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Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada

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Abstract

• *Context* Understanding the range of possible climate change impacts on forests and the interactions between them is vital to sustainable forest management.
• *Aims* We examine whether the combined influence of climate change and timber harvest will affect tree species distribution and productivity beyond predictions based on climate alone.
• *Methods* We used the landscape disturbance model LANDIS-II to simulate two climate and two harvest scenarios in 14,000 ha of managed watersheds.
• *Results* The elevated temperature led to a decline in the abundance of boreal species and a substantial increase in some temperate and pioneer species. Importantly, the interaction of climate change and timber harvest yielded changes in the distribution of some species that would not be expected based on climate alone. Conversely, some late-successional species exhibited resistance to climate-driven changes in their distribution. Climate change caused an increase in forest productivity when harvest was simulated, but a decrease in no-harvest scenarios. A time lag in forest response was likely responsible for this decrease in the absence of widespread mortality.
• *Conclusions* The finding that disturbance may drive the range expansion of early-successional broadleaved species and cause a decline of red spruce has implications for forest community associations, as well as for forest management where conifers are favoured for pulp production.

Contribution of the co-authors James Steenberg was responsible for the experimental design, running the data analysis, and writing the paper. Peter Duinker and Peter Bush were responsible for supervising the work and providing input and manuscript revisions.

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1 Introduction

Climate change poses numerous threats to forests around the globe due to changes in forest productivity, shifting ranges and abundances of tree species, and changes in natural disturbance regimes (Dale et al. 2001; McKenney et al. 2007; McMahon et al. 2010). 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 (Intergovernmental Panel on Climate Change (IPCC) 2007). Understanding the range of possible impacts on forest ecosystems and interactions between them will be critical in ensuring their future functioning and the continuing provision of the services upon which society has become dependent.

Climate change, particularly increased atmospheric carbon dioxide (CO_2) and temperature and altered precipitation rates, is predicted to affect the distribution, phenology, and physiology of trees, as well as the functioning of forest ecosystems (McKenney et al. 2007). In addition to anticipated shifts in tree-species ranges, a restructuring of many forest communities is possible due to changes in abundance and relative dominance. Such severe changes in forest composition could affect complex ecosystem processes like competition and succession in unforeseen ways (Gustafson et al. 2010), particularly when extensive disturbance from timber harvest is factored in as an additional source of uncertainty.

Several studies on the effects of climate change in transitional forest regions between boreal and temperate zones suggest declines in the abundance and productivity of colder-climate boreal tree species and increases in warmer-climate temperate species (Ravenscroft et al. 2010;

Steenberg et al. 2011). However, it is also held that climate alone is understandably not sufficient to predict changes in forest composition (Lo et al. 2010). Changes in climate, natural disturbance regimes, and forest management practices may interact in unforeseen ways, favouring species outside of their range of climatic tolerance (Landhäusser et al. 2010). We explore whether the combined influence of climate change and timber harvest in a transitional forest region will affect tree species distribution and productivity beyond predictions based on climate alone.

Increases in temperature, atmospheric CO_2, and growing season length have also been predicted and observed to benefit the metabolic processes of trees, mainly photosynthesis and respiration, leading to increases in forest productivity (McMahon et al. 2010). 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). The cumulative effects of climate change on forest productivity are still not fully understood as studies often have variable or conflicting findings with high levels of uncertainty and regional variability.

Many studies speculate that given the rate of climatic change and the long generation time of trees, a lag in forest response will occur and be detrimental to forest productivity. This essentially equates to a gap in fundamental and realized niche, whereby forests may persist in suboptimal states (Scheller and Mladenoff 2005). The extent of these lag effects may be influenced by several factors, namely genetic and phenotypic diversity (Aitken et al. 2008), migration rates and barriers to dispersal (Scheller and Mladenoff 2005), and the level of disturbance and mortality (Kuparinen et al. 2010). We investigate the role of tree mortality associated with timber harvest in the existence and size of a response lag, and the associated influence on forest productivity.

We simulated the effects of climate change and timber harvest on the forests of two watersheds in central Nova Scotia, Canada (Fig. 1) using the landscape disturbance model LANDIS-II (Scheller et al. 2007). The study objectives include: (1) assessing the effects of a severe climate change scenario on forest composition, age structure, and productivity, (2) examining the influence of timber harvest on the response of the forests to the changing climate, and (3) assessing the restructuring of current forest ecosystems that are associated with particular ecosites. Specifically, we address the following questions. Can the combined influence of climate change and timber harvest in transitional forest regions affect tree species distribution and productivity beyond predictions based on climate alone? Are different forest community associations within a landscape more vulnerable to the changing climate? How will timber harvest influence the rate of forest response to climate change?

2 Methods

2.1 Study area and forest ecosystem classification

The study area consists of two discrete watersheds: The 7,100-ha Pockwock Lake watershed and the 7,000-ha Lake Major watershed located in central Nova Scotia, Canada (Fig. 1). The Pockwock and Lake Major watersheds are managed by Halifax Water to supply a small amount of timber, but are also managed to supply potable water for the Halifax Regional Municipality. The watersheds have an elevation ranging between 17 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 growing-degree days (GDD; Neily et al. 2003). The GDD data used in the study were obtained from several sources, all of which use a threshold base temperature of 5 °C (see Section 2.3).

The Acadian Forest Region where the study area is situated is a transitional region between boreal and temperate forests. Characteristic communities in the absence of anthropogenic disturbance are mixedwood in composition, with long-lived, shade-tolerant species like red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), balsam fir (*Abies balsamea*), and white pine (*Pinus strobus*). Edaphic site conditions and frequent disturbance favour communities of black spruce (*Picea mariana*), tamarack (*Larix laricina*), and shorter-lived early- to mid-successional broadleaved species such as red maple (*Acer rubrum*), northern red oak (*Quercus rubra*), white birch (*Betula papyrifera*), and aspen (*Populus* spp.). The main natural disturbances in the region are windthrow, insects, and diseases. Both stand-initiating disturbances caused by catastrophic windstorms and hurricanes and gap disturbances from smaller wind events are key disturbance agents in the region. Major insect pests include spruce beetle (*Dendroctonus rufipennis*) and more recently the introduced brown spruce longhorn beetle (*Tetropium fuscum*) that can cause landscape-scale disturbance when there is an abundance of host species (Loo and Ives 2003). Current harvest practices in central Nova Scotia generally consist of even-aged management focused on softwood pulp production.

