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Study of landscape change under forest harvesting and climate warming-induced fire disturbance

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Abstract

We examined tree species responses under forest harvesting and an increased fire disturbance scenario due to climate warming in northern Wisconsin where northern hardwood and boreal forests are currently predominant. Individual species response at the ecosystem scale was simulated with a gap model, which integrates soil, climate and species data, stratified by ecoregions. Such responses were quantified as species establishment coefficients. These coefficients were used to parameterize a spatially explicit landscape model, LANDIS. Species response to climate warming at the landscape scale was simulated with LANDIS, which integrates ecosystem dynamics with spatial processes including seed dispersal, fire disturbance, and forest harvesting. Under a 5 °C annual temperature increase predicted by global climate models (GCM), our simulation results suggest that significant change in species composition and abundance could occur in the two ecoregions in the study area. In the glacial lake plain (lakeshore) ecoregion under warming conditions, boreal and northern hardwood species such as red oak, sugar maple, white pine, balsam fir, paper birch, yellow birch, and aspen decline gradually during and after climate warming. Southern species such as white ash, hickory, bur oak, black oak, and white oak, which are present in minor amounts before the warming, increase in abundance on the landscape. The transition of the northern hardwood and boreal forest to one dominated by southern species occurs around year 200. In the sand barrens ecoregion under warming conditions, red pine initially benefits from the decline of other northern hardwood species, and its abundance quickly increases. However, red pine and jack pine as well as new southern species are unable to reproduce, and the ecoregion could transform into a region with only grass and shrub species around 250 years under warming climate. Increased fire frequency can accelerate the decline of shade-tolerant species such as balsam fir and sugar maple and accelerate the northward migration of southern species. Forest harvesting accelerated the decline of northern hardwood and boreal tree species. This is especially obvious on the barrens ecoregion, where the intensive cutting regime contributed to the decline of red pine and jack pine already under stressed environments. Forest managers may instead consider a conservative cutting plan or protective management scenarios with limited forest harvesting. This could prolong the transformation of the barrens into prairie from one-half to one tree life cycle.

Keywords: Climate warming; Landscape model; LANDIS; Fire; Forest harvesting; Wisconsin

1. Introduction

Climate warming will alter ecological processes at many scales (Richie, 1986; Manabe and Wetherall, 1987; Roberts, 1989; Gates, 1990; Foley et al., 1994; Sykes and Prentice, 1996; Iverson et al., 1999). The

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direct impacts of warming on tree physiology at small scales can accumulate and alter species migration patterns at large scales (Davis et al., 1991; Leishman et al., 1992; Pitelka, 1997; Clark et al., 1998; He et al., 1999a). Increased temperatures can also alter ecosystem processes such as soil organic matter mineralization dynamics, which in turn further affects species growth and establishment (Pastor and Post, 1986; Running and Nemani, 1991).

Ecological models are useful tools for studying the complex interactions and feedbacks involved in climate warming. The majority of forest ecological models are either gap models or ecosystem process models (Waring and Running, 1998). Gap models are individual-based, JABOWA/FORET-types plot models (Botkin et al., 1972; Shugart, 1984). They are typically based on empirical equations developed from measurements made on trees and stands, and simulate forest dynamics at plot scales ranging from 10 to 100 m^2 (e.g. Urban et al., 1993; Fischlin et al., 1995; Bugmann, 1996). Ecosystem process models often operate from watershed to regional scales and simulate key processes involved in the carbon, water and nitrogen cycles of forests. Individual species are generally not tracked (Aber et al., 1995; Landsberg and Gower, 1997; Prentice et al., 1992). With few exceptions (Keane et al., 1989; Urban et al., 1999; Pacala et al., 1996), gap and ecosystem process models typically do not incorporate landscape level dynamics, a set of unique, spatially-explicit interactions operating at scales between those simulated by gap and the upper bounds of ecosystem process models. Forest landscape processes include seed dispersal, fire and windthrow, insect defoliation, and forest harvesting. They typically operate at large spatial (10^4–10^6 ha) and temporal (10^2–10^3 years) scales, shaping spatial patterns and driving change, recovery, and feedbacks in ecosystems (Turner et al., 1997; Mladenoff et al., 1993). In gap models, landscape processes are assumed to be either constant (e.g. constant seed rain) or random (e.g. random disturbance) (Botkin, 1993; Shugart, 1997). In ecosystem process models, climatic variables are usually the sole drivers of vegetation dynamics. Other drivers such as fire disturbance and timber harvesting, which are also important in boreal forest and other systems (Bonan and Shugart, 1989; Suffling, 1995; Larsen, 1997; Flannigan et al., 1998), are not typically included. These assumptions have substantially limited the spatial applications of ecosystem models.

In northern portions of the US Great Lakes states, Minnesota, Wisconsin, and Michigan, forests are mostly young due to historical cutting during the mid 19th to early 20th centuries (Mladenoff and Pastor, 1993). Natural disturbance incidence such as fire, which used to be an important factor driving forest compositional change and shaping landscape patterns (Loucks, 1970), is less frequent than historic disturbance regimes. The probability of fire disturbance will increase as forests age (He and Mladenoff, 1999a). In boreal forest ecosystems fire frequency has been predicted to increase further due to climate warming (Flannigan and Van Wagner, 1991; Flannigan et al., 1998; Suffling, 1995; Larsen, 1997). At the same time, forests in some ownership classes are under increasingly intensive management. Forest harvesting alters species composition and age structure at landscape scales in a more systematic way than fire disturbance. The interaction of these factors can make forest successional trajectories that differ from those derived under current conditions (Davis and Botkin, 1985; Zabinski and Davis, 1989; Guetter and Kutzbach, 1990; Pastor and Mladenoff, 1992).

