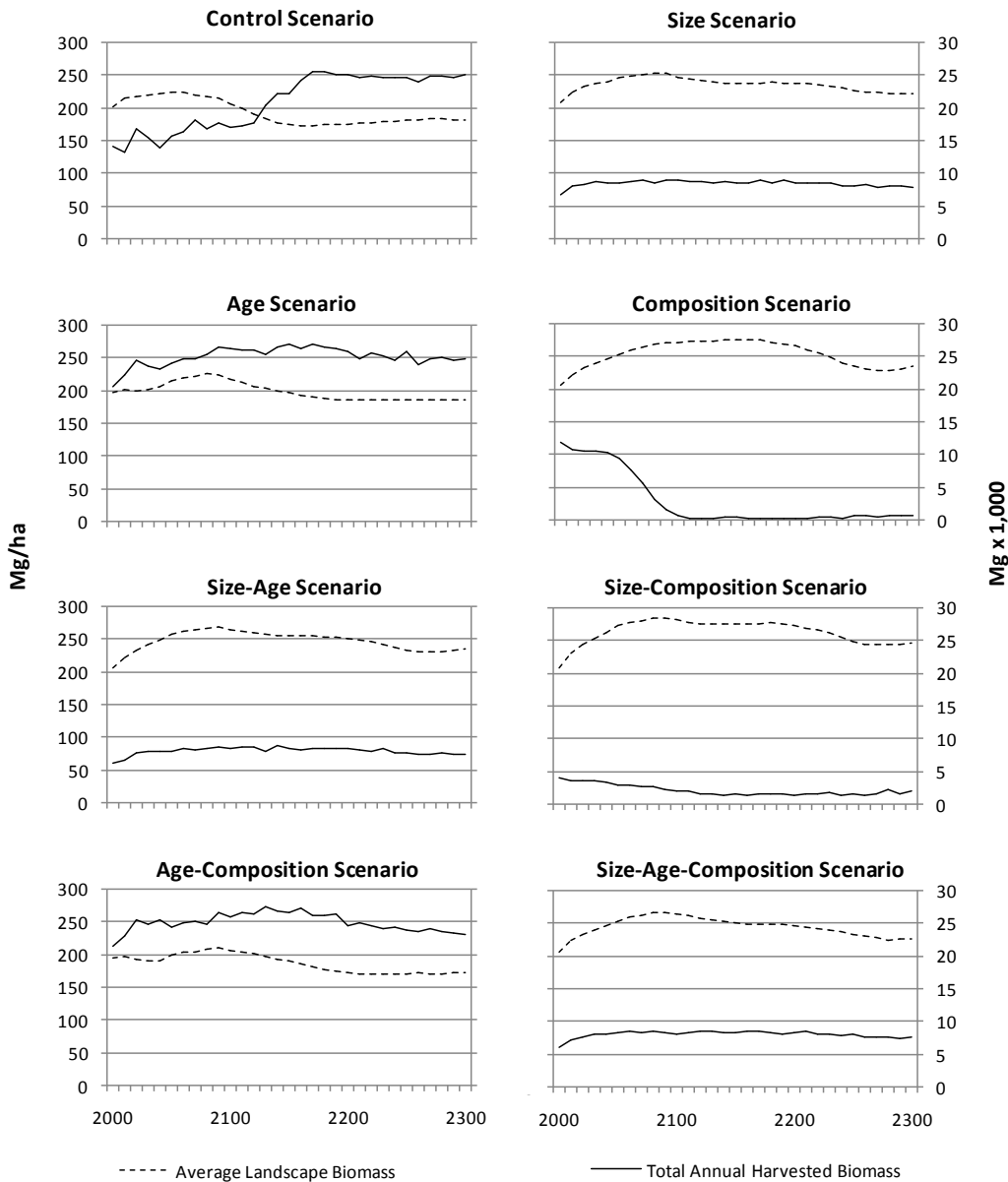


Figure 14 Time-series graphs of AGB (Mg/ha) and HB (Mg/yr) of the entire study area for all eight scenarios between simulation years 2000 and 2300.

4.3.2. Forest Age Response Category

As with the timber supply response category, there was considerable variation in how each adaptation treatment performed in the age category (Table 12). Not surprisingly, the control scenario had the youngest forest age, least amount of OGF, and smallest OGF patch sizes, with an average cover age of 67 yr, OGF area of 624.8 ha, and average OGF patch size of 0.2 ha. The composition treatment led, without question, to the oldest forest and most OGF, as was evident in both the composition scenario (243 yr and 9,407.5 ha) and the size-composition scenario (240 yr and 9,702.6 ha), though when the composition treatment was combined with the age treatment, there was a large decrease in cover age, OGF, and average OGF patch size, as was evident in the age-composition scenario. The size treatment also led to an older forest with more OGF, with an average cover age of 160 yr and 6,504.0 ha of OGF, though not as old as with the composition treatment. However, the size treatment appears to be more robust in maintaining an older forest in combination with other treatments than the composition treatment, as is evident in the size-age, size-composition, and size-age-composition scenarios. The age treatment led the youngest forest, least amount of OGF, and smallest average OGF patch size outside of the control scenario, with a cover age of 95 yr, OGF area of 2,281.9 ha, and average OGF patch size of 1.0 ha in the age scenario. However, when combined with the size treatment in the size-age and size-age-composition scenarios, this effect was reduced. There were no incongruencies in the relationship between average OGF patch size, OGF area, and forest age in any of the scenarios.

It should be stated that average forest cover age may be slightly exaggerated due to the fact that age was averaged using the oldest cohort on every site, as opposed to the average of all cohorts on every site. In addition to the inappropriateness of taking an average of averages, we found that the latter calculation had the opposite effect of understating patterns in forest age.

Table 12 Average forest cover age (yr), total OGF area (ha), and average OGF patch size (ha), where old-growth is defined as a continuous patch of sites using

an eight-nearest-neighbour classification, with a cover age greater than or equal to 125 yr (Nova Scotia Department of Natural Resources [NSDNR], 2008).

Scenario	Average cover age (yr)	Total OGF area (ha)	Average OGF patch size (ha)
Control scenario	67 (± 33)	624.8	0.2 (± 2.1)
Size scenario	160 (± 69)	6,504.0	7.9 (± 93.9)
Age scenario	95 (± 43)	2,281.9	1.0 (± 5.7)
Composition scenario	243 (± 94)	9,407.5	22.5 (± 320.5)
Size-age scenario	178 (± 75)	7,417.2	9.6 (± 157.1)
Size-composition scenario	240 (± 94)	9,702.6	28.2 (± 364.4)
Age-composition scenario	92 (± 42)	2,091.4	0.8 (± 4.2)
Size-age-composition scenario	171 (± 73)	7,108.2	7.6 (± 134.9)

4.3.3. Forest Composition Response Category

The most apparent pattern in the spatial representation of forest composition (Figure 15) was the almost complete loss of the priority removal category at simulation year 2300 in all scenarios in comparison to year 2000 in the control scenario. In this display, all scenarios appeared equally effective in the removal of the species included in the priority removal category. However, this can be largely attributed to the almost complete climate-driven extirpation of the ubiquitous balsam fir, as well as white birch and black spruce (Table 13). In year 2300 of the control scenario, there was a high dominance of the opportunistic removal category, especially in comparison with the adaptation scenarios. This was primarily due to the increasing landscape presence of red maple, as well as large-tooth aspen, white pine, and trembling aspen.

Table 13 Change in landscape presence (%) between simulation year 2000 and 2300 for the major tree species in all scenarios. S: size, A: age, C: composition.

Species	Control scenario	S scenario	A scenario	C scenario	S-A scenario	S-C scenario	A-C scenario	S-A-C scenario
Balsam fir	-93	-91	-94	-84	-92	-90	-87	-91
Red maple	59	35	55	-5	32	-4	54	34
Sugar maple	-13	14	22	24	25	27	20	24
Yellow birch	-22	-17	-22	-27	-18	-29	-20	-18
White birch	-31	-31	-32	-30	-34	-33	-31	-34
American	-6	12	19	20	21	22	16	20

Species	Control scenario	S scenario	A scenario	C scenario	S-A scenario	S-C scenario	A-C scenario	S-A-C scenario
beech								
Black spruce	-23	-23	-23	-26	-24	-25	-25	-24
Red spruce	-53	-18	-26	3	-8	4	-27	-9
White pine	35	27	38	-2	27	-3	17	22
Large-tooth aspen	37	11	28	-2	7	-4	34	8
Trembling aspen	22	7	18	-2	4	-2	21	5
Red oak	3	3	4	3	4	3	4	4
Eastern hemlock	-2	18	-2	21	22	27	-4	21

In comparing the single-treatment scenarios, the composition scenario appeared most effective in the promotion of the conservation category and control of the opportunistic category. Red maple, white pine, and the aspen species all experience a small decrease in landscape presence, ranging from -2% to -5%, as opposed to increases ranging from 4% to 59% in the other adaptation scenarios. Increases in the landscape presence of conservation target species occurred with all species except for yellow birch, which in fact had a decrease of 27% in landscape presence with the composition treatment. These trends are visible in the response category maps, but what is not visible is the smaller decrease in landscape presence of priority-removal species, such as balsam fir and white birch in comparison to other adaptation scenarios.

The size and age treatments both performed similar to each other and the control scenario in removing species of the priority category from the landscape. The size scenario was much more effective in controlling the increases in landscape presence and abundance of the species in the opportunistic removal category. Although the difference was not as pronounced as with the opportunistic removal category, the size treatment also seemed more effective in promoting and maintaining the distribution of conservation target species. Exceptions were sugar maple and American beech.

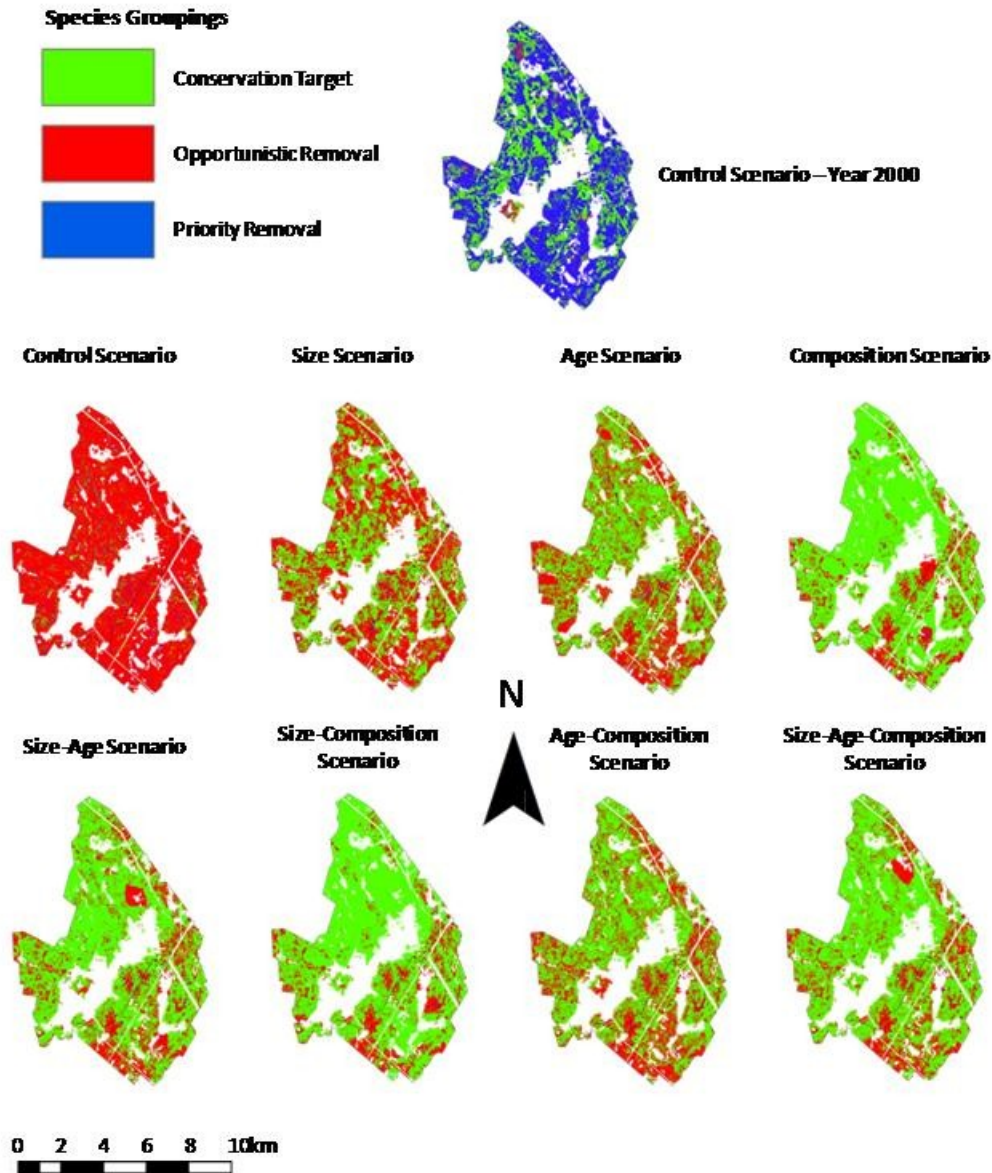


Figure 15 Spatial representation of the three groups of species based on their response to climate change in the Pockwock watershed at simulation year 2300 in all scenarios. The conservation-target species consisted of sugar maple, yellow birch, American beech, red spruce, red oak, and eastern hemlock. The opportunistic-removal species consisted of red maple, white pine, large-tooth aspen, and trembling aspen. The priority-removal species consisted of balsam fir, white birch, tamarack, white spruce, black spruce, and red pine.

There was little variation in the spatial orientation of the species groupings among the combinational scenarios, though the size-composition scenario appeared to be the most effective in the forest composition response category and the age-composition

scenario appeared to be the least. In limiting the advancement of the opportunistic species, the size-composition scenario was the most effective and the age-composition scenario was the least. In the maintenance and promotion of conservation-target species, again the size-composition scenario was most effective and the age-composition scenario was least, though once again the exception was yellow birch, which had the largest decrease in landscape presence at 29% in the size-composition scenario. All of the combinational scenarios were comparable in the removal of the priority species, and were all within 4% landscape presence of each other at simulation year 2300.

Given that these adaptation scenarios were simulated for 300 yr, we believed it was also valuable to explore the temporal dynamics in the management of species groupings, as some scenarios may be more adept in achieving management goals in a shorter time frame (Figure 16). In the no-adaptation control scenario there was a considerable increase in landscape presence of the opportunistic-removal species of 59%, and an even higher decrease in the priority-removal species of 93%. The conservation-target species also decreased in landscape presence by 18%. The age scenario and the age-composition scenario both led to similar increases in the opportunistic-removal species over time, reaching a maximum landscape presence of approximately 90% towards the end of the second century of simulation. Both the composition scenario and the size-composition scenario maintained the opportunistic-removal species at a range similar to the initial conditions over the entire simulation, ranging between 20% and 30% landscape presence.

Beyond the control scenario, which had a decrease in conservation-target species after the first century of simulation, there was no obvious winner in increasing the landscape presence of conservation-target species. In all scenarios where an increase in landscape presence was observed, a levelling-off at approximately simulation year 2050 at a value between 60% and 80% occurred. The age-composition scenario was the most effective in the rapid removal of the priority species, decreasing landscape presence of these species to less than 20% before simulation year 2100.

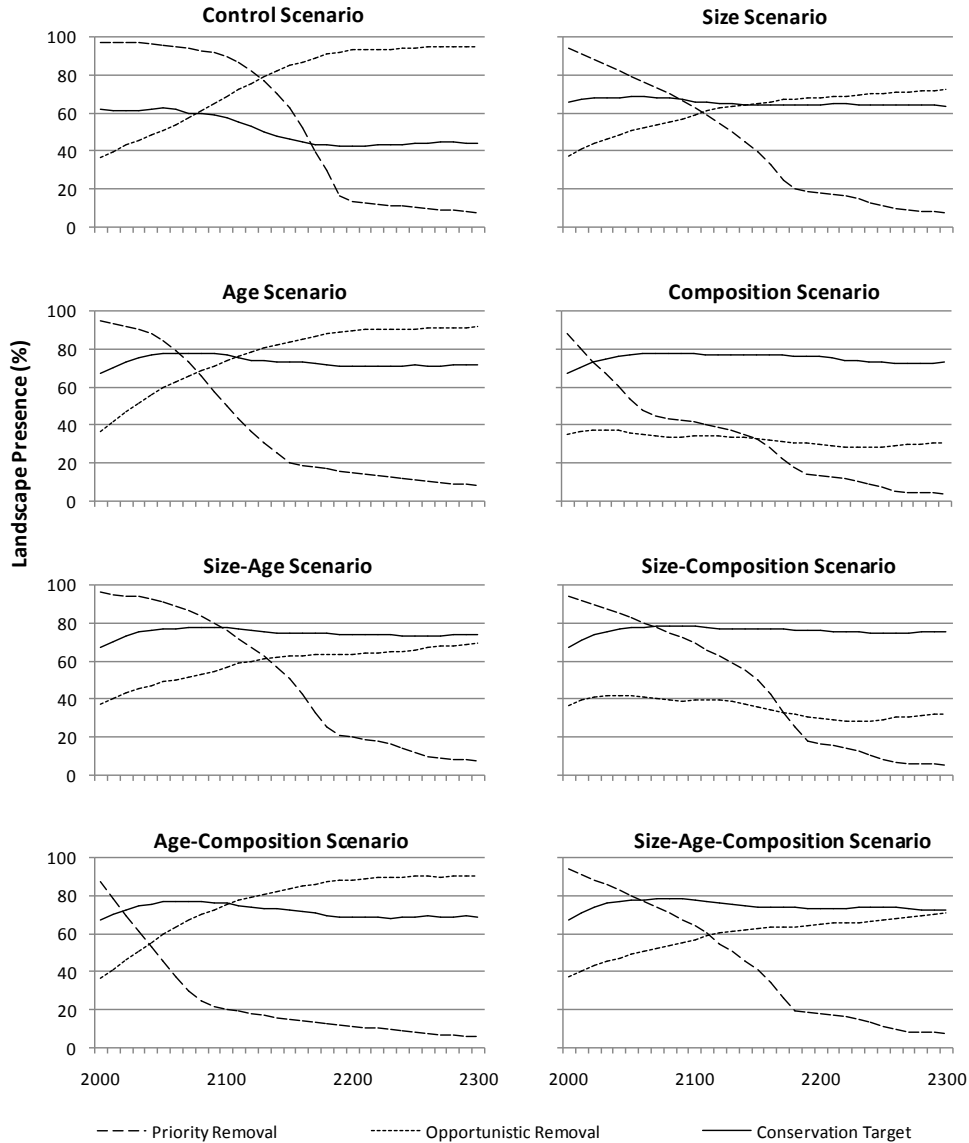


Figure 16 Time-series graphs of landscape presence (%) of the three species groupings for the entire study area between simulation year 2000 and 2300. The conservation-target species consisted of sugar maple, yellow birch, American beech, red spruce, red oak, and eastern hemlock. The opportunistic-removal species consisted of red maple, white pine, large-tooth aspen, and trembling aspen. The priority-removal species consisted of balsam fir, white birch, tamarack, white spruce, black spruce, and red pine.