We also incorporated the forest ecosystem classification of Nova Scotia into the modelling framework, which is a stand-level classification of ecosites based on site, soil, and vegetation (Keys et al. 2003). It was used to delineate site conditions in the study area (Table 1) using a geospatial multi-criteria evaluation based on soil type, surficial
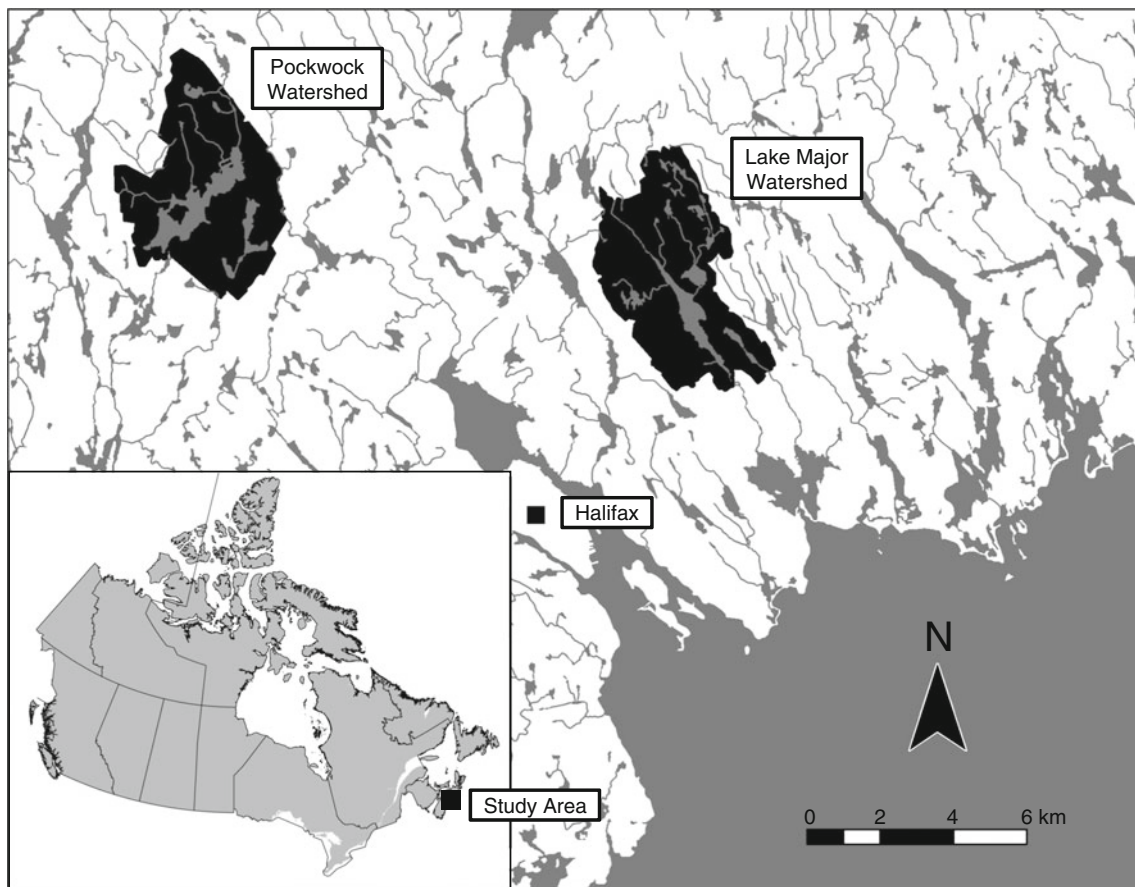
Fig. 1 The Pockwock and Lake Major watersheds in central Nova Scotia, Canada

geology, drainage, slope, and topographic position index (Keys et al. 2003).

2.2 Simulation models

Our study employed two simulation models: a forest landscape and disturbance model, LANDIS-II (Scheller et al. 2007), and an ecosystem process model, PnET-II (Aber and Federer 1992; 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 and is stratified into areas of similar abiotic conditions called ecoregions, which in this study were the nine ecosites (Table 1). Trees are not individually represented, but rather aggregated into age cohorts of a given species, whereby any site (cell) can have multiple species-age cohorts. A series of tree species life history attributes included in the simulation is used to model successional processes. Succession, biomass accumulation, dispersal, age-related mortality, and biomass decay are driven by a central succession module. Tree species growth rates, represented by aboveground net primary productivity

(ANPP), and establishment probabilities (P_{est}) values were calculated using PnET-II for each tree species in each ecosite. There are multiple optional disturbance modules. We simulated timber harvest, as well as background wind and insect disturbances.

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, photosynthetically active radiation, and atmospheric CO_2 concentrations (Aber and Federer 1992; Xu et al. 2009). PnET-II has been coupled with LANDIS-II and its predecessors in several studies to calculate the ANPP and P_{est} input parameters based on current and future climates (Scheller and Mladenoff 2005, 2008; Xu et al. 2009; Gustafson et al. 2010; Ravenscroft et al. 2010; Steenberg et al. 2011). PnET-II calculates the LANDIS-II input ANPP as the combination of wood and foliar NPP. Variation in ANPP between ecosites is driven by latitude and soil water holding capacity (cm) input parameters. The P_{est} values are calculated within PnET-II using light and water availability and optimal GDD for each tree species, as described by Xu et al. (2009).