Over the past several years, we have developed a modeling approach to overcome some previous modeling constraints. LANDIS, a spatially explicit model, was developed to simulate forest change over large, heterogeneous landscapes and long time scales (Mladenoff et al., 1996; Mladenoff and He, 1999; He et al., 1999b). LANDIS (1) simulates large landscapes that are heterogeneous in terms of site conditions (e.g. ecoregions or other land classes) and initial vegetation (species/age class); (2) simulates spatial processes including fire, windthrow, forest harvest, and their interactions; (3) includes species-level forest dynamics with mechanistic realism and modest input parameter needs; (4) accommodates a range of study scales and a variety of resolutions of map input data; and (5) allows parameterization with empirical data and calibration that reflects historical distributions (He and Mladenoff, 1999a).

In this study, we use LANDIS to simulate stochastic fire and common forest harvesting practices in combination with species-level succession. We apply the model to a large landscape in northern Wisconsin and compare individual species trajectories simulated under current climate conditions and fire regimes (with harvesting) with trajectories simulated under warming climate conditions and increased fire disturbance (with harvesting). Such comparisons reveal potential response of tree species to possible warming climates while incorporating fire and management practices.

2. Materials and methods

2.1. Study area and environmental data

We chose as our study area a 400,000 ha landscape in northwestern Wisconsin (47.0°N 92.0°W, Fig. 1). Our study area contains two ecoregions that are delineated from surficial geology and mesoclimatic gradients (Host et al., 1996): a glacial lake plain (lakeshore) and barrens outwash ecoregions. The lakeshore ecoregion has moderate to well-drained silt-clay, while the barrens ecoregion, which is part of the larger Wisconsin Pine Barrens, contains very well-drained sand. Both ecoregions underwent extensive forest cutting in the past, and are largely composed of young, secondary forests (Mladenoff and Pastor, 1993). In the lakeshore ecoregion, characteristic north temperate species ('northern hardwoods') include sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), basswood (*Tilia americana*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*). Boreal species include balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*, *P. grandidentata*), paper birch (*B. papyrifera*), jack pine (*P. banksiana*), and red pine (*P. resinosa*). Species of more southern distribution are rare and include sparsely distributed white oak (*Q. alba*), bur oak (*Q. macrocarpa*), and white ash (*Fraxinus americana*). In the barrens ecoregion, common species include red pine, jack pine, northern red oak, northern pin oak (*Q. ellipsoidalis*), paper birch, red maple, and aspen. Currently about 65% of the study area is forested. The forested areas have multiple ownership, with about 40% state and national forest, about 35% county forest, and 25% privately owned forest. Public-owned forests are primarily located in the lakeshore ecoregion, while most privately owned forests are found in the barrens ecoregion.

2.2. The LANDIS model

2.2.1. Overall model design and structure

The major modules of the LANDIS model are forest succession, seed dispersal, wind and fire disturbances, and harvesting (He et al., 1999b). LANDIS is a raster-based model. Each raster unit or cell is a spatial object that tracks: (1) the presence or absence of 10-year-old cohorts of individual species; (2) fuel

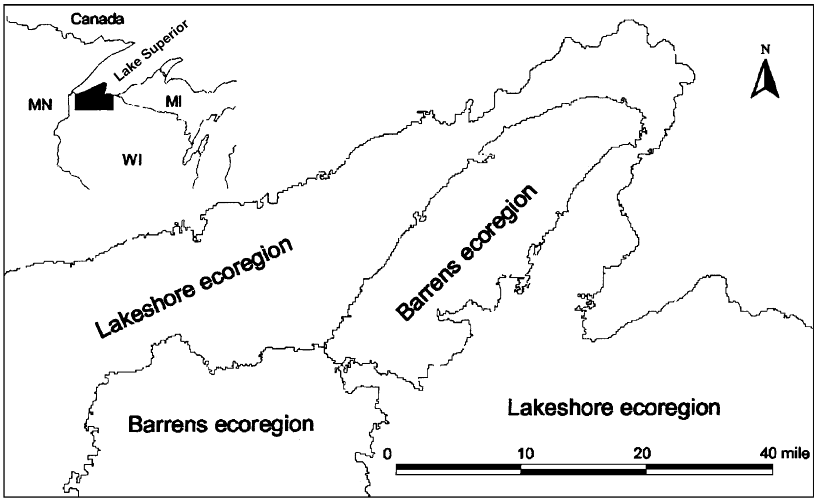

Fig. 1. The study area is stratified into two distinct ecoregions.

levels based on fuel accumulation and decomposition characteristics; (3) mean fire/wind return interval; (4) the time since last fire/wind/harvest disturbance; and (5) species establishment ability in particular environments. For each cell, species birth, growth, death, regeneration, random mortality, and vegetative reproduction are simulated at 10-year time step. At landscape scales, seed dispersal, disturbances, and forest harvesting are simulated at each iteration. To simulate heterogeneous landscapes, ecoregions derived from other climate and soil GIS data layers are used to stratify the landscape (He et al., 1998). At a given focal resolution such as within each ecoregion, environmental variables such as climate and soils are assumed homogeneous, as are some characteristics such as mean fire return intervals, fuel decomposition rates, and species establishment (Mladenoff and He, 1999; He et al., 1999a).