4.4. Discussion

In recent years several options for climate change adaptation have been explored, such as the control of undesirable or climatically unfavoured species, partial cutting and

reduced harvest intensity, maximization of forest structural complexity and diversity, insect and disease control, provenance testing, and assisted migration/anticipatory planting (Parker et al., 2000; Dale et al., 2001; Noss, 2001; Volney & Hirsch, 2005; Spittlehouse, 2005; Johnston et al., 2009). Adaptive measures to climate change also frequently refer to the necessity for flexibility and continual learning of forest management institutions and policies through adaptive management (Duinker & Trevisan, 2003; Johnston et al., 2010). However, examples of specific adaptation strategies, especially at the operational scale, are relatively rare in the literature, due to both a lack of research and understanding, as well as the lack of documentation by forest practitioners across Canada (Johnston et al., 2010). This has created a knowledge gap between forest and climate change research and operational decision-making. The goal of this study is to help in bridging this gap using a modelling approach to climate change adaptation that can aid in the forest management planning of Halifax Water in the management of its forested watersheds in central Nova Scotia. This study explores climate change adaptation in timber harvesting through a spatially and temporally broad landscape-ecology lens, so that it may act as a precursor to more technical adaptation for future implementation, monitoring, and re-evaluation in the watersheds.

A limitation of this study was the lack of exploration into changes of natural disturbance regimes. The frequency and severity of windstorms, hurricanes, and insect and disease outbreaks is a predicted impact of climate change in Nova Scotia (Williamson et al., 2009). However, a dynamic and climate-sensitive simulation of wind and bark-beetle disturbances was not feasible using the modelling framework employed by this study. While we strongly recommend this as an area for further research, we felt that this study was a valid and useful approach, as it incorporated the direct impacts of climate change on forest structure, composition, and productivity while investigating different aspects of forest management adaptation to climate change. The alteration of natural disturbance regimes due to climate change is an indirect source of climate change impacts, and as such does not invalidate the approach taken and could be further developed using the foundations established with this study.

4.4.1. Timber Supply Response Category

While the primary objective of these watersheds is the supply of clean water, they are still managed forests, and as such there is an interest in forest productivity and timber supply. The harvest and landscape biomass data were aimed towards evaluating the adaptation treatments in this response category. First, it should be established that LANDIS-II is a mechanistic model used to look at forest ecosystem dynamics, not a predictive empirical growth and yield model (Scheller et al., 2007). As such, the results of this study are not meant to predict future timber yields in response to climate change adaptation, but rather to analyze the landscape-level response in forest productivity and get a coarse measure of the trade-offs with timber supply due to adaptation in the three different aspects of timber harvesting (Porté & Bartelink, 2002).

In the absence of adaptation, climate change caused an increase in timber supply – a frequent prediction in the literature, though often associated with high levels of uncertainty and variability (Heimann & Reichstein, 2008; Williamson et al., 2009). In targeting climate change adaptation towards timber harvesting, it was obvious that some adaptive measures were more beneficial for the timber supply, while others were quite costly. The age adaptation treatment, which excluded younger cohorts from harvests, was the most effective in maintaining timber supply at levels similar to the historical-based timber harvests of the control scenario. What was surprising was that HB was often greater than the control scenario, and reached an elevated equilibrium nearly a century before the control simulations. This suggests that this treatment was successful in encouraging more rapid succession to mature forest stands by maintaining regeneration and a seed-producing crop. However, it was costly to other forest values at the prescribed intensity of these simulations.

The selection harvesting and FEC-based management of the size treatment by its very nature is expected to lead to a decrease in timber supply, especially in the short term (Puettmann et al., 2009). But what was encouraging for the advent of FEC-based management in Nova Scotia was that the timber supply in scenarios simulating the size treatment reached a stable equilibrium in the changing climate. Low-intensity forestry has been suggested as one method to promote forest resistance and resilience to climate change (Noss, 2001).

The composition treatment appeared to have caused an almost complete collapse of timber supply. By constructing forest management decisions around the associated response of individual species to climate change, this adaptation treatment was directed towards facilitating and promoting transition to inevitable changes in climate and forest dynamics. This is a risk-laden approach, as it necessitates the acceptance of inevitable change, which is exceedingly difficult with the high levels of uncertainty surrounding climate change (Spittlehouse, 2005; Millar et al., 2007).

The driving force behind this sharp decline of timber supply after the first century of composition-directed adaptation is more likely due to the decline of target species than forest ecosystem collapse, as the other response categories indicate. There is an extreme segregation of target species in this treatment, where the removal of any conservation-target species is forbidden. Therefore, once the priority-removal species are cleared from the landscape due to the changing climate and rapid removal, the supply of opportunistic-removal species was quickly exhausted under the prescribed harvest intensity of this treatment, and the timber supply collapsed.

What was interesting about the combination of adaptation treatments in this response category was that some treatments had not only more influence on timber supply than others, but were more robust in their influence on timber supply. In all scenarios that simulated the size treatment, similar timber supply and forest productivity trends were observed. In the absence of the size treatment, the age treatment appeared to be more influential in this response category than did the composition treatment. All adaptation treatments except the age treatment led to an increase in AGB, which is not surprising given the elevated harvested biomass removed annually. Landscape biomass and AGB are related to forest ecosystem productivity, and can be indicative of the health of a forest (Friend, 2010). However, in these modelling experiments AGB is highly influenced by HB, and as such it would be imprudent to infer forest ecosystem integrity from these data.

4.4.2. Forest Age Response Category

The second category through which we examined the forest response to climate change adaptation was forest age, as it provided some insight into the level of ecosystem

integrity resulting from these adaptation treatments. Forest age is also related to the provision of forest ecosystem services, including water supply, and old-growth is often linked with the health of a water supply (Herbert, 2007). However, a direct link between water quality and forest age in the Acadian Forest Region and the study area has not been sufficiently studied, and this is well outside the scope of this study. Ecologically, old forests are critical for wildlife habitat of many species, especially cavity-dwelling species (Spence et al., 1996; Mosseler et al., 2003) and OGF is highly beneficial for the conservation of biodiversity and structural complexity (Lindenmayer & Franklin, 2002). OGF, despite initial contention in the literature, also contributes to climate-change mitigation through carbon capture (Harmon et al., 1990; Luysaert et al., 2008). Finally, in a regional context, OGF is very rare in Nova Scotia and the Acadian Forest Region (Mosseler et al., 2003; Owen et al., 2008), and it will be important to consider climate change in recent provincial OGF conservation initiatives (Colin Stewart Forest Forum Steering Committee, 2009).

The considerably older forests and greater OGF area and patch size observed in the scenarios incorporating the composition treatment can be easily attributed to the fact that six of the 16 tree species included in the modelling (all of which were long-lived) were excluded from timber harvesting. Yet this by no means negates the role of species-directed adaptation in maintaining older stand ages and OGF. While operational adaptation will likely not be as extreme as this landscape-scale adaptation treatment, the maintenance and monitoring of some OGF reserves directed towards ecologically significant species favoured in, or robust to, the altered climate may help to satisfy the previously described forest values associated with OGF and promote further establishment of climatically adapted forest in the coming decades and centuries (Halpin, 1997; Noss, 2001). Old forests with high connectivity also facilitate migration of favourable species that may be adapted to the warming temperatures, so connected areas of OGF may be an important facilitator of climate change adaptation (Noss et al., 2001; Scheller & Mladenoff, 2008).

The size treatment was markedly more effective in maximizing forest age, OGF area, and average OGF patch size than the age treatment, because the age treatment was targeted towards natural regeneration and the age of sexual maturity/seed production,

while the size treatment emphasized selection management and small opening sizes. Recall that the age treatment was not meant to maintain a healthy forest age structure in a changing climate, but rather was the directing of climate change adaptation towards stand-age-related aspects of timber harvesting. This is also true of the size and composition adaptation treatments.

In the combinational scenarios, again the influence of a single adaptation treatment was most apparent. As with the timber supply category, the size treatment was the most influential when simulated, followed by the age treatment. Also as before, the exception was the composition treatment having a greater influence when combined with the size treatment, although the influence was far more pronounced in this response category.

Forest complexity refers to compositional and structural diversity (McElhinny et al., 2005; Smith et al., 2008), and the structural complexity of forests increases with age (Odum, 1969; Brassard et al., 2008). This lends more credit to this response category as the concept of forest complexity is never far from the climate change adaptation research (Millar et al., 2007; Bradford & Kastendick, 2010). Complexity is important for the adaptive capacity and resilience of forest ecosystems because higher functional diversity means many more species and structures that can respond differently to climate change, giving more overall stability, and ensuring the ability to continually provide ecosystem services (Bradford & Kastendick, 2010).