Table 1 The major tree species and moisture, nutrient, and natural disturbance regimes for each of the nine ecosites found in the watersheds (Keys et al. 2003)

Ecosite[a]	Major species	Natural disturbance regime	Area (ha)
Dry-poor conifer	Black spruce	Frequent, stand-replacing	718
Fresh-poor conifer	White pine, black spruce, jack pine	Frequent, stand-maintaining	989
Moist-poor conifer	Black spruce, red pine, white pine	Frequent, stand-maintaining	567
Wet-poor conifer	Black spruce, red spruce, balsam fir	Frequent to infrequent, stand-replacing	309
Fresh-medium conifer	Red spruce	Infrequent, stand-replacing	5,317
Moist-medium mixedwood	Red spruce, eastern hemlock, balsam fir	Infrequent, stand-replacing	1,814
Fresh-rich deciduous	Sugar maple, yellow birch, red maple, red spruce	Gap dynamics	1,182
Moist-rich mixedwood	Red maple, sugar maple, red spruce, yellow birch	Infrequent, stand-replacing	61
Wet-rich deciduous	Red maple, balsam fir, yellow birch, red spruce	Infrequent, stand-replacing	12

[a] The naming convention of the ecosites refers to moisture regime, nutrient regime, and cover type, respectively

2.3 Model initialization and parameterization

The initial forest structure and composition for the study were derived from the provincial forest resource inventory (FRI) data (Nova Scotia Department of Natural Resources (NSDNR) 2010). The forest consists of 512 stand types 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. The study area, at just over 14,000 ha, is relatively small compared to those typically modelled using LANDIS-II, which usually range from 10,000 ha to 1,000 km^2. Therefore, the model was run at a fine spatial resolution (20 m) to capture a finer level of ecosystem complexity and spatial variability.

The 16 tree species included in the modelling have an array of parameters that define their respective life cycles, competitive abilities, biology, and climatic ranges (Table 2) and were obtained from several sources (Burns and Honkala 1990; Aber et al. 1997; Goodale et al. 1998; Scheller and Mladenoff 2005; Xu et al. 2009; Bourque et al. 2010), as well as from consultation with local experts in forest ecology. Due to the uncertainty surrounding the full effects of CO$_2$ 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 and Mladenoff 2008; Gustafson et al. 2010).

We selected a 10-year time step for the succession, wind, biological disturbance, and harvest disturbances in all scenarios. 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). The biological disturbance module was parameterized to simulate bark beetle disturbance of both

the native spruce bark beetle and introduced brown spruce longhorn beetle (Magasi 1995). Beetle outbreak was considered chronic, with low rates of mortality occurring at every time step. White spruce (*Picea glauca*), 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 (2010). Both the wind and biological disturbance modules were insensitive to changes in climate. Consequently, the effects of the changing climate on these forms of natural disturbance were not addressed by the study.

The timber harvest disturbance module was parameterized to mimic even-aged clear-cutting, which is typical of the region. Stands eligible for harvest were delineated using the original NSDNR FRI polygons used to parameterize initial forest conditions (NSDNR 2010), with a mean size of 4.2 ha. Harvest priority was assigned based on stand age, with the oldest stands receiving the highest harvest priority. A 10-year adjacency rule was used, meaning that neighbouring stands cannot be harvested for an additional 10 years. Total biomass of every species-age cohort was removed from each site within a harvested stand. Natural regeneration after harvest was driven by species-specific P_{est} parameters, seed dispersal, and existing cover species. No planting schedules were simulated. An annual allowable harvest area of 1.5 % of the watersheds was used as it was the level of harvest where simulated forest composition, as defined by relative species abundance, was most consistent with recent FRI data for the region (Townsend 2004).

2.4 Experimental design

We simulated two harvest scenarios and two climate scenarios: (a) current climate-no harvest, (b) climate change-no harvest, (c) current climate-harvest, and (d) climate change-harvest. Each scenario was run for 300 years, representing the period from 2000 to 2300, meaning an additional 200 years of

Table 2 Key tree species input parameters

Species	P_{est}[a]	ANPP[b]	Longevity (years)	Shade tolerance	Seed disp.[c]	GDD$_{min}$[d]	GDD$_{max}$[e]
Balsam fir	−0.39	−152	150	5	30	563	2,011
Red maple	0.63	36	200	3	100	1,260	6,600
Sugar maple	−0.04	18	300	5	100	1,222	3,100
Yellow birch	−0.32	28	300	4	100	1,100	2,900
White birch	−0.44	−85	100	2	200	484	2,036
American beech	0.17	11	250	5	20	1,300	3,500
Tamarack	−0.46	0	150	1	30	560	2,386
White spruce	−0.10	−258	150	3	40	280	1,911
Black spruce	−0.33	−342	200	4	80	300	2,200
Red spruce	−0.37	−87	300	5	100	800	2,900
Red pine	−0.13	−10	200	2	20	1,400	2,300
White pine	0.14	−134	300	3	60	1,100	3,400
Large-tooth aspen	−0.02	−46	100	1	1,000	743	3,169
Trembling aspen	−0.04	−46	100	1	1,000	800	3,000
Northern red oak	0.16	11	250	3	30	1,525	3,878
Eastern hemlock	0.24	26	400	5	30	1,222	3,800

[a] Change in the probability of establishment between 1961–2000 baseline values and the 2091–2100 values

[b] Change in aboveground net primary productivity (Mg/ha per year) between 1961–2000 baseline values and the 2091–2100 values

[c] Effective seed dispersal (m)

[d] Minimum growing-degree days

[e] Maximum growing-degree days

simulation after the Third Generation Coupled Global Climate Model (CGCM3) climate profile. This was done in order to attain steady-state conditions and examine forest composition and structure after most of the original cohorts had been removed by disturbance or age-related mortality (He et al. 1999; Steenberg et al. 2011). LANDIS-II was also run for 500 years in a spin-up cycle in order to reach steady-state conditions prior to the implementation of the four scenarios. Background wind and bark beetle disturbances were simulated in all scenarios.