2.2.2. Spatial processes simulated in LANDIS

Currently LANDIS simulates four spatial processes: fire, windthrow, seed dispersal, and harvesting (Mladenoff and He, 1999), with insect disturbance under development. Fire and windthrow disturbances are stochastic processes based on the distributions of mean disturbance return intervals and mean disturbance sizes characterized for various ecoregions (He and Mladenoff, 1999a). For example, fire in certain ecoregions is more frequent than in others. Fire is a 'bottom-up' disturbance with small, young trees more susceptible to damage than large, older trees. LANDIS simulates fire intensity as five classes, from low intensity ground fires to high intensity crown fires. Correspondingly, tree species are grouped into five fire-tolerance classes. Fire severity is the interaction of susceptibility based on species age classes, species fire tolerance, and fire intensity. The latter is determined by the time since the last fire on the site, a surrogate for the amount of fuel accumulation (He and Mladenoff, 1999a).

Windthrow is a 'top–down' disturbance and the probability of mortality due to wind increases with tree age and size. Windthrow events interact with fire disturbance by increasing potential fire intensity class at a site due to increased fuel loads. Interactions between these two disturbances can be interesting and complex. Based on our simulation results, windthrow becomes more important on mesic landtypes with longer-lived species, and where fire frequency is low (Mladenoff and He, 1999).

In the LANDIS harvest module, a landscape is divided into forest management areas that represent spatial zones to which specific management goals are assigned. Within each management area, the landscape is divided into stands of various forest types. Each stand contains a group of grid cells, and each cell is populated with a specific combination of species and age cohorts. Management practices are the combination of temporal, spatial, and species components (Gustafson et al., 2000): (1) when or how often to harvest a stand; (2) how to allocate a harvest based on stand ranking, which in turn is based on ecological or economic criteria; and (3) how to harvest a species age cohort (shelterwood, selection, and clear-cutting). The combination of these three components covers most forest management practices currently being used across a wide spectrum of ownership (Gustafson et al., 2000).

LANDIS simulates seed dispersal in a spatially explicit manner. Seed dispersal probability is modeled using an exponential distribution in which for each species the effective and maximum dispersal distances control the shape of seedling distribution (He and Mladenoff, 1999b). When seeds successfully arrive at a site, the shade-tolerance rank of the seedling relative to those of species already existing on the site determines whether the seedling will be successfully recruited. The species establishment coefficient (0–1), which quantifies how different environmental conditions favor or inhibit the establishment of a particular species (He et al., 1999a), determines if the seedling can establish and survive. Species with high establishment coefficients have higher probabilities of establishment. The establishment coefficient for a given species may vary from one ecoregion to another. These coefficients which are provided as input to LANDIS are derived either from the simulation results of a gap model (He et al., 1999a) such as LINKAGES (Pastor and Post, 1985), or from estimates based on existing experimental data (Shifley et al., 2000).

2.3. Input data and simulation scenarios

For LANDIS input, we derived maps of 23 tree species from a species-level forest classification based on Landsat TM satellite imagery (Wolter et al., 1995). This was integrated with a quantitative ecoregion classification (Host et al., 1996), and age class data from regional US Department of Agriculture Forest Service Forest Inventory and Analysis (FIA) data (Hansen et al., 1992; He et al., 1998). We also estimated the disturbance regime for each ecoregion based on the literature (e.g. Heinselman, 1973, 1981; Lorimer and Gough, 1988; Frelich and Lorimer, 1991) and existing historical data of the study area. In the lakeshore ecoregion, fire disturbance is infrequent with a mean fire return interval of approximately 1000 years. In the barrens ecoregion, fire is much more frequent with a 200-year mean fire return interval. To simulate an increased fire disturbance regime under warming conditions, we used a doubled fire disturbance scenario by halving the fire return intervals to 500 and 100 years in the lakeshore and the barrens ecoregions, respectively, based on estimates from Flannigan and Van Wagner (1991), Flannigan et al. (1998), Suffling (1995) and Larsen (1997). Current forest management is different in the two ecoregions for the study area (Wisconsin Department of Natural Resources, 1990). We treated each ecoregion as a distinct forest management area. In the barrens ecoregion, 30% of the management area was simulated as clear-cutting on a 40-year rotation. Stands in the barrens ecoregion are relatively homogeneous and therefore were randomly selected for harvest (Table 1). In the lakeshore ecoregion, we simulated group selection every decade, in which 75% of the stands in the management area were selected for harvest with 10% of each stand being harvested (Table 1). Stands in the lakeshore ecoregion are highly heterogeneous and therefore the oldest stands were ranked first for harvest (Table 1). For both ecoregions, forest stand boundaries were derived by classifying all species age class maps using a LANDIS reclassification algorithm.

We have complete map data of monthly precipitation and temperature of 30-year average, growing season length, soil organic matter and texture (soil water holding capacity) for each ecoregion. Species response to warming conditions at ecosystem-scales was simulated using the LINKAGES model, with simulation results quantified as species establishment coefficients (He et al., 1999a). To incorporate climate warming factors in LINKAGES, we used a scenario of a linear annual temperature increase over 100 years to a total increase of 5 °C in the annual mean, and no obvious precipitation changes (Schlesinger and Mitchell, 1987). The temperature increase was evenly distributed among months. The increased mean annual temperature was held constant after 100 years. Other climate change scenarios such as those with detailed monthly temperature and precipitation predictions can be used as alternatives.