4.4.3. Forest Composition Response Category

The final and most complex response category in this study was the forest composition category, as it provides some insight into how effective each adaptation treatment was in achieving their guiding principles of climate-change resilience, resistance, and transitioning described in Section 4.1 (Millar et al., 2007). This is an important area to evaluate, as severe changes in forest composition were predicted in the study area as a result of climate change (Steenberg, 2010), with a sharp decline in colder-climate boreal species near the southern limit of their range and increase in warmer-climate temperate species and early-successional broadleaved species (He et al., 1999; McKenney et al., 2007; Bourque & Hassan, 2008; Bourque et al., 2010; Steenberg,

2010). In a managed forest, much importance is placed upon forest composition, as management decisions and forest management plans are highly dependent on assumptions of what trees will grow where. Climate-induced changes in forest composition due to the northward shift of tree species ranges will compromise our ability to utilize forest ecosystem resources (Spittlehouse, 2005).

The almost complete extirpation of boreal species such as the prominent balsam fir and white birch occurred in all scenarios, with and without adaptive measures, in a relatively similar spatial pattern, though the composition treatment appeared to be the most temporally effective in facilitating this change. This brings to light the question of whether active management in the expedited removal of these species should be employed. The forests' lag in response-time to the rapidly changing climate could enable these tree species to persist in the suboptimal climate leading to a less productive forest in a degraded and depauperate state (Scheller & Mladenoff, 2005; Aitken et al., 2007). It has even been suggested that increased mortality may accelerate genetic adaptation of trees to the altered climate (Kuparinen et al., 2010). Management decisions for the current generation of forests over the next 50 to 100 years will be important, as these forests are already growing and will be less affected than future forests, and this lag may enable them to persist past a climate threshold, leading to catastrophic ecosystem collapse (Spittlehouse, 2005; Stephens et al., 2010). This approach is certainly risk-laden, and there may be ecological consequences, particularly for species that occupy a relatively unique niche, such as lowland black spruce.

The other side of this issue is the use of assisted migration/anticipatory planting, provenance testing, and seed transfer zones to find species, phenotypes, and genotypes that may be better adapted to anticipated future climates (Johnston et al., 2009; McKenney et al., 2009). This approach focuses climate change adaptation towards the regeneration side of forest management rather than the mortality side, and, though possible within the LANDIS-II framework, was not within the scope of this study. What is certain is that in the face of climate change, a redefinition of what spatial and taxonomic scales we consider to be 'native' may be necessary.

The threat of regional extirpation of important tree species and the introduction of newly adapted ones is a prominent subject of study (He et al., 1999; Scheller &

Mladenoff, 2008; Johnston et al., 2009). Much less attention is given to the threat of native species that are well adapted to the changes in climate and may have aggressive range expansions, threatening species and ecosystem diversity, particularly in areas that have dispersal barriers for newly adapted species from other regions, such as Nova Scotia and the study area. Climate change has been predicted to favour a wider distribution of early-successional pioneer species (Ravenscroft et al., 2010; Steenberg, 2010). There is the threat of a loss of species and ecosystem diversity due to the climate-driven increases in landscape presence and abundance, and the competitive release of highly favoured and aggressively competitive species, such as red maple and aspen species, with the decline of the boreal species.

These species were classified as an opportunistic-removal category, in light of redirection or intensification of management activities towards them. Once again, the compositional adaptation treatment surpassed the others in this response category. Red maple, which was the most prolific species in all forest ecosystems in face of climate change (Steenberg, 2010), had a 5% decrease in landscape presence in this scenario compared to a 59% increase in the control scenario. In fact, all opportunistic-removal species were found at less than their original range in current climate conditions (simulation year 2000) with the composition treatment. This exemplifies yet another important issue: these species are still ecologically and economically valuable, especially in areas with poor site conditions (Simpson, 2009), and the adaptive measures employed in this treatment were not meant to reduce or remove these species from the landscape, but rather to limit their climate-driven advancement into areas more typical of tolerant long-lived species. As such, the decrease in landscape presence of these species that occurred in some scenarios due to the composition treatment may be seen as an adverse effect and could in part explain the sharp decline in timber supply seen in these scenarios.

The conservation of tolerant and long-lived, late-successional species not only contributes to forest ecosystem complexity and biodiversity, but may impede the advancement of some of these aggressive competitors in the new climate and impede forest ecosystem homogenization (Scheller & Mladenoff, 2005; Scheller & Mladenoff, 2008; Steenberg, 2010). The only sharp decline in the conservation-target species was in the control scenario, though the composition treatment did maintain their distribution

marginally higher. However, the distribution of the conservation-target species at the individual species level tells a different story. Some of the longer-lived species were fairly robust to the changes in climate and stable between scenarios, such as sugar maple, eastern hemlock, and red oak, while others were highly sensitive to adaptation treatments. Two of these species that are of special concern are red spruce and yellow birch. Red spruce is a species of particular economic and ecological importance in the Acadian Forest Region (Loo & Ives, 2003) whose distribution was halved in the study area due to climate change. Higher-extraction adaptation treatments such as the age treatment still led to a considerable reduction of red spruce, while the composition treatment was able to maintain or even enhance its distribution. Yellow birch was slightly anomalous in this respect and responded inversely to other conservation-target species. This was likely due to shade exclusion by other climax species within LANDIS-II, as is supported by Steenberg (2010).

It is vital to consider forest composition in assessing vulnerability to climate change. In the simplest context, a more diverse forest composition will have more resilience to climate change because a forest that is diverse at the species, population, and genetic levels is more likely to contain some elements that are resistant or adapted to the changing conditions (Millar et al., 2007). Maintaining reserves of representative forest types will be highly valuable in the adaptation of forests to climate change, especially in transitional regions such as the Acadian Forest Region (Noss, 2001). However, the composition treatment, though highly effective in achieving many of the management goals and objectives described in this study, is a risk-laden approach to climate change adaptation. The increased removal of boreal species no longer favoured in the region's climate involves a level of risk, but may be a necessary step in climate change adaptation. In facilitating forest transition to the changing climate, this treatment is heavily dependent upon the predicted climate change impacts explored in the Steenberg (2010) study. While measures were taken in this study to account for some of the uncertainty associated with climate prediction (Ravenscroft et al., 2010), there is still much uncertainty in the response of forests and the forest sector to the changing climate.

4.4.4. Interrelatedness

It was hoped that by combining climate change adaptation treatments in experimental simulation modelling, we could realize the diverse benefits of all adaptation treatments across multiple areas of forest management values. The three values-based response categories used to investigate climate change adaptation in the Pockwock and Lake Major watersheds have diverging values, especially between the timber supply response category and the forest composition and age response categories. It is therefore inevitable that there will be trade-offs among them. The combinational scenarios were meant to minimize trade-offs between forest management goals and objectives in a changing climate. Moreover, some of the adaptation treatments may seem contradictory, such as promoting rapid succession to tolerant climax forest communities to promote resistance to climate change, while directing timber harvests towards individual species to facilitate transition to the changing climate. As with minimizing trade-offs between management values and objectives, the combination of different adaptation treatments was meant to minimize risk due to uncertainty with a bet-hedging strategy for climate change adaptation (Millar et al., 2007).

In the examination of the combined adaptation treatments within each response category, one treatment, most often the size treatment, was more influential than the others, and the forest response to climate change closely followed the pattern of that treatment when combined with others. This produced obvious and solitary winners in each response category; the age treatment was most effective in maintaining the timber supply, while the composition treatment was most effective in the forest age and composition response categories. However, the beneficial attributes of combining these adaptation treatments were realized when these scenarios were analyzed across response categories. In this area, the stability of the size treatment across scenarios and the influence of the treatment on other treatments became beneficial, despite never being the most effective in any one response category.

Without question, the final experimental scenario, which combined the size, age, and composition adaptation treatments, is critical to understand in order to realize the interrelatedness of timber-harvest adaptation to climate change and trade-offs between forest management goals and objectives. This scenario represented the middle ground in

climate change adaptation across the response categories just as the size treatment did. The key difference was that with the addition of the age and composition adaptation treatments, there was a slight improvement in each response category towards the associated management target. Hence, the trade-off between the response categories was minimized.

4.5. Conclusions

Forest productivity is often predicted to benefit from climate change (McMahon et al., 2010). In the absence of any adaptive measures to climate change, we observed a simulated increase in timber supply, though the impacts on forest age and composition were severe. The age treatment was most effective in the timber supply response category, and even yielded a simulated timber supply greater than in control conditions. The size treatment led to a lowered but stable timber supply, while the composition treatment caused almost a complete collapse of timber supply in the face of climate change. We believe this was not due to forest ecosystem collapse under this approach, but rather the nature of the simulated adaptation treatment, as it proved more efficacious when combined with other adaptation treatments. In combination with other adaptation treatments, the size treatment was the most influential on simulated timber supply and forest biomass.

Old forests may be highly beneficial in promoting forest resistance and resilience to climate change (Noss, 2001), and may facilitate the migration of climatically favoured species into new regions if connectivity is high (Scheller & Mladenoff, 2005). Forest structural complexity, which increases with stand age, has also been linked with climate change resilience (Millar et al., 2007; Bradford & Kastendick, 2010). The composition treatment vastly exceeded the other adaptation treatments in maximizing forest age, OGF area, and OGF patch size due to the exclusion of the longer-lived climax species from timber harvesting. The size treatment was more effective than the age treatment, and was once again the most influential on forest age when combined with other adaptation treatments.