We simulated the forest landscape under both a current climate and high-emissions climate change scenario to incorporate a broad range of prediction (Ravenscroft et al. 2010). The no-change scenario used the current climate conditions, an average of the 1961–2000 climate output from the Canadian Regional Climate Model (CRCM) for the study area, with total annual precipitation ranging between approximately 1,000 and 1,400 mm and mean annual temperature ranging between approximately 4 and 6 °C. Simulating multiple climate change scenarios with additional general circulation models (GCMs) and emissions scenarios, particularly an additional moderate climate change scenario, would have been favourable. However, downscaled data from the CRCM were only available for one GCM, the CGCM3, under the SRES-A2 emission scenario. Downscaled data from the CRCM were necessary due to the smaller size of the study area. This limits our study to the single climate change scenario and is an important limitation of the study and source of uncertainty in our results. Uncertainty in the response of forests to multiple GCMs and emission scenarios has been documented using LANDIS-II by Xu et al. (2009).

The emissions scenario used to simulate climate change was the SRES-A2 scenario, from the IPCC Fourth Assessment Report, which predicts atmospheric CO_2 levels stabilizing at 850 ppm by the year 2100 (IPCC 2007). When downscaled in the CRCM, this leads to a 5.8 °C increase in mean annual temperature and a 7-mm increase in total annual precipitation in the study area (Canadian Centre for Climate Modelling and Analysis (CCCMA) 2009). The historic and climate change data were retrieved from the CCCMA (2009). The CRCM is a downscaling tool for GCM data that functions at a regional scale of 46 horizontal km in North America and is driven by the CGCM3 (CCCMA 2009). Monthly means of maximum temperature, minimum temperature, total precipitation, photosynthetically active radiation, and atmospheric CO_2 were input in PnET-II to model ANPP and P_{est} for subsequent input into LANDIS-II.

In the climate change scenarios, the climate-driven changes in the ANPP and P_{est} variables were quantified every 10 years 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. Scenarios were run for the additional 200-year period beyond the climate profile in order to attain steady-state conditions in the future climate, allowing cohorts from the first century to reach mortality (He et al. 1999). However, uncertainty will of course be higher in the final 200 years of simulation (Scheller and Mladenoff 2005). The 500-year spin-up cycles were simulated under the 1961–2000 climate, using the same ANPP and P_{est} values simulated in current climate scenarios. Timber harvest was simulated in the spin-up cycle for the harvest scenarios only. This does present a limitation for the effectiveness of comparing the initial influence of climate change between harvest and no-harvest scenarios since initial scenario conditions are different. However, it was found to be a more valid approach than beginning timber harvest simulation at scenario implementation.

2.5 Data analysis

Scenarios were replicated four times in order to assess the model variability within each scenario arising from the stochastic variation in disturbances, dispersal, and establishment. LANDIS-II model output had very low stochastic variability, and the relative standard error in all of the response variables never exceeded 1 %. Consequently, we randomly selected one replicate from each scenario for analysis (Ravenscroft et al. 2010). The use of replicates to examine between-scenario variation may not be a valid approach when model stochastic variability is low (Scheller and Mladenoff 2005). Moreover, additional replicates can be misleading as they can be used to shrink standard error (Scheller and Mladenoff 2005). However, the validity of the inherently low stochastic variability within LANDIS-II may be an issue that warrants further study.

We examined the effects of the changing climate on forest composition, productivity, and age structure in the nine different ecosites (Table 1) and in the entire study area. The landscape presence (percentage), defined as the proportion of active sites with one or more age cohorts of a given species present, was calculated at simulation year 2300. Four ecosites were selected for analysis as they were both extensive in the watersheds and represented key examples from ecosite groups that responded similarly to climate change. The biomass response variable was total living aboveground biomass (AGB) of all tree species, expressed in Mg/ha. Biomass was graphed as a time series for the 300-year simulation for the entire study area to observe any temporal patterns. AGB was also calculated at year 2300 for the nine ecosites. The age response variable was the area covered (ha) by five seral stages for the entire study area, similar to Gustafson et al. (2010). The five seral stages were establishment (0–40 years), early seral (41–100 years), mid-seral (101–140 years), late seral (140–200 years), and old growth (>200 years).

A rigorous quantitative validation of a modelling study of this nature is essentially impossible. 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). Forest models with broad spatial and temporal scales, such as LANDIS-II, use a combination of the literature and expert consultation to assess model reliability and validity (Vanclay and Skovsgaard 1997). In this study, model output from the no-harvest simulations was compared to the literature of historical conditions (Loo and Ives 2003) and old growth (Mosseler et al. 2003), and model behaviour was found to be consistent with climax forest composition. Forest composition, biomass, and age structure were assessed for consistency by local forest researchers and practitioners. For the harvest scenarios, model behaviour in terms of forest composition, AGB, and age structure was generally consistent with the literature, expert opinion, and provincial forest inventory reports (Townsend 2004).

3 Results

3.1 Forest composition

Results from the current climate-no harvest scenario compared well with pre-settlement conditions of the Acadian Forest Region from the literature (Loo and Ives 2003) and expert consultation, with a dominance of shade-tolerant, longer-lived species typical of climax communities, including red spruce, eastern hemlock, American beech, sugar maple, and balsam fir (Fig. 2). Timber harvest disturbance in the current climate-harvest scenario led to a much higher landscape presence of the early- to mid-successional species, such as white pine, northern red oak, red maple, white birch, large-tooth aspen (*Populus grandidentata*), and trembling aspen (*Populus tremuloides*).