Individual tree species response to the climate warming was analyzed by comparing LANDIS simulation results under current and warming climate conditions. The warming conditions used the doubled fire disturbance regime and the species establishment coefficients derived in LINKAGES for the warming climate (He et al., 1999a). The forested

Table 1
Forest management plan simulated for the two ecoregions[a]

	Lakeshore ecoregion	Barrens ecoregion
Harvesting methods	Group selection	Clear-cutting
Minimum stand age (years)	60	50
Stand ranking method	Oldest first	Random
Initial harvesting decade (years)	10	10
Harvesting interval (years)	10	40
Final harvesting decade (years)	300	300
Harvest target (proportion to MA)	75%	30%
Stand proportion	10%	100%
Mean group size (cells)	20	NA
Standard deviation (cells)	10	NA

[a] The simulation plan is based on the forest management practices on the barrens and lakeshore ecoregions in northern Wisconsin. MA stands for management area, corresponding to ecoregion in this study. Cells are in 60 m × 60 m resolution.

landscape was simulated for 300 years under both sets of climatic conditions from the same starting point. For simulations under warming conditions, differences between species establishment coefficients for current and warming climate were linearly interpolated for each decade (one LANDIS iteration) over the first 100 years of the 300 years simulation, reflecting the 5 °C temperature increase scenario (Schlesinger and Mitchell, 1987). The model was then run for the remaining 200 years to examine the consequences of climate warming.

We simulated the dynamics of 23 species and summarized results for those that were most abundant on the forested landscape. All simulation results were calibrated following an approach proposed in He and Mladenoff (1999a), to ensure that the simulated fire disturbance regimes closely matched historical distributions reported in the literature (e.g. Heinselman, 1973, 1981; Lorimer and Gough, 1988; Frelich and Lorimer, 1991). Individual species abundance at every 10-year time step was calculated as the percentage of cells in the forested landscape containing a given tree species. Trajectories of species abundances across 300 years under different simulation scenarios were plotted for comparisions. To generalize tree species response under each scenario, we calculated mean species abundance as the average abundance from these individual time steps over the period of simulation.

3. Results

3.1. Effects of forest harvesting and fire disturbance

LANDIS simulated all harvesting prescriptions for every decade and generates species-specific harvesting outputs for each treatment. The effects of forest harvesting can be observed directly from maps generated for each species at every 10-year iteration. At the beginning of the simulation, forests were generally young due to historical forest cutting (Mladenoff and Pastor, 1993) and species age-class distributions were relatively homogeneous (He et al., 1998). Sugar maple was an abundant species that covers much of the forested portion of the lakeshore ecoregion (Fig. 2a), while aspen was less abundant (Fig. 2c). In the lakeshore ecoregion, every decade approximately 75% of the stands in a management area were treated with group selection (Table 1). Within each stand, small areas comprising 1/10 of the stand were harvested. Thus, at year 10 a small portion of sugar maple along with other species was removed. This had little impact on sugar maple in the lakeshore ecoregion as the sugar maple age class distribution remained relatively unchanged (Fig. 2b). However, the effects of this treatment were reflected in the age-class distributions of other species such as aspen. As an early successional species, aspen was shade-intolerant and needs open space to establish. At year 0, aspen in the 0–10 year age class was absent. At year 10, small patches of aspen in this class appeared at places where group selection was applied (Fig. 2d) in this ecoregion.

In the barrens ecoregion, clear-cutting on stands older than 50 years were implemented on a 40 year rotation over 30% of the area (Table 1). As in the lakeshore ecoregion, clear-cutting favored shade-intolerant species. On the very well-drained sandy soils, jack pine established readily while other early successional species such as aspen and paper birch did not due to their low reproduction probabilities. At year 0, jack pine was largely constrained to the central part of the barrens ecoregion (Fig. 2e), and red oak and red maple populated the north. After the first clear-cutting at year 10, young jack pine patches were seen regenerated in the clear-cuts (Fig. 2f). In general, forest harvesting changed species composition and age structure throughout the simulation.

Fire had a more dramatic impact on changing species composition and age class distribution than harvesting. Multiple fires with high intensity were simulated at year 30 on the barrens ecoregion under warming conditions (Fig. 2g). These fires, varying in shape and size, interacted with vegetation and the spatial configuration of the landscape. Like clear-cutting, fires created open space and allowed jack pine to establish on the barrens. Consequently, young jack pine age cohorts occurred on the fire patches (Fig. 2h). Repeated but stochastic fire disturbance is often a disruption in forest successional dynamics in the barrens ecoregion (Vogl, 1970; Radeloff et al., 1998).

3.2. Individual species response to climate warming

The abundance of quaking aspen and paper birch, two early successional boreal species, decreased with