The provision of forest ecosystem services that we depend on as a society is closely linked to forest composition (Spittlehouse, 2005). Understanding possible

changes in forest composition and developing adaptive strategies to maintain sensitive species, remove undesirable ones, and facilitate the migration of new ones was a key theme of forest management adaptation to climate change in this study. The composition treatment was a novel and relatively extreme adaptive measure in transitioning forests to the changing climate, and was the most effective in attaining the forest composition management objectives. This approach may be useful in providing directional insight for less rigid, operationally feasible approaches. However, there is risk associated with this concept due to the uncertain nature of climate change and forest response. The composition treatment was again most effective in controlling the advancement of highly competitive, early successional species that are favoured by the warmer climate, but may have in fact exhausted their supply and reduced their abundance in the landscape, leading to the observed decline in timber supply with this treatment. The conservation-target species were the most stable between scenarios, though were maintained marginally better with the composition treatment. However, at the individual species level, the composition treatment was far superior in maintaining the threatened red spruce population.

The age treatment was designed to build resistance to climate change by promoting rapid succession to climax Acadian forest communities. However, in examining the forest response categories we can conclude that the age treatment was the least effective in meeting adaptation targets.

A general theme in model results was that climate change adaptation that maintains forest-composition values and OGF in the future in light of the predicted impacts in the study area will necessitate a trade-off with timber supply. Given the influential and stable nature of the size adaptation treatment on the forests of the watersheds and on the other adaptation treatments, it was the most effective at minimizing trade-offs between management goals and objectives when combined with the age and composition treatments.

This study of climate change adaptation is a scratch on the surface of the depth to this topic, but we believe it still provides insight into future approaches to climate-smart management of the studied watersheds. We recognize that the landscape-scale approach to incorporation and analysis of climate change adaptation in this study was useful in

exploring three broad themes of adaptation, but as such was not operationally feasible. The objective of this study is to examine landscape trends in response to climate change adaptation, so that the results of this study could directly inform further decision-making around more technically advanced and operationally feasible forest management adaptations in the Halifax Water watersheds. This study may also contribute to the design, forecasting, and implementation of alternative management approaches to begin a cycle of adaptive management suited to the uncertain conditions of climate change (Duinker & Trevisan, 2003; Van Damme et al., 2003). However, given the importance of these watersheds as a water supply to the Halifax Regional Municipality, it is recommended this be a passive management approach.

The provision of a healthy water supply is an ecosystem service of great import, and it is closely related to the forest. The management of the forest ecosystems within the Pockwock and Lake Major watersheds must incorporate climate change adaptation for Halifax Water to sustainably manage its watersheds in the coming decades and centuries in the face of climate change. The findings of this study suggest that a multi-faceted and tool-rich approach to climate change adaptation will be the best strategy to contend with the risk and uncertainty of the future.

4.6. References

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CHAPTER 5 CONCLUSIONS

5.1. Project Summary and Conclusions

In this study I assess forest vulnerability to climate change in the Pockwock and Lake Major watersheds, the two principal watersheds managed by Halifax Water for the supply of clean water to the HRM. Specifically, the purpose of the study is to investigate the potential effects of climate change on the forest ecosystems within the watersheds managed by Halifax Water using a modelling approach, and to develop a conceptual framework of climate change adaptation to increase forest resilience in the face of climate change.

I used the LANDIS-II forest landscape and disturbance model for the design and simulation of two modelling experiments. The first experiment was focused on climate change impacts on the forests of the watersheds, and was the subject of the first manuscript chapter. The second experiment implemented climate change adaptations to simulated impacts from the first experiment and the literature into the timber-harvest regimes of the watersheds. This was the subject of the second manuscript chapter. The ecosystem process model PnET-II was linked to climate prediction data for the study area, downscaled from the CCCMA's CGCM3 for the more extreme SRES-A2 climate change scenario. This enabled the incorporation of climate-driven changes in tree-species growth and establishment in LANDIS-II.

5.1.1. Climate Change Impacts

The effects of climate change were apparent within the forest ecosystems of the Pockwock and Lake Major watersheds. Changes in forest composition were considerable at the watershed and ecotype scale, and were the most apparent impact of the changing climate. These included:

- A decrease in landscape presence and abundance of colder-climate boreal species, such as balsam fir, white birch, black spruce, white spruce, red pine, and tamarack.

- An increase in landscape presence and abundance of warmer-climate temperate species, such as red maple, white pine, American beech, and red oak.

These trends in forest composition were present in all experimental scenarios simulating climate change, regardless of forest management activities. The sensitivity of transitional forest regions such as the Acadian Forest Region to climate-driven changes in forest composition has been observed in modelling studies in other transitional forest regions (Pastor & Post, 1988; Neilson, 1993; Scheller & Mladenoff, 2005). Furthermore, the response of some of these Nova Scotian tree species to climate change is consistent with other studies conducted in the region and in the province (McKenney et al., 2007; Bourque & Hassan, 2008; Bourque et al., 2010). However, there are important landscape processes, such as succession, competition, dispersal, and disturbance, which were not included in the climate-envelope approach taken in these studies (Hampe, 2004). The importance of these processes becomes evident in some forest responses to climate change, such as:

- The increase in landscape presence of early-successional, pioneer species, such as large-tooth and trembling aspen, due to competitive release from other less-favoured species.
- The variable response of some ecologically and economically important species to the changing climate, such as red spruce and yellow birch, which was heavily influenced by forest management activities.

The aggressive colonization of these early-successional and highly competitive species in areas typically associated with long-lived, late-successional species observed in this study may be a threat to species and ecosystem diversity (Ravenscroft et al., 2010). The successional role and longevity of tree species typical of climax Acadian forest communities also appeared to influence their response to climate change:

- The distribution of the longer-lived, shade-tolerant, and late-successional species such as sugar maple, eastern hemlock, red oak, and American beech was found to be more robust to the changing climate.

The use of FEC is a valuable tool for managing forests sustainably (Treitz & Howarth, 2002), and is currently under development in Nova Scotia (Keys et al., 2003). As such, the impacts of climate change on different FEC ecotypes will be important for the advancement of this management approach. Moreover, climate change may affect forest composition at the individual-tree level, not the community level (Webb & Bartlein, 1992), so exploring the restructuring of ecotypes will be critical. Ecotype-scale analysis of climate change impacts in the watersheds revealed that:

- Conifer-dominated and nutrient-poor ecotypes were highly susceptible to climate-driven changes in forest composition.
- Mixedwood and broadleaved ecotypes with richer nutrient regimes were more robust to changes in forest composition, but experienced a greater loss in forest ecosystem resilience, as indicated by species richness and age-class evenness.

Since the effects of climate change on natural disturbance regimes were not simulated in this study, this analysis of vulnerability to natural disturbances using species richness and structural complexity was an important measure.

Forest productivity and biomass, as measured by changes in the aboveground living biomass of trees over time, was also affected by climate change, with:

- An increase in forest productivity in younger, actively managed forests with climate change.
- A decline in overall AGB of unmanaged forests.

An increase in forest productivity is frequently predicted in a warmer, wetter climate with higher atmospheric CO₂ concentrations (McMahon et al., 2010). However, these predictions are highly uncertain and regionally variable, and did not include the simulation of climate-induced changes in natural disturbance regimes. Furthermore, changes in forest composition may be the driver for much of the observed changes in AGB, especially at the ecotype scale. Interestingly, the reduction in AGB of the unmanaged forest landscape due to climate change supports the theory that younger

forests with an abundance of early-successional broadleaved species may experience considerable increases in productivity, but there will be no change or even a decrease in the total biomass potential of old-growth forests (Williamson et al., 2009).

The response of forest age to climate change was found to be of little importance in comparison to the implications of forest-generational longevity:

- There was little to no effect of climate change on forest age, as represented by the spatial delineation of seral stages. The impacts of timber harvesting were far more evident.
- There was a time-lag in forest response to climate change due in part to the long lifespan of trees and lower mortality rates in unmanaged forests.

Climate change, as simulated in this study, does not cause mortality of the colder-climate boreal species predicted to have decreases in landscape presence. As such, in the absence of large-scale disturbance and mortality these climatically unfavoured species may impede the colonization of climatically favoured species, leading to degraded and less productive forest ecosystems (Scheller & Mladenoff, 2005).

5.1.2. Climate Change Adaptations

Climate change may result in an increased timber supply in the study area, but the impacts described above threaten many other forest-ecosystem functions and values associated with these watersheds. Incorporating adaptation to climate change into forest management will be vital in the continual and sustainable provision of forest ecosystem services (Spittlehouse, 2005). Climate change adaptations, based on the simulated impacts of this study and the literature, were directed towards three components of timber harvesting: the canopy-opening size of harvests, the age of harvested trees within a stand, and the composition of harvested trees within a stand. The response of the annually harvested tree biomass in LANDIS-II varied depending on what adaptation treatment was simulated:

- The timber supply benefited from the changes in climate when simulating historic harvest patterns in the absence of any adaptive measures.

- The age treatment was the most effective in maintaining or even enhancing the timber supply.
- The size treatment, based on the FEC management guidelines of Nova Scotia and the current Halifax Water FMP, maintained a stable timber supply, though at a considerably lower level.
- The composition treatment targeted different tree species for removal or conservation depending upon their response to climate change and forest management values, and led to a severe decline of the timber supply.