Forest composition responded to climate change in both the presence and absence of timber harvest. In the climate change-no harvest scenario, 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, northern red oak, and eastern hemlock had smaller increases (<5 %). Tamarack, white spruce, red pine (*Pinus resinosa*), large-tooth aspen, and trembling aspen were either absent or sparsely distributed in the no-harvest scenarios, and had negligible changes in distribution.
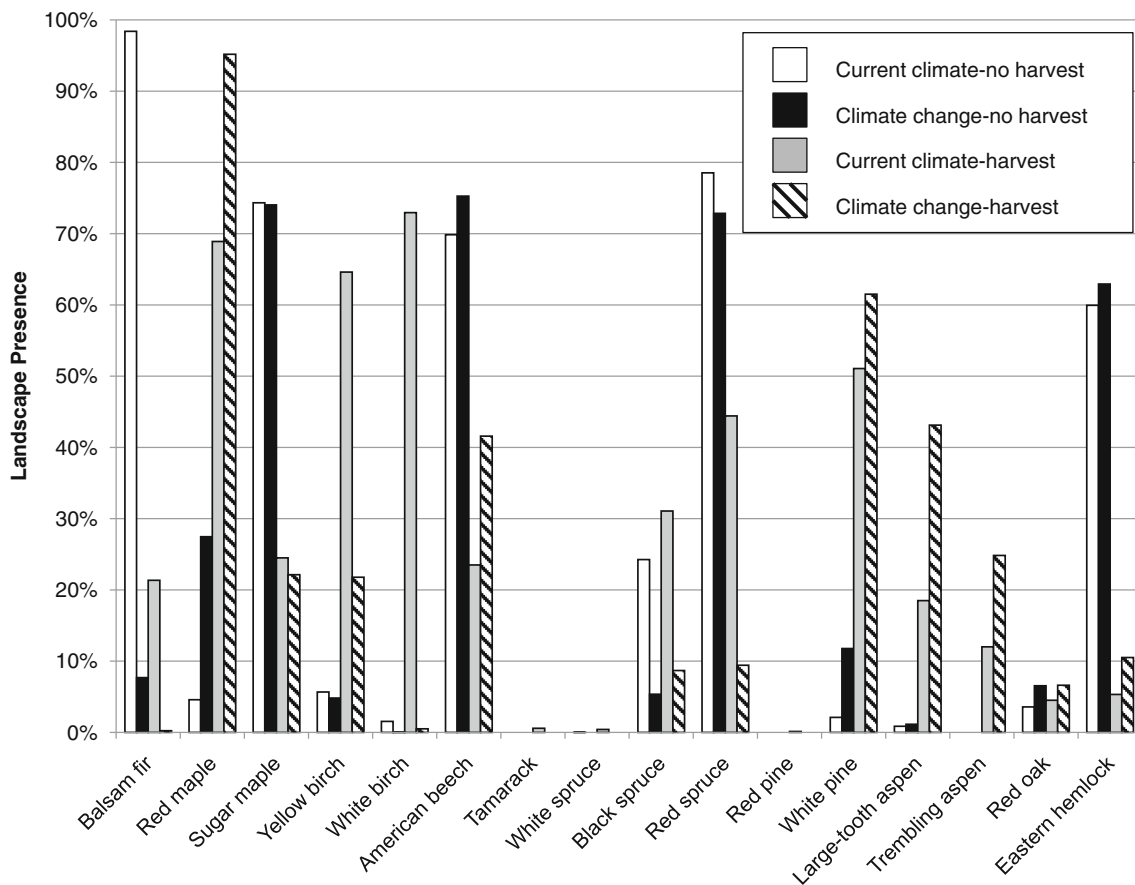
Fig. 2 Landscape presence of the 16 tree species in the entire study area at simulation year 2300 for all four scenarios

Timber harvest in the climate change-harvest scenario had the effect of amplifying the response in landscape presence of some tree species to climate change. Yellow birch had a decrease of 43 % compared to 1 %, and red spruce had a loss of 35 % compared to 6 %. The aspen species had much larger increases in their landscape presence than in the climate change-no harvest scenario (25 % for large-tooth aspen and 13 % for trembling aspen), again likely due to the introduction of timber harvest.

Analysis of the nine ecosites illustrated important implications for the stand-level response of forest composition to climate change (Fig. 3). Between the no-harvest scenarios, the most striking change was the loss of balsam fir in every ecosite. However, another important finding was that there was no major loss of spruce and no major increase of intolerant hardwoods (red maple, white birch, trembling aspen, and large-tooth aspen) in the fresh-medium conifer and fresh-rich deciduous ecosites, as was seen in the nutrient-poor coniferous ecosites.

In the comparison between harvest scenarios, spruce was found to decline in all ecosites, and intolerant hardwoods increased in all ecosites, in contrast to the no-harvest scenarios. The tolerant hardwoods (sugar maple, yellow birch,

American beech, and northern red oak) were resistant to climate change with and without timber harvest in the fresh-medium conifer and fresh-rich deciduous ecosites. Finally, the presence of pine, specifically white pine, and subsequent increase in the climate change-harvest scenario was in contrast to the no-harvest scenarios. The substantial increase in tolerant hardwoods in the dry-poor conifer ecosite in this scenario was due entirely to the increase of northern red oak.