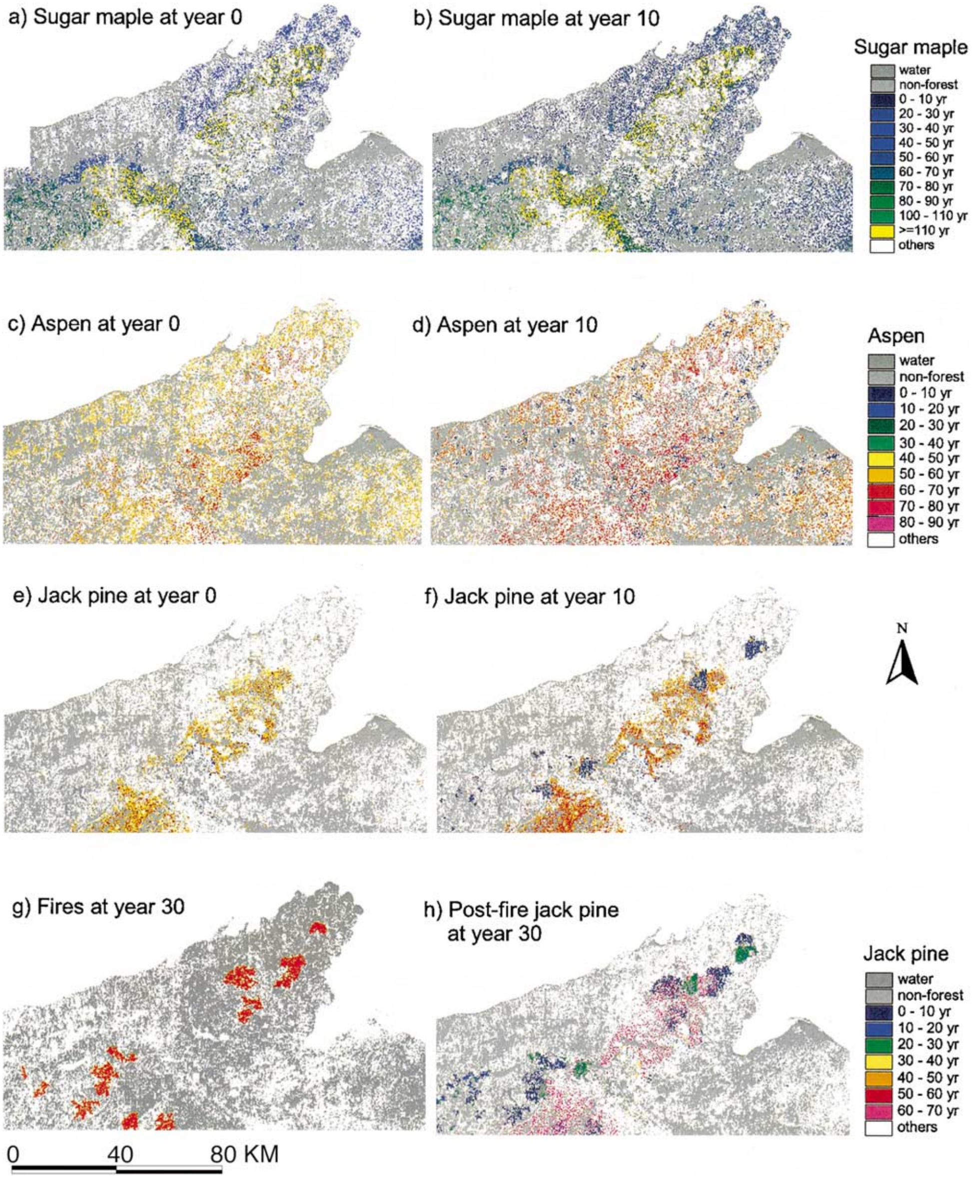

Fig. 2. Effects of group selection harvesting in the lakeshore ecoregion at year 10 on species age class distribution, showing sugar maple at (a) year 0; (b) year 10; (c) aspen at year 0; and (d) year 10, respectively. Effects of clear-cut harvesting at year 10 and fire disturbance at year 30 on species age class distribution in the barrens ecoregion showing (e) jack pine at year 0; (f) post-harvest jack pine at year 10; (g) fires simulated at year 30; and (h) post-fire jack pine at year 30.

an increased fire frequency under warming conditions (Fig. 3a). Starting at 42% of the landscape, the abundance of aspen fluctuated through time due to fire disturbance and reached 27% of the landscape under current conditions. Under unfavorable warming conditions, it declined dramatically to about 1% of the landscape (Fig. 3a). Paper birch abundance also declined under warming conditions. Paper birch abundance began at 31% of the landscape and decreased significantly for the first 100 years of climate