The response of forest age to climate change adaptation is an important consideration for forest managers, as it is related to climate change resistance and resilience, forest complexity, and forest values (Lindenmayer & Franklin, 2002; Millar et al., 2007).

- The composition treatment greatly exceeded the other treatments in maximizing forest age, OGF area, and OGF patch size.
- The size treatment was more effective than the age treatment in satisfying management values and objectives associated with forest age.

Drastic changes to forest composition due to climate change are a major impact expected in the study area. The response of individual tree species to the altered climate may lead to a reordering of forest communities and ecosystems. Therefore, tree species were grouped and analyzed according to their response to climate change, not their community associations, to assess the effects of different adaptive measures on forest composition. These species groupings responded in varying ways to the timber-harvest adaptations:

- The composition treatment was the most effective in controlling the proliferation of opportunistic-removal species that were highly favoured in the altered climate, and at maintaining climatically sensitive species like red spruce.

- The distribution of conservation-target species was more stable between adaptation treatments and scenarios (excluding the control scenario), although scenarios involving the composition treatment were marginally more effective in increasing their landscape presence over time.
- The drastic decline of priority-removal species occurred within all simulated scenarios, but once again the composition treatment was marginally more effective in hastening their decline in landscape presence.
- The size treatment was once again more effective than the age treatment in the attainment of management goals relating to forest composition.

The experimental combination of the different adaptation treatments was meant to minimize trade-offs between forest management values and objectives and to yield the benefits of incorporating climate change resistance, resilience, and transitioning (Millar et al., 2007). In comparing the effectiveness of adaptation treatments across forest response categories in addition to within them, new patterns were observed:

- The size treatment was the most influential treatment on forest response when combined with other treatments, and as such was the most effective in minimizing the trade-offs between response categories.
- The final experimental scenario, which combined all three adaptation treatments, was comparable to the size treatment in minimizing trade-offs between management goals and objectives, but was slightly more effective in each evaluation category, suggesting that addressing all areas of adaptation will be important.

The conceptually broad and landscape-scale approach to the implementation and analysis of climate change adaptation in this study was meant to illustrate forest-landscape trends in response to adaptive measures in timber harvesting within the scale and scope of LANDIS-II. As such, they are not operationally feasible as they stand, but are valuable for directing more refined, technical adaptations in future research and forest management planning at Halifax Water. What appears evident is that a multi-faceted and tool-rich approach to climate change adaptation will best prepare forest managers at Halifax Water for the uncertainty of climate change in the coming years.

5.2. Management Recommendations

Several management recommendations to Halifax Water have been developed in response to the findings of this study:

- Practice even-aged forest management in conifer-dominated, nutrient-poor ecosystems with frequent stand-replacing disturbance regimes. This approach will contribute to forest transition to the changes in climate and may be useful in mitigating the negative effects of time-lags in forest response to climate change.
- Increase the removal of colder-climate boreal species in the short term, such as balsam fir, white birch, red pine, and (in some areas) black spruce and tamarack.
- Increase the removal of early-successional and more temperate species in the long term, such as red maple, white pine, large-tooth aspen, and trembling aspen, especially in areas where they compete with longer-lived, tolerant species.

Management actions based on the response of ecotypes and individual tree species to climate change will be important in facilitating forest transition in response to the changes in climate, though by nature is a risk-laden approach. Furthermore, despite current controversy around the issue, the increased abundance of some temperate and early-successional species may favour management activities towards forest biomass products in the future (Spittlehouse, 2005).

- Focus considerable management initiatives into the canopy-opening size of timber harvests using a combination of clear-cutting, group selection, and individual tree selection, based on the management guidelines of the Nova Scotia FEC (Keys et al., 2003; McGrath, 2007; 2009).
- Consider the opening size, stand age, and stand composition of timber harvests in the watersheds, and as such integrate a more diverse set of approaches to climate change adaptation.

The size adaptation treatment proved effective in building timber-supply stability in the face of climate change, without significant trade-offs with other forest management values. The incorporation of FEC management guidelines may also be effective in promoting forest resilience to climate change by building stand complexity. Further

incorporation of the age and composition adaptation treatments was the most effective strategy for minimizing trade-offs between forest management values and objectives.

- Focus selection harvesting in tolerant mixedwood and broadleaved ecosystems and maintain long-lived late-successional species in the watersheds.

This will help promote the distribution of tolerant species that are robust to climate change, such as eastern hemlock and sugar maple, and maintain the distribution of climatically sensitive species, such as red spruce. Furthermore, these longer-lived, late-successional species were often more robust to climate change in the watersheds, so planting species with similar life histories native to the region, such as butternut, basswood, and silver maple, may prove effective.

- Experiment with provenance testing and anticipatory planting of other tolerant Acadian Forest Region species where site conditions are suitable.
- Monitor forest conditions and management effectiveness, especially at the regeneration and mortality stages of forest succession, as these will be the most sensitive stages to climate change.
- Utilize the adaptive management paradigm to maintain flexibility in the forest management planning and policy at Halifax Water to contend with the uncertainty of climate change and the developing nature of scientific research.

The results of this study may provide a foundation for the cyclical forecasting, implementation, monitoring, and refinement of existing and alternative forest management strategies under the adaptive management framework (Duinker & Trevisan, 2003; Van Damme et al., 2003). However, given the ecological risk of alternative-approach implementation and the high societal value of these watersheds as the water supply to a major urban centre, this would likely require passive adaptive management techniques. The passive adaptive management approach implies the implementation of one alternative approach to monitor and compare with no-change conditions, and is often recommended in areas with high ecological risk or severe consequences of improper management, such as a water supply (Duinker & Trevisan, 2003).

5.3. Further Research

Upon completion of this modelling-based study of climate change in the forests of the Pockwock and Lake Major watersheds, I have identified some areas for future research that could directly relate to the findings of this study. The first is the further investigation and dynamic modelling of natural disturbances and their associated response to climate change. The increase in the frequency and severity of natural disturbance events are a major impact of climate change predicted in most forest regions (Dale et al., 2001). This could have further implications for the observed changes in forest composition and productivity observed in this study. There is potential for the development of the LANDIS-II framework to be effective in this area.

Tree species reproduction and regeneration will also likely be affected by climate change. This study incorporated climate-driven changes in seedling establishment, but not in seed production or dispersal, and as such may overestimate these parameters, as climatic stress may lead to lower tree-species fecundity (Price et al., 2001). A dynamic simulation of all aspects of tree-species reproduction and regeneration would be a valuable area for further research.

Another major area recommended for future research is collaboration with hydrologists and hydrological models. The relationship between forest dynamics, climate change, and water supply are exceedingly complex and warrant further research. This study has found that the principal watersheds managed by Halifax Water are vulnerable to the changing climate, while other studies have highlighted existing and predicted impacts of climate change on the hydrology of forested watersheds managed for water supply (Jones et al., 2009). The relationship between these two rich topics of research is an area of understanding vital to future water security and key management objectives of Halifax Water.

5.4. Concluding Comments

Climate change poses a threat to forests across Canada and indeed the entire planet, and the findings of this study suggest that the forests of the Pockwock and Lake Major watersheds are no exception. Across the forest sector there is a general awareness

of climate change and realization of its impacts on forests (Johnston et al., 2010). The findings of this study were consistent with many similar research initiatives, but shed some new light on climate change impacts in the Acadian Forest Region and central Nova Scotia using the powerful modelling approach provided by LANDIS-II and PnET-II. We are now at a point where adaptation can and must be incorporated into forest management planning.

Halifax Water has a unique opportunity to take a leadership role in climate change adaptation, as its managed forests are not constrained by rigid timber-driven management, as other managed forest landscapes may be. Trials of new and controversial approaches to climate change adaptation that facilitate the transition to an altered climate could be implemented at smaller scales and contrasted with more traditional or resistance-based approaches between managed watersheds. What is clear is that action must be taken to adapt to the likely impacts of climate change in the forested watersheds managed by Halifax Water in order to ensure the continual supply of forest ecosystem services like water and timber to society.

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APPENDIX A LANDIS-II AND PnET-II PARAMETERS

Table 1 List of abbreviations and scientific names of species modelled or mentioned in this study.

Species	Binomial	Abbreviation
Trees		
Balsam fir	<i>Abies balsamea</i>	BF
Red maple	<i>Acer rubrum</i>	RM
Silver maple	<i>Acer saccharinum</i>	-
Sugar maple	<i>Acer saccharum</i>	SM
Yellow birch	<i>Betula alleghaniensis</i>	YB
White birch	<i>Betula papyrifera</i>	WB
American beech	<i>Fagus grandifolia</i>	BE
Butternut	<i>Juglans cinerea</i>	-
Tamarack	<i>Larix laricina</i>	TL
White spruce	<i>Picea glauca</i>	WS
Black spruce	<i>Picea mariana</i>	BS
Red spruce	<i>Picea rubens</i>	RS
Red pine	<i>Pinus resinosa</i>	RP
White pine	<i>Pinus strobus</i>	WP
Large-tooth aspen	<i>Populus grandidentata</i>	LA
Trembling aspen	<i>Populus tremuloides</i>	TA
Red oak	<i>Quercus rubra</i>	RO
Basswood	<i>Tilia americana</i>	-
Eastern hemlock	<i>Tsuga canadensis</i>	EH
Biological disturbance agents		
Spruce budworm	<i>Choristoneura fumiferana</i>	-
Beech scale insect	<i>Cryptococcus fagisuga</i>	-
Mountain pine beetle	<i>Dendroctonus ponderosae</i>	-
Spruce beetle	<i>Dendroctonus rufipennis</i>	-
Beech bark disease fungus	<i>Neonectria faginata</i>	-
Brown spruce longhorn beetle	<i>Tetropium fuscum</i>	BSLB

Table 2 Tree species life history parameters used in LANDIS-II (Burns & Honkala, 1990 [parameters except those marked]; Scheller & Mladenoff, 2004₁; Scheller & Mladenoff, 2005₁; Scheller & Mladenoff, 2008₁; Xu et al., 2009₂).