3.2 Biomass

Landscape AGB responded to climate change and to the interaction of climate change with timber harvest. Interestingly, there was a divergent response of forest biomass to climate change with and without timber harvest (Fig. 4). In the no-harvest scenarios, mean AGB of the entire landscape at year 2300 decreased from 258 to 240 Mg/ha with climate change. In the harvest scenarios, 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 harvest and no-harvest scenarios increased with the onset
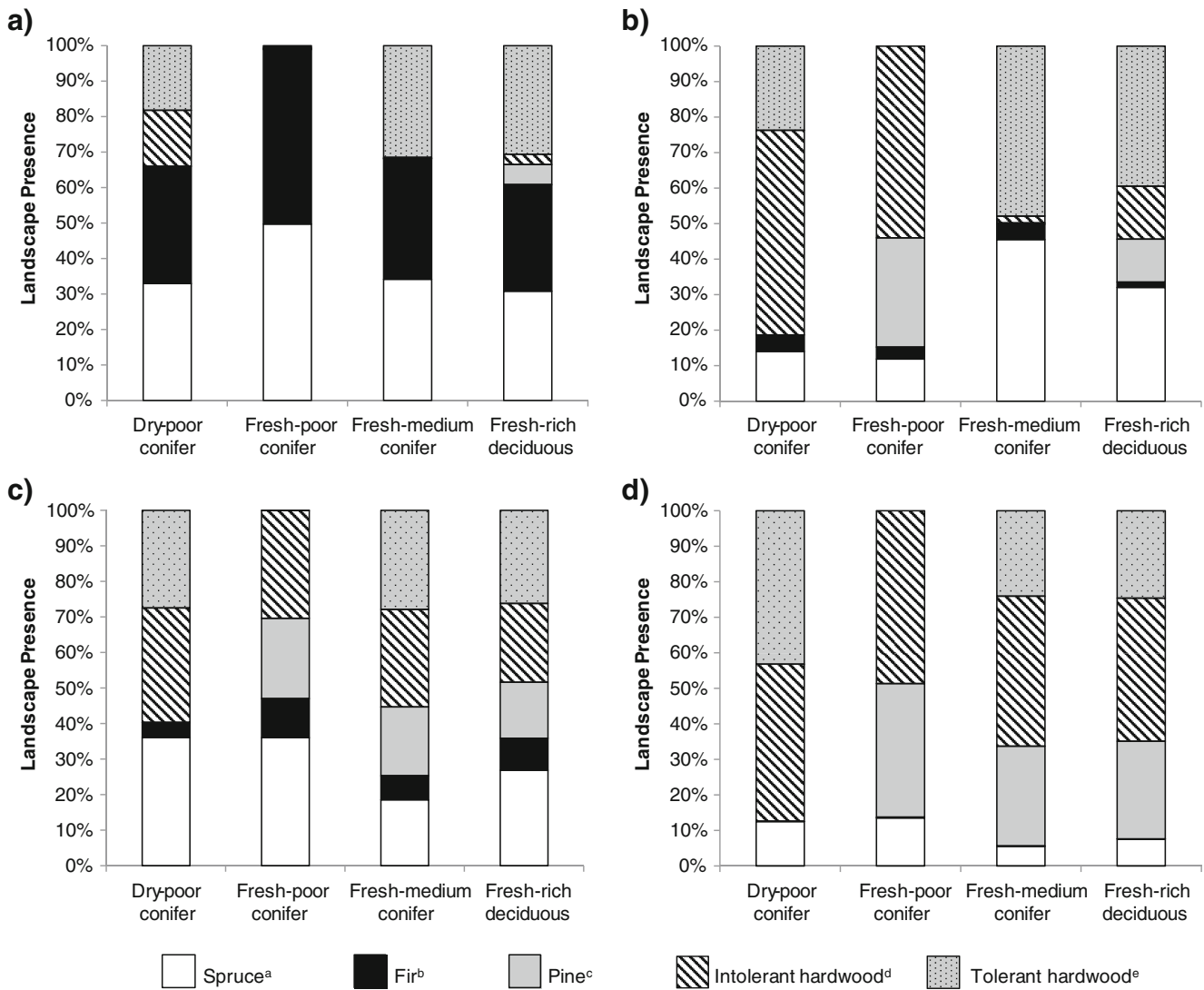
a)

b)

c)

d)

☐ Spruce[a]   ■ Fir[b]   ▨ Pine[c]   ▧ Intolerant hardwood[d]   ▦ Tolerant hardwood[e]

Fig. 3 Landscape presence of major species groups in four key ecosites in the **a** current climate-no harvest, **b** climate change-no harvest, **c** current climate-harvest, and **d** climate change-harvest scenarios. [a]Spruce (red spruce, black spruce, and white spruce); [b]fir (balsam fir); [c]pine (white pine and red pine); [d]intolerant hardwoods (red maple, white birch, trembling aspen, and large-tooth aspen); [e]tolerant hardwoods (sugar maple, yellow birch, American beech, and northern red oak)

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 the no-harvest scenarios, AGB decreased by 19 Mg/ha by year 2300, and in the harvest scenarios, AGB increased by 15 Mg/ha by year 2300. The higher initial AGB values at year 2000 for the no-harvest scenarios can be attributed to the fact that timber harvest was not simulated in the spin-up cycle, as it was for the harvest scenarios.

There was some divergence amongst ecosites in comparison to the trends in landscape AGB (Fig. 5). The dry-poor ecosite was the only ecosite where AGB responded positively to climate change in the absence of timber harvest. Conversely, with timber harvest present, the fresh-medium conifer and fresh-rich deciduous ecosites

had smaller changes in AGB than the nutrient-poor ecosites, and the fresh-rich deciduous ecosite in fact had a decline in AGB.

3.3 Age structure

As expected, timber harvest significantly reduced the area of older seral stages, leading to a much younger forest, primarily in the establishment and early seral stages (Fig. 6). However, the notable influence of climate change on the distribution of seral stages was in the no-harvest scenarios. There was a considerable increase in the area of late seral forest and a decline in the area of early- and mid-seral forest in the climate change-no harvest scenario in comparison to the current climate-no harvest scenario. Conversely, there

Fig. 4 Time-series graph of mean average aboveground biomass (Mg/ha) in the four scenarios for the entire study area over the 300-year simulations
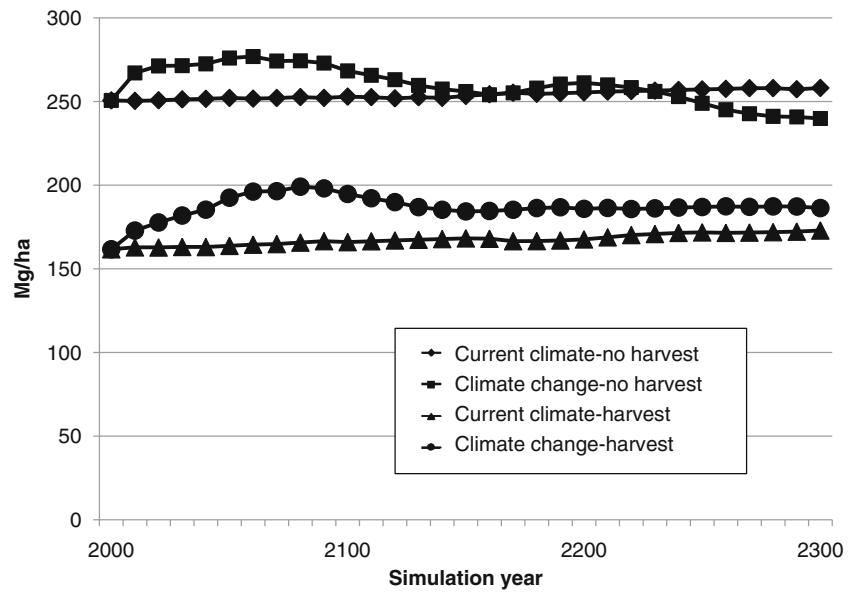
was almost no change in the extent of seral stages between the harvest scenarios.