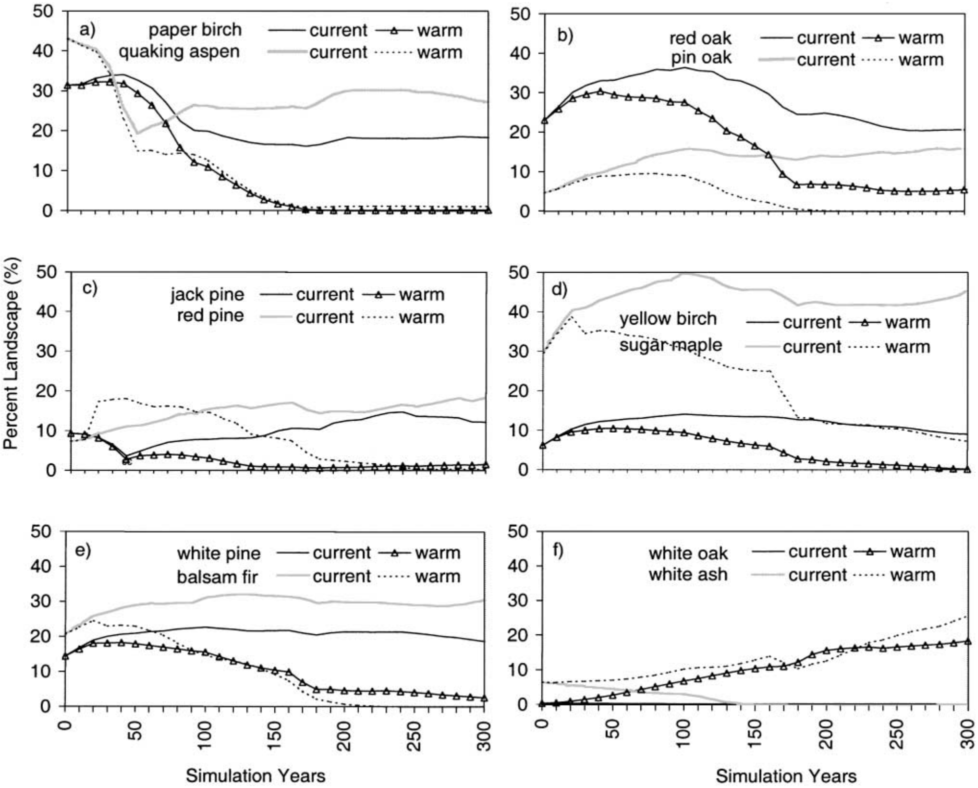

Fig. 3. LANDIS simulated abundance of 10 selected species over 300 years under periodic harvesting (Table 1) and both current climate and warmer climate.

warming. It continued to decrease on the landscape for another 100 years or so until its abundance approached 0 (Fig. 3a).

Northern red oak was not favored in either ecoregion under warming conditions. However, its reproduction probabilities did not decrease as significantly as other northern hardwood species (He et al., 1999a). This is due to its greater drought tolerance and its ability to persist in the dry environment associated with the warming conditions. The decrease of red oak abundance did not become significant until after the 100-year climate warming period. Red oak abundance stabilized at 6% of the landscape under warming conditions as compared to 25% of the landscape under current conditions (Fig. 3b). Pin oak was less abundant than red oak and it behaved similarly to red oak under the warming conditions. With an unfavorable environment under warming conditions, pin oak abundance approached 0 after year 200 (Fig. 3b).

Red pine and jack pine both decreased under warming conditions. Jack pine, largely distributed in the barrens ecoregion, maintained its abundance at 13% of the landscape under current conditions (Fig. 3c). However, under warming conditions, jack pine abundance started at 10% of the landscape and decreased to 4% at year 40 due to species competition. It declined further to <2% of the landscape and never recovered as it did under current conditions (Fig. 3c). The abundance of red pine was also low at the beginning of the simulation due to historical cutting. Starting at about 8% of the landscape, red pine abundance increased to 20% at year 300 under current conditions. With warming, red pine initially benefited from the decline of other northern hardwood species, and its abundance quickly increased to 18%. However, red pine eventually declined under the warming conditions and its abundance approached 0 at about year 300 (Fig. 3c).

Sugar maple, the most abundant late successional species in the landscape, was able to increase in abundance under current, favorable conditions with low fire frequencies. Starting at 30% of the landscape, sugar maple abundance increased to 45% at the end of the 300-year simulation (Fig. 3d). Under warming conditions, sugar maple abundance was significantly lower due to a decrease in its establishment ability under warmer climate conditions as well as the doubled fire disturbance regime. Sugar maple gradually decreased to 10% of the landscape (Fig. 3d). Yellow birch, another late successional species, occurred on 10% of the landscape under current conditions. With warming conditions, its abundance declined to less than 2% of the landscape. With a relatively long mean longevity, the decline process was gradual (Fig. 3d).

White pine was able to maintain its abundance at approximately 20% of the landscape under current conditions (Fig. 3e). Similar to sugar maple and yellow birch, white pine abundance declined with warming conditions and it became a minor species covering about 3% of the landscape (Fig. 3d). Balsam fir, a shade-tolerant species started at 20% of the landscape, increased in abundance under current conditions (Fig. 3e), but decreased linearly to 0% under warming conditions (Fig. 3e).

For all southern species, we found increases in species abundance. White ash, starting around 7% of the landscape at year 0, increased to 28% of the landscape at year 300 under warming conditions (Fig. 3f). Similarly, white oak initially presented as a minor species under current conditions, increased substantially with warming to 20% of the landscape at year 300 (Fig. 3f). Other southern species including black oak, hickory, and bur oak increased in a similar fashion. The invasion of the southern species under climate warming involves interactive processes of fire disturbance, harvesting, seed dispersal, and species competition. As mid-shade-tolerant species, they need fire to remove the dominant shade-tolerant sugar maple and balsam fir and create open spaces. Fire along with warming conditions made the northward migration of these southern species possible, especially over the first 200 years. Afterwards, their increasing rates tended to become stable, indicating that possible equilibrium may be achieved in longer time frames than in our model simulation.

3.3. Changes in forest species composition

The current forest composition and age class structure is an artifact of past land use. Thus, it took approximately 50 years for some tree species in the landscape to undergo substantial changes and stabilize for the remaining 200 years (Fig. 4a). This suggests that under current climate, harvesting treatments, and fire disturbance regimes, forest succession dynamics can reach a relatively stable state on both the lakeshore and the barrens ecoregions. Currently, sugar maple is the most abundant species occurring on 40% of the landscape, followed by aspen (30%), balsam fir (29%), red oak (28%), paper birch (21%), white pine (20%), red pine (15%), pin oak (13%), yellow birch (12%), and jack pine (10%). The proportions of other species are all under 5% (Fig. 4a).