Species	Longevity (yr)	Sexual maturity (yr)	Shade tolerance (1 to 5)	Effective seed dispersal (m)	Maximum seed dispersal (m)	Vegetative reproduction probability	Maximum age of vegetative reproduction (yr)	Leaf longevity (yr)
Balsam fir	150 ₁	251	5 ₁	30 ₂	160 ₁	0	0	4 ₁
Red maple	200	101	3 ₁	100 ₁	200 ₁	0.5 ₂	150	1 ₁
Sugar maple	300 ₁	401	5 ₁	100 ₂	200 ₁	0.1 ₂	100	1 ₁
Yellow birch	300 ₁	401	4 ₁	100 ₁	400 ₁	0.1	180	1 ₁
White birch	100	301	2 ₁	200 ₂	5000 ₁	0.5 ₂	70	1 ₁
American beech	40	30	5	20	1000	0.8	40	1 ₁
Tamarack	150	40	1	30	60	0	0	1 ₁
White spruce	150	30	3 ₁	40	300	0	0	4 ₁
Black spruce	200 ₂	30	4	80 ₂	200	0.5	200	4 ₁
Red spruce	300	30	5	100	300	0	0	4 ₁
Red pine	200	351	2 ₁	20	275 ₂	0	0	2,3 ₁
White pine	300	402	3 ₁	60	210	0	0	3 ₁
Large-tooth aspen	100	10	1 ₁	1000	5000 ₁	0.9 ₂	100	1 ₁
Trembling aspen	100	20	1 ₁	1000	5000 ₁	0.9 ₂	100	1 ₁
Red oak	250 ₁	251	3 ₁	30 ₁	3000 ₁	0.5	200	1 ₁
Eastern hemlock	400	30	5 ₁	30 ₁	100 ₁	0	0	3 ₁

Table 3 Canopy parameters used in PnET-II (Aber et al., 1996₁; Goodale et al., 1998₂; Scheller & Mladenoff, 2005₃; Xu et al., 2009₃).

Species	Canopy light attenuation constant ₁	Foliar N content (gN/gLeaf) ₃	Foliar retention (yr) ₃	Specific leaf weight (SLW; g m ⁻²) ₁	Change in SLW with foliar mass (g m ⁻² g ⁻¹) ₁	Maximum relative growth rate for foliage (yr ⁻¹) ₂
BF	0.50	1.6	4	280	0	0.3
RM	0.58	2.4	1	100	0.2	0.3
SM	0.58	2.5	1	100	0.2	0.3
YB	0.58	2.4	1	100	0.2	0.3
WB	0.58	2.3	1	100	0.2	0.3
BE	0.58	2.5	1	100	0.2	0.3
TL	0.50	1.6	1	280	0	0.3
WS	0.50	1.5	4	280	0	0.3
BS	0.50	1.5	4	280	0	0.3
RS	0.50	1.5	4	280	0	0.3
RP	0.50	1.5	2.3	280	0	0.3
WP	0.50	2.2	3	280	0	0.3
LA	0.58	2.5	1	100	0.2	0.3
TA	0.58	2.5	1	100	0.2	0.3
RO	0.58	2.5	1	100	0.2	0.3
EH	0.50	1.2	3	280	0	0.3

Table 4 Photosynthesis parameters used in PnET-II (Aber et al., 1996₁; Goodale et al., 1998₂).

Species	Conifers	Broadleaves
AmaxA (nmol CO ₂ gleaf ⁻¹ s ⁻¹) ₁	5.3	-46
AmaxB (nmol CO ₂ gleaf ⁻¹ s ⁻¹) ₁	21.5	71.9
Respiration fraction of photosynthesis ₂	0.1	0.1
Half-saturation light level (nmol PAR m ⁻² s ⁻¹) ₂	200	200
Daily Amax fraction of early morning instantaneous rate ₂	0.76	0.76
Factor of respiration increase per 10 ^o C change ₂	2	2

AmaxA is the intercept of the relationship between foliar nitrogen and maximum photosynthesis and AmaxB is the slope of the relationship between foliar nitrogen and maximum photosynthesis, both in nmol CO₂ gleaf⁻¹ s⁻¹.

Table 5 Water balance and soil respiration parameters used in PnET-II (Baldocchi et al., 1988₁; Aber et al., 1996₂; Aber et al., 1997₂).

Parameter	All species
Photosynthesis constant A (DVPDA) ₂	0.05
Photosynthesis constant B (DVPDB) ₂	2
WUE constant ₁	10.9
Fraction of water lost to drainage ₃	0.1
Soil water release parameter (d ⁻¹) ₁	0.04

Parameter	All species
SoilRespA	27.46
SoilRespB	0.06844

SoilRespA is the slope of the relationship between monthly mean temperature ($^{\circ}\text{C}$) and soil respiration ($\text{gC m}^{-2} \text{ month}^{-1}$) and SoilRespB is the intercept of the relationship between monthly mean temperature ($^{\circ}\text{C}$) and soil respiration ($\text{gC m}^{-2} \text{ month}^{-1}$).

Table 6 Carbon allocation parameters used in PnET-II (Goodale et al., 1998₁).

Parameter	All Species
C fraction of foliar mass ₁	0.45
Root AllocationA ₁	0
Root AllocationB ₁	2
Growth respiration fraction ₁	0.25
Ratio of fine root respiration ₁	1
Fraction of wood respiration ₁	0.07
Fraction of C reserved after bud allocation ₁	0.75

Root AllocationA is the intercept of the relationship between foliar and root allocation and Root AllocationB is the slope of the relationship between foliar and root allocation.

Table 7 Decomposition parameters used in PnET-II (Aber et al., 1997₁)

Parameter	Pines	Other conifers	Broadleaves
Fraction of annual live wood mortality	0.025	0.025	0.025
Fraction of annual deadwood transfer to soil organic matter	0.1	0.1	0.1
Fraction of mass lost as CO ₂ in decomposition	4	4	4
Fine root turnover coefficient A	0.789	0.789	0.789
Fine root turnover coefficient B	0.191	0.191	0.191
Fine root turnover coefficient C	0.0211	0.0211	0.0211
Maximum nitrogen content in plant N pool (g m^{-2})	20	20	20
Decomposition constant for soil organic matter (yr^{-1})	0.075	0.075	0.075
Fraction of mineralized N re-immobilized as a function of soil organic matter C:N – coefficient A	151	151	151
Fraction of mineralized N re-immobilized as a function of soil organic matter C:N – coefficient B	-35	-35	-35
Minimum N concentration in root litter (%)	1.2	1.1	1.2
Minimum N concentration in foliar litter (%)	0.4	0.35	0.8
Minimum N concentration in wood litter (%)	0.2	0.2	0.2
Maximum fractional increase in N concentrations	0.7	0.6	0.6

Table 8 Optimum and minimum temperature for photosynthesis parameters used in PnET-II (Aber et al., 1996₁; Scheller & Mladenoff, 2005₂; Xu et al., 2009₂).

Species	Optimum temperature for photosynthesis (°C)	Minimum temperature for photosynthesis (°C) ₁
BF	19.6 ₂	2.0
RM	25.1 ₂	4.0
SM	25.0 ₂	4.0
YB	24.0 ₂	4.0
WB	18.8 ₂	4.0
BE	24.0 ₂	4.0
TL	19.6 ₂	2.0
WS	17.8 ₂	2.0
BS	17.5 ₂	2.0
RS	24.0 ₁	2.0
RP	21.5 ₂	2.0
WP	22.5 ₂	2.0
LA	20.0 ₂	4.0
TA	20.0 ₂	4.0
RO	24.0 ₂	4.0
EH	24.0 ₁	4.0

Table 9 Minimum and maximum GDD for each species (Pastor & Post, 1988₁; Scheller & Mladenoff, 2005₁; Bourque et al., 2010₂).

Species	Minimum GDD	Maximum GDD
BF	563 ₂	2011 ₂
RM	1260 ₁	6600 ₁
SM	1222 ₁	3100 ₁
YB	1100 ₂	2900 ₂
WB	484 ₁	2036 ₁
BE	1300 ₂	3500 ₂
TL	560 ₁	2386 ₁
WS	280 ₁	1911 ₁
BS	300 ₂	2200 ₂
RS	800 ₂	2900 ₂
RP	1400 ₂	2300 ₂
WP	1100 ₂	3400 ₂
LA	743 ₁	3169 ₁
TA	800 ₁	3000 ₂
RO	1525 ₂	3878 ₂
EH	1222 ₁	3800 ₁

Table 10 Simulated P_{est} values from PnET-II for the average climate conditions from 1961 to 2000, used for the LANDIS-II spin-up cycles, initial time steps, and all current climate scenarios.