4 Discussion

Climate change had a considerable effect on forest composition in the study area both with and without timber harvest. Many of the colder-climate boreal species suffered extreme declines or even extirpation from the study area. The almost complete disappearance of balsam fir and white birch and considerable decline of black spruce are evidence of this.

White spruce, red pine, and tamarack are other boreal conifers that were 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 warmer-climate temperate species were climatically favoured in the study area, 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 when timber harvest was simulated. White pine, American beech, eastern hemlock, and northern red oak were also more widely distributed.

Fig. 5 Average aboveground biomass (Mg/ha) of four key ecosite in the four scenarios at simulation year 2300
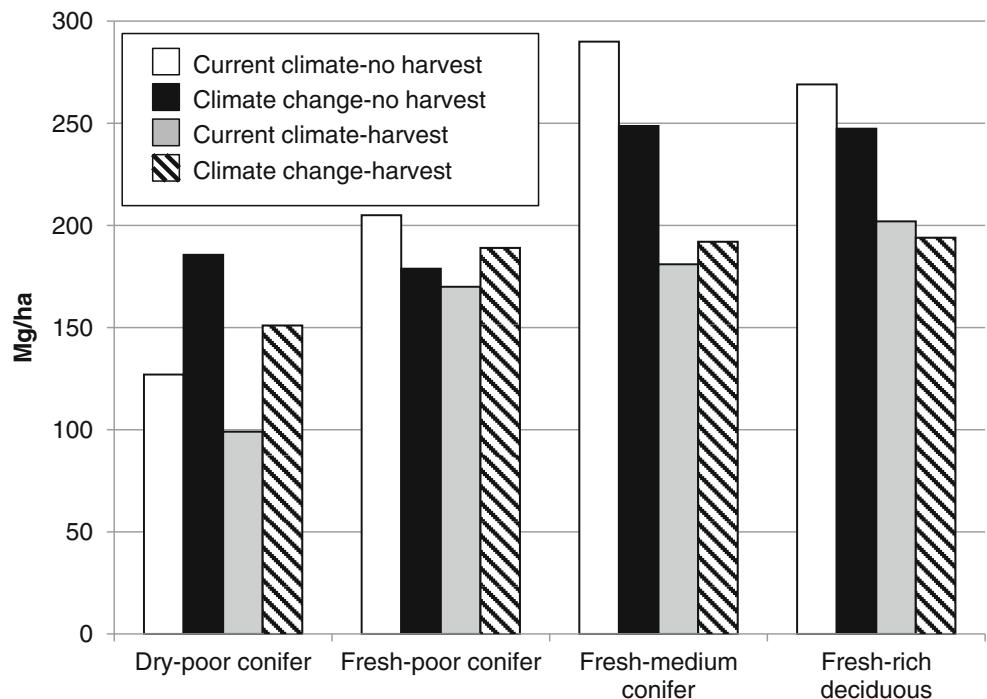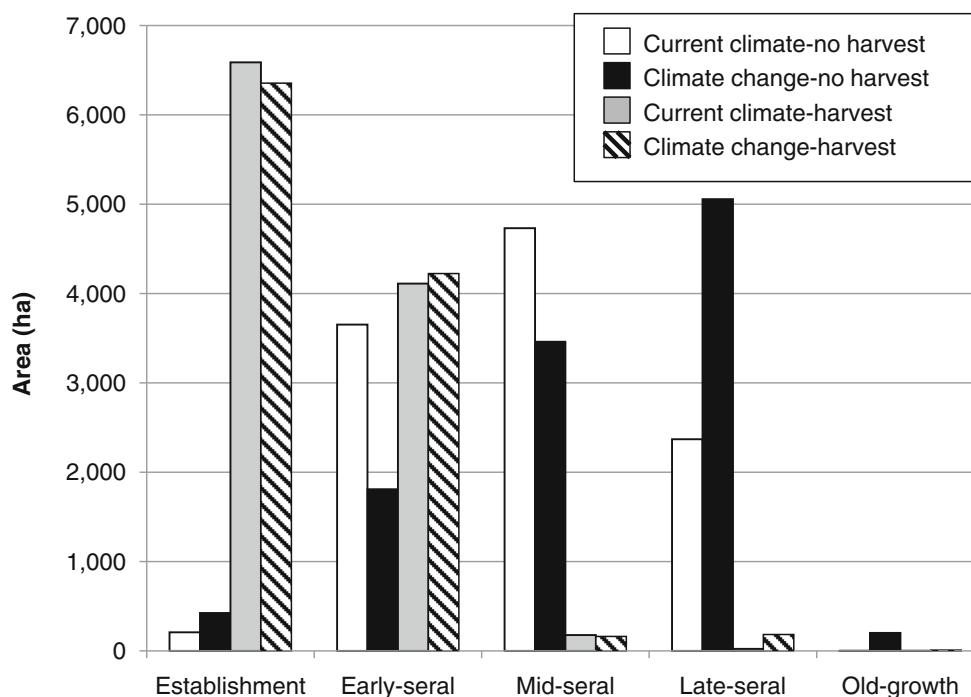
Fig. 6 Seral stage representation of the study area in the four scenarios at simulation year 2300

These changes in tree-species distribution are consistent with recent continental-scale modelling studies (McKenney et al. 2007) as well as some studies specific to Nova Scotia and the Acadian Forest Region (Bourque et al. 2010; Steenberg et al. 2011). Moreover, several studies using LANDIS-II to explore the impacts of climate change on tree-species distributions in transitional boreal-temperate forests in northern Minnesota and Wisconsin have had similar findings (Sheller and Mladenoff 2005, 2008; Ravenscroft et al. 2010). However, the interaction of climate change and timber harvest yielded some unanticipated changes in forest composition.