Under warming conditions, changes in forest species composition on the landscape occurred. Abundant boreal and northern hardwood species such as red oak, sugar maple, white pine, red pine, jack pine, balsam fir, paper birch, yellow birch, and pin oak declined substantially during the warming process. Such declines extended another 100 years after warming. Southern species such as white ash, hickory, bur oak, black oak, and white oak, were present in minor amounts at the beginning of the simulation, and gradually increased in abundance on the landscape (Fig. 4b). Due to climate warming, northern species experienced a decrease in establishment and a corresponding decrease in abundance. Abundance of southern species increased in the area, but only to a moderate degree. The transition of species composition on the landscape from one dominated by northern hardwood and boreal species to one dominated by southern species occurred shortly before year 200. Overall, the total percent forest cover decreased under warming conditions (Fig. 4b). This was also reflected by comparing harvesting results under the current and warming scenarios. The age-cohort harvested, species-specific data recorded by LANDIS in the harvesting log file can be converted into actual timber volume by species using age-volume look-up tables (e.g. Shifley et al., 2000). Because a complete table does not exist for our study area, we assumed that forests are largely even-aged and tree density is relatively uniform within an ecoregion (but could vary among ecoregions). Thus, the number of age cohorts

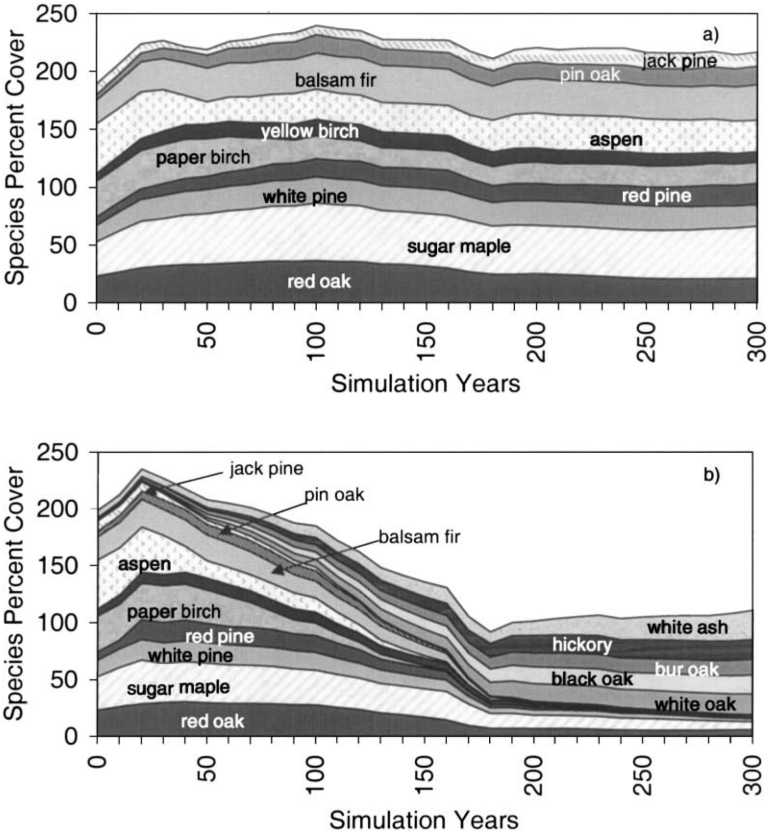

Fig. 4. Transitions of major species composition simulated by LANDIS, species abundance as percent area under periodic harvesting (Table 1) with (a) the current; and (b) the warming climate conditions. The sum of species percentage on the landscape is larger than 100% because percent area portrays species presence, not dominance, and therefore, multiple species can occur on a single site.

harvested responded linearly to the number of sites harvested as well as the number of trees. As percent forest cover decreased under warming conditions, the amount of timber available for harvest (biomass) also decreased.

Sugar maple, aspen, balsam fir, red oak, paper birch, white pine, and red pine comprised most timber production under current conditions (Fig. 5a). Under warming conditions, a transition in timber production to southern species occurred from year 100 to 200, when white ash, hickory, bur oak, black oak, and white oak became the major species (Fig. 5b). Note that the minimum stand ages for harvesting were 60 on the lakeshore ecoregion and 50 on the barrens ecoregion. Therefore, at every 100 years, most stands ranged from 0 to 90 years and the average stand age was 45 years, falling below the minimum age requirement. Thus, there was a significant drop in the number of species age cohorts harvested every 10 decades (Fig. 5a and b).

For the barrens ecoregion, the clear-cutting rotation was 40 years. Red oak, red pine, white pine, red maple, balsam fir, and jack pine provided most of timber production under current conditions. With poor reproduction of red oak and balsam fir in this ecoregion, jack pine abundance increased and so did the number of jack pine age cohorts harvested (Fig. 5c). Under current conditions, red pine and jack pine provided most of the timber production (Fig. 5c). Under warming conditions, abundances for all species declined. With current species being unable to reproduce successfully under warming conditions, the number of age cohorts harvested dropped dramatically with the majority of them reaching their longevity and dying (Fig. 5d). This