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
BF	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4	0.4
RM	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
SM	0	0	0	0	0.5	0.5	0.5	0.5	0.5
YB	0	0	0	0.6	0.6	0.6	0.6	0.6	0.6
WB	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
BE	0	0	0	0	0.4	0.4	0.4	0.4	0
TL	0.7	0	0.7	0.7	0	0	0.7	0.7	0.7
WS	0	0	0	0	0	0	0.3	0.3	0.3
BS	0.5	0.5	0.5	0.5	0	0	0.5	0.5	0
RS	0	0	0	0.7	0.7	0.6	0.7	0.7	0.6
RP	0	0.6	0.6	0	0	0	0	0	0
WP	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
LA	0	0	0	0	0	0.35	0.35	0.35	0
TA	0	0	0	0	0	0.35	0	0.35	0
RO	0.2	0	0	0	0	0	0	0.2	0
EH	0	0	0	0	0.4	0.4	0.4	0.4	0.4

Table 11 Simulated P_{est} values from PnET-II for the final 2091 to 2100 period, under the SRES A2 scenario and used in all LANDIS-II climate-change scenarios.

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
BF	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
RM	0.835	0.835	0.834	0.836	0.835	0.834	0.836	0.834	0.835
SM	0	0	0	0	0.43	0.429	0.431	0.428	0.428
YB	0	0	0	0.126	0.127	0.126	0.127	0.127	0.127
WB	0	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
BE	0	0	0	0	0.773	0.773	0.773	0.774	0
TL	0.01	0	0.01	0.01	0	0	0.01	0.01	0.01
WS	0	0	0	0	0	0	0.01	0.01	0.01
BS	0.01	0.01	0.01	0.01	0	0	0.01	0.01	0
RS	0	0	0	0.109	0.109	0.108	0.109	0.109	0.109
RP	0	0.01	0.01	0	0	0	0	0	0
WP	0	0.654	0.653	0.654	0.654	0.654	0.654	0.655	0.654
LA	0	0	0	0	0.218	0.217	0.218	0.218	0
TA	0	0	0	0	0.122	0.122	0	0.122	0
RO	0.912	0	0	0	0	0	0	0.911	0
EH	0	0	0	0	0.831	0.832	0.83	0.832	0.832

Table 12 Simulated ANPP values from PnET-II for the average climate conditions from 1961 to 2000, used for the LANDIS-II spin-up cycles, initial time steps, and all current climate scenarios.

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
BF	4.54	7.31	6.91	8.16	7.65	7.05	7.72	7.41	7.33
RM	4.08	6.28	5.96	6.85	6.53	6.08	6.58	6.37	6.3
SM	0	0	0	0	6.84	6.32	6.89	6.64	6.57
YB	0	0	0	6.76	6.45	6	6.5	6.29	6.22

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
WB	0	4.87	4.71	5.14	4.95	4.77	4.96	4.9	4.88
BE	0	0	0	0	6.76	6.25	6.82	6.57	0
TL	4.05	0	5.97	6.7	0	0	5.97	6.7	5.97
WS	0	0	0	0	0	0	6.66	6.47	6.41
BS	4.05	6.25	5.97	6.7	0	0	6.48	6.31	0
RS	0	0	0	8.82	8.18	7.52	8.26	7.92	7.82
RP	0	5.1	4.85	0	0	0	0	0	0
WP	0	8.06	7.55	9.32	8.52	7.72	8.62	8.19	8.08
LA	0	0	0	0	6.1	5.68	6.14	5.94	0
TA	0	0	0	0	6.1	5.68	0	5.94	0
RO	4.14	0	0	0	0	0	0	6.57	0
EH	0	0	0	0	5.81	5.5	5.84	5.69	5.65

Table 13 Simulated ANPP values from PnET-II for the final 2091 to 2100 period, under the SRES A2 scenario and used for all LANDIS-II climate-change scenarios.

Species	ET1	ET2	ET3	ET4	ET5	ET6	ET7	ET8	ET9
BF	3.44	5.75	5.41	6.56	6.04	5.53	6.1	5.83	5.76
RM	3.93	6.62	6.19	7.71	7	6.34	7.08	6.74	6.64
SM	0	0	0	0	7.1	6.43	7.18	6.83	6.74
YB	0	0	0	7.51	6.83	6.19	6.91	6.58	6.49
WB	0	3.98	3.76	4.51	4.18	3.84	4.22	4.04	3.99
BE	0	0	0	0	6.95	6.3	7.03	6.69	0
TL	0	0	0	0	0	0	0	0	0
WS	0	0	0	0	0	0	3.92	3.78	3.73
BS	1.79	2.72	2.61	2.89	0	0	2.81	2.74	0
RS	0	0	0	8	7.28	6.61	7.36	7.01	6.92
RP	0	5.03	4.73	0	0	0	0	0	0
WP	0	6.69	6.26	7.79	7.07	6.41	7.16	6.81	6.71
LA	0	0	0	0	5.67	5.18	5.72	5.48	0
TA	0	0	0	0	5.67	5.18	0	5.48	0
RO	3.89	0	0	0	0	0	0	6.69	0
EH	0	0	0	0	6.2	5.66	6.26	5.98	5.91

Table 14 Ecoregional parameters, including major species, soil WHC, and moisture, nutrient, and natural disturbance regimes for each of the nine ecotypes found in the watersheds (Keys et al., 2003₁).

Ecotype	Moisture regime ₁	Nutrient regime ₁	Major species*	Natural disturbance regime ₁	WHC (cm) ₁	Area classified (ha)
ET1 Dry-Poor Conifer	Very dry	Very poor	BS	Frequent, stand-replacing	1.55	718

Ecotype	Moisture regime ₁	Nutrient regime ₁	Major species*	Natural disturbance regime ₁	WHC (cm) ₁	Area classified (ha)
ET2 Fresh-Poor Conifer	Fresh to dry	Poor to very poor	WP, BS, JP	Frequent, stand-maintaining	5.27	989
ET3 Moist-Poor Conifer	Fresh/moist to moist	Poor to very poor	BS, RP, WP	Frequent, stand-maintaining	4.48	567
ET4 Wet-Poor Conifer	Moist/wet to wet	Medium to very poor	BS, RS, BF	Frequent to infrequent, stand-replacing	8.02	309
ET5 Fresh-Medium Conifer	Fresh/moist to dry	Medium to poor	RS	Infrequent, stand-replacing	6.11	5317
ET6 Moist-Medium Mixedwood	Fresh/moist to moist/wet	Medium to poor	RS, EH, BF	Infrequent, stand-replacing	4.73	1814
ET7 Fresh-Rich Deciduous	Moist/Fresh to dry	Rich to medium	SM, YB, RM, RS	Gap dynamics	6.31	1182
ET8 Moist-Rich Mixedwood	Fresh/moist to moist/wet	Rich to medium	RM, SM, RS, YB	Infrequent, stand-replacing	5.51	61
ET9 Wet-Rich Deciduous	Moist/wet to wet	Very rich to medium	RM, BF, YB, RS	Infrequent, stand-replacing	5.31	12

Table 15 Wind disturbance event parameters (Seymour et al., 2002₁; Keys et al., 2003₁)

Ecoregion	Maximum size (ha) ₁	Minimum size (ha) ₁	Mean size (ha) ₁	Rotation period (yr) ₁
ET1	100	1	50	125
ET2	100	1	50	300
ET3	100	1	50	125
ET4	100	1	50	300
ET5	3785	0.2	54	855
ET6	3785	0.2	54	855
ET7	0.1	0.04	0.04	50
ET8	3785	0.2	54	855
ET9	3785	0.2	54	855

Table 16 Wind event severity parameters, with five being to most severe and one being the least severe (Scheller & Domingo, 2007₁).

Event severity	Percent of species longevity impacted ₁
Five	0% to 100%
Four	20% to 100%
Three	50% to 100%
Two	70% to 100%
One	85% to 100%

Table 17 Bark beetle disturbance parameters (Magasi, 1995₁; Neily et al., 2007₁; NSDNR, 2010₁).

Species	Host age (yr) ₁	Susceptibility/mortality age (yr) ₁
WS	60	70
RS	100	150

Table 18 Percent of total possible aboveground biomass necessary of each shade class in each ecotype (Keys et al., 2003 [open seral, edaphic, or climatic climax communities]₁; Scheller & Mladenoff, 2004₂; Scheller, 2010₂).

Ecotype ₁	Shade class 1 ₂	Shade class 2 ₂	Shade class 3 ₂	Shade class 4 ₂	Shade class 5 ₂
ET1	0% to 20%	21% to 50%	51% to 80%	81% to 100%	100%
ET2	0% to 20%	21% to 40%	41% to 60%	61% to 90%	91% to 100%
ET3	0% to 20%	21% to 40%	41% to 60%	61% to 90%	91% to 100%
ET4	0% to 20%	21% to 40%	41% to 60%	61% to 90%	91% to 100%
ET5	0% to 20%	21% to 30%	31% to 40%	41% to 50%	51% to 80%
ET6	0% to 20%	21% to 30%	31% to 40%	41% to 50%	51% to 80%
ET7	0% to 20%	21% to 30%	31% to 40%	41% to 50%	51% to 80%
ET8	0% to 20%	21% to 30%	31% to 40%	41% to 50%	51% to 80%
ET9	0% to 20%	21% to 40%	41% to 60%	61% to 90%	91% to 100%