Red spruce is a commercially and ecologically important tree species in the Acadian Forest Region, and as a dominant late-successional species is one of the defining characteristics of the region (Mosseler et al. 2003). In the absence of timber harvest, red spruce suffered a minimal change in distribution with climate change and maintained its dominance in the forests of the study area. However, when timber harvest was simulated, the decrease in landscape presence 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 interaction of timber harvest and climate change was likely responsible for these declines that were absent with climate change only. Conversely, some late-successional species like sugar maple and eastern hemlock remained robust to climate change when timber harvest was simulated.

Some early-successional species also exhibited a response to the interaction of climate change and timber harvest that would not be expected based on climate alone.

Large-tooth aspen and trembling aspen were both found to be climatically unfavoured for the study area. Bourque et al. (2010) also found that trembling aspen suffered a decrease in its potential range in Nova Scotia. However, with the extensive timber harvests simulated in the climate change-harvest scenario, these species experienced a considerable increase in their landscape presence under climate change. These discrepancies can most likely be attributed to the widespread mortality of key competitors from timber harvest and the competitive release of the aspens. This is an important finding as it suggests that a species could potentially flourish outside of its climate envelope due to changes in competitive relationships. Landhäusser et al. (2010) also found that the current advancement of aspen to higher altitudes in the upper foothills region of Alberta, Canada can likely be attributed to the interaction of climate change and forest management practices.

Early-successional broadleaved species pose a serious existing threat to the biodiversity of the watersheds due to the long history of forest management in the area (Loo and Ives 2003). 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 2004). 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 more robust in their 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 and Mladenoff 2005). Ecosites with an abundance of resistant, late-successional species saw a reduced climate-induced advancement of pioneer species, and a smaller loss of red spruce and yellow birch. However, there is a risk of a time lag in forest response to climate change due to these resistant species, and a potential for slowing adaptation to climate change exists (Millar et al. 2007; Kuparinen et al. 2010).

Competition for light and nutrient resources between climatically favoured species, climatically unfavoured species, and resistant late-successional species also has implications for forest productivity. 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 and Mladenoff 2005; Scheller and Mladenoff 2008). The resistance of some species like sugar maple and eastern hemlock may be seen as favourable to the management of these watersheds. However, the presence of boreal species that are no longer favoured on the landscape in the changing climate could impede colonization by other species due to light and nutrient competition, leaving an abundance of forest communities in a depauperate state with lowered productivity. Consequently, low mortality rates in these species may perpetuate a time lag in the full response of the study area to climate change.

A time lag in the response of forest composition to climate change in the absence of timber harvest disturbance may explain the decrease in biomass observed in the climate change-no harvest scenario. More of the climatically unfavoured boreal species were present on the landscape in the absence of timber harvest for a longer period and likely slowed the advancement of newly favoured species. This theory is supported by the seral stage representation of the study area, where more late-seral forest was found under climate change in the climate change-no harvest scenario. 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 time-frame. Conversely, the divergent response of AGB with and without timber harvest may also support the existing theory that the change in climate accelerates forest productivity, but has no beneficial effects and may even be detrimental to the total biomass capacity of forests (Körner et al. 2005).

The increase in AGB in the majority of ecosites and in the entire landscape when climate change and timber harvest were simulated was most likely due to the fact that timber harvest greatly increased the abundance of early- and mid-successional species in the watersheds and removed the older boreal cohorts from impeding establishment of these species. Many of these species experienced climate-induced increases in growth rates. As such, the response in productivity in extensively harvested forests would be more rapid than in old forests. Red maple in particular experienced much higher productivity and comprised almost two thirds of the total AGB in the watersheds in the climate change-harvest scenario.

Ecosites 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 ecosites, 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 and the effects of timber harvest were much more influential on AGB. Our findings do support a restructuring of existing forest communities that are associated with particular site conditions.

A limitation of this study was the lack of inclusion of the effects of climate change on natural disturbance regimes in the region, which are predicted to increase in frequency and severity (Dale et al. 2001). While background wind and bark beetle disturbance were simulated, the effects of climate change on their dynamics were not incorporated. However, forest response variables were found to be relatively insensitive to variation in wind and bark beetle disturbance in comparison to timber harvest disturbance (Steenberg et al. 2011). One other limitation and a key source of uncertainty in our model output data was the simulation of only one climate change scenario. Uncertainty in simulated forest response arising from multiple climate change scenarios has been investigated using LANDIS-II by Xu et al. (2009).

5 Conclusions

The interaction of climate change and timber harvest has yielded some unanticipated changes in forest composition. These include the decline of mid- and late-successional species that were relatively uninfluenced in their distribution by climate change alone. In instances where these climatically vulnerable species are of high commercial importance, there is considerable threat of rapid decline at current harvest levels. Timber harvest disturbance may also be driving the expansion of early-successional, broadleaved species beyond their climatic range. The restructuring of forest community associations will certainly have serious implications for the functioning of these ecosystems, but there are also some major implications for the use of forest ecosystem classification as a decision-support tool for forest managers. The community associations described in the classification framework were developed from historic forest conditions and growth patterns,

and thus rely on the now invalid assumption of a relatively stable climate. A classification framework that is derived from less climatically sensitive vegetation variables and more climatically robust site variables may be more appropriate for forest ecosystem classification under climate change, though more generalized in nature.

The notion that disturbance may drive or accelerate the range expansion of aspen species has far-reaching implications for forest community associations, as well as for forest management where conifers are favoured for pulp production. Maintaining late-succession species or reserves of old-growth forest in management areas may be a tool for slowing or impeding the advancement of climatically favoured early-successional species. However, this also brings risk of a time lag in forest transition to the changing climate as low mortality in climatically unfavoured species may impede adaptation.

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