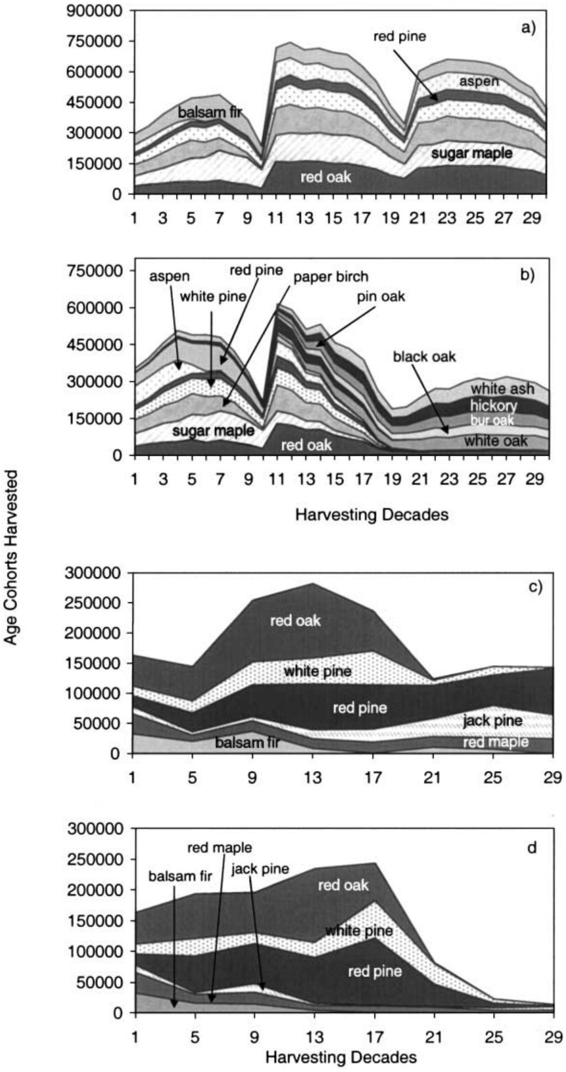

Fig. 5. Comparisons of forest harvesting results by ecoregions. The lakeshore ecoregion under (a) current climate; (b) warming climate; and the barrens ecoregion under (c) current climate; and (d) warming climate, respectively.

suggests that the barrens ecoregion could transform into a region with only grass and shrub species after 250 years under warming conditions.

4. Discussion

We present a modeling framework to evaluate the impact of climate warming and management on forest species at landscape scales. Individual species responses to the warming climate conditions were derived from previous simulation results of LINKAGES, a gap model, which integrates soil, climate, and species data (He et al., 1999a). The LANDIS model does not directly simulate climate variables. Rather it integrates species response at gap scales simulated by the LINKAGES model and simulates interactions of species-specific dynamics such as competition and succession with large spatial processes such as seed dispersal and disturbance. Thus, the cumulative effects of climate warming on tree species at regional scales can be examined in terms of species abundance and species migration pattern (He et al., 1999a). Furthermore, with the capability of simulating landscape processes, the increased fire disturbance frequency under warming conditions can be incorporated, which increases the realism and accuracy compared with results from simulations where fire disturbance is assumed to be negligible. The LANDIS model can also be used as a tool to examine consequences of various forest management plans and practices on forest species composition and landscape patterns, as it can incorporate spatially explicit constraints.

LANDIS simulation results indicate significant decreases in abundance across the landscape for most boreal and northern hardwood species. These results are consistent with corresponding biomass decreases simulated at smaller gap scales by the LINKAGES model (He et al., 1999b). However, at broader scales, species response to warming can be further complicated by landscape processes. Increased fire frequency can accelerate the decline of shade-tolerant boreal species such as balsam fir (Fig. 3e). On the other hand, species vital attributes such as longevity, shade and fire tolerance, and effective and maximum seeding distances can also affect species successional trajectories under a warming climate. Boreal and northern hardwood species that have long longevity and drought tolerance can delay the impacts of climate warming by 100 to a few 100 years, as was shown for red oak (Fig. 3b), sugar maple (Fig. 3d), and yellow birch (Fig. 3d). In addition, landscape processes such as fire can accelerate the northward migration of southern species including white ash, white oak, bur oak, and hickory (Fig. 3f).

Although our modeling experiments do not alter management regime in response to the climate warming, the results indicate that forest harvesting also accelerates the decline of northern hardwood and boreal tree species. This is especially obvious on the barrens ecoregion, where the intensive cutting regime contributed to the decline of red pine and jack pine already under stressed environments. Forest managers may instead consider a conservative cutting plan or protective management scenario with forest harvesting limited only to budworm infected stands. This could prolong the transformation of the barrens into prairie for one-half to one tree life cycle. For red pine this ranges about 100–200 years, assuming that mature trees are more tolerant to an unfavorable environment caused by the warming than young trees (Loehle and LeBlanc, 1996). Nevertheless, because of the increased fire regimes simulated under warming conditions, species abundance would become much lower than that under current climate even with conservative forest cutting regimes, unless fire suppression is included in forest management scenarios.

Landscape modeling is a recent endeavor, challenged by the complex interactions of ecological processes and large spatial and temporal dimensions. The majority of landscape models simulate only landscape processes and do not incorporate species-specific dynamics (e.g. Baker et al., 1991; Gardner et al., 1996). Models such as LANDIS and LANDSIM (Roberts, 1996) that incorporate species information typically employ a simplified vegetation representation (Mladenoff et al., 1996; Mladenoff and He, 1999). LANDIS tracks only species age-cohort presence or absence, not individual trees, and therefore it is a semi-quantitative model. For example, the actual number of seeds per unit area of a species arriving at a given site is not simulated as in other small-scale models that track individual trees (e.g. Ribbens et al., 1994). Simulations that represent tree density at large spatial scales pose challenges and warrant further study (He et al., 1999b). Furthermore, the exact simulated location of a species in a given year is not deterministic because of the stochastic components implemented in seed dispersal and fire disturbance and the method used for model parameterization (He et al., 1998). A particular spatial event should not be considered as a prediction of the model. However, the abundance information summarized for each species is the result of the complex interaction of spatial processes (dispersal, fire disturbance, and forest harvesting), species response to warming conditions, landscape configuration, and the initial spatial distribution of each species. At the ecoregion or landscape level, species abundance and distribution information generalized from the model simulation can be an overall estimation of a landscape pattern outcome.

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