Forest Landscape Response to Different Harvest Scenarios under Climate Warming – A Spatial Simulation Study

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Abstract

This study examined forest landscape responses to climate warming in a large (~0.5 million ha) boreal and northern hardwood forest region in northern Wisconsin, U.S.A. We examined whether it contributed to the decline of currently predominant tree species and whether harvests can be used as effective means to prolong the transformation of current forest landscapes to those under warmer conditions. We used a modeling approach by linking a spatially explicit landscape model (LANDIS) with a gap model (LINKAGES). Individual tree species responses at stand scales were simulated with LINKAGES, which integrated soil, climate and species data. Such responses were quantified as inputs for LANDIS, which was then used to integrate large spatial processes such as disturbance and harvesting with ecosystem processes. This protocol allowed us to examine regional forest landscape response to climate warming at the species level with greater realism than by using gap models or landscape transition models alone.

Our simulation results suggest that forest landscapes in two ecoregions of northern Wisconsin would experience a significant change under a climate-warming scenario that a 5°C temperature increase occurs over next 100 years. In the lakeshore ecoregion, with more favorable water and nutrient conditions, currently dominant boreal and northern hardwood forests would transform into southern hardwood forests. This result is consistent with the general trends simulated by other models for this region, but shows that landscape transition takes much longer time. By incorporating realistic initial seed source and simulating spatially explicit seed dispersal, our results suggest that the landscape transition is gradual and becomes apparent during 2150-2300 in contemporary time assuming warming occurs from the beginning of this century.

Forest harvesting plays an important role in delaying the decline of boreal forests and northern hardwoods. The greatest differences in resulting landscapes under different harvest scenarios (clear cutting group selection, and selection cutting) occurred starting around year 2150. However, harvest does not alter the long-term impacts of climate warming, as the proportions of various cover types simulated under different harvest scenarios at year 300 are very similar.

At year 2300 in the lakeshore ecoregion, formerly dominant paper birch, yellow birch, sugar maple, balsam fir, and quaking aspen forests were replaced largely by southern oak species (bur oak, white oak, and black oak), white ash, and hickory. Boreal forests in this ecoregion completely disappeared, while northern hardwoods became a minor cover type compared to southern hardwood forests. A more dramatic transformation occurred in the barrens ecoregion. More than 98% of jack pine and red pine forests disappeared. Because southern hardwood species may be unable to reproduce and establish under warming conditions, the barrens ecoregion could transform into an area with only grass and shrub species.

I. INTRODUCTION

Forest landscapes in northern Wisconsin, U.S.A., have experienced extensive human disturbance. Forest cutting and other land use activities have profoundly altered the natural distribution and composition of dominant forest types, which, otherwise, are strongly correlated with environmental gradients (Graumlich and Davis 1993, Kimmerer 1989). The landscapes today are fragmented and disturbed, and their successional paths are not well-understood at large scales (Pastor and Mladenoff 1992, Mladenoff and Pastor 1993). Climate warming and natural disturbance further complicate successional trajectories on these landscapes as suggested elsewhere (Foley et al. 1994, Suffling 1995, Larsen 1997, Pitelka et al. 1997, Flannigan et al. 1998). This complexity makes computer simulation modeling a useful tool to assess landscape response across large spatial and temporal scales (Mladenoff and Baker 1999, He and Mladenoff 1999).

For the past three decades, numerous forest ecological models have been developed to study forest vegetation dynamics, including gap models (Botkin 1993, Shugart 1997), ecosystem process models (Parton et al. 1987, 1988, Running and Coughlan 1988, Running and Gower 1991, Aber and Federer 1992, Aber et al. 1995), and individual tree-based models (Pacala et al. 1993, 1996, Urban et al. 1999). With few exceptions, all these models do not directly incorporate landscape processes, a set of contagious and spatially explicit interactions such as natural disturbance, forest harvesting, and species migration. Landscape processes typically operate from thousands to millions of hectares in space, and from decades to thousands of years in time (Pickett and White 1985, Clark 1991, Turner 1990, Li et al. 1993, Holling 1992, Portnoy and Willson 1993, Houle 1998). In gap models, landscape processes are assumed to be constant (e.g., constant seed rain) or random (e.g., random disturbance) (Pastor and Post 1985, Urban et al. 1992, Fischlin et al. 1995, Bugmann 1996). In ecosystem process models, climatic variables are usually the driving factors of vegetation

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dynamics. Other drivers such as fire disturbance, which is found equally important to climate drivers in systems such as the boreal forest (e.g., Li et al. 1997), are not considered. Individual tree-based models try to incorporate both gap level mechanisms and spatial interactions. However, they are typically limited areas smaller than 500 ha (e.g., Pacala et al. 1996, Caspersen et al. 1999), limited by current computing capacity. When these models are applied to larger landscapes, spatially inexplicit scaling-up of the simulation results is required (Keane et al. 1996, Acevedo et al. 1995, Urban et al. 1999). Clearly, new modeling approaches are needed to study landscape-scale dynamics. One is represented by the LANDIS model, a landscape disturbance and succession model (Mladenoff and He 1999, He et al. 1999a). LANDIS is similar to LANDSIM (Roberts 1996), a polygon-based landscape model, but is a raster-based model suitable for complex spatial processes. In LANDIS, it is realized that not all ecological processes can be optimized. Detailed individual tree information and within-stand processes can be simplified, while large-scale questions such as landscape pattern, species distribution, and disturbances can be adequately addressed (see the LANDIS section in Materials and Methods).

We have conducted various pilot studies with the LANDIS model, including model sensitivity analysis, mechanisms of seed dispersal, fire and windthrow disturbance, and a harvest component (Mladenoff and He 1999, He and Mladenoff 1999, He et al. 1999a, Gustafson et al. 2000). We have extensively explored the spatially explicit and stochastic simulation of fire disturbance and forest succession, and shown how historical fire distributions can be simulated with results validated against empirical data (He and Mladenoff 1999). In simulating forest species response to potential climate warming, we have developed a protocol for linking a gap model to LANDIS (He et al. 1999b). Individual tree species responses at stand or plot scales can be simulated with the gap model, which integrates soil, climate and species data, stratified by ecoregions. Such responses are quantified as species establishment coefficients that are used to parameterize LANDIS. LANDIS is then used to integrate large spatial processes with ecosystem processes. This protocol allows us to examine large-scale species response to climate warming more realistically than using gap models or landscape models alone, especially under transient climate conditions (He et al. 1999b).

Recently, we have examined tree species responses under forest harvesting and an increased fire disturbance scenario due to climate warming in northern Wisconsin (He et al. 2002). Under a warming scenario of annual temperature increase by 5°C over next 100 year predicted by a GCM (Schlesinger and Mitchell 1987), we found that significant change in species composition and abundance could occur in forests of northern Wisconsin. Increased fire frequency would accelerate the decline of shade-tolerant species such as balsam fir and sugar maple and produce increase of species such as white oak and hickory (He et al. 2002).

In this study, we intend to further examine landscape level responses to climate warming. Specifically, we will investigate whether forest harvesting contributes to the decline of tree species already under environmental stresses and whether harvests can be used as effective means to delay the transformation of current forest landscapes to those expected under warmer conditions. We will examine how forest landscapes in northern Wisconsin would evolve under warming conditions by incorporating natural fire regimes based on studies of historical fires and different forest harvesting scenarios.

II. MATERIALS AND METHODS

Study area

The study area is located in northwestern Wisconsin (47.0°N 92.0°W, Figure 1) and covers approximately a half million hectares. About 65% of the area is forested and includes some of the Chequamegon National Forest and some county, state, and private forestland. There are two distinct ecoregions derived from surficial geology and mesoclimatic gradients (Host et al., 1996): a glacial lake plain (lakeshore) and a barrens outwash ecoregion. The lakeshore ecoregion has moderate to well-drained silt, while the barrens ecoregion contains very well drained sand. In the lakeshore ecoregion, characteristic boreal species include balsam fir (*Abies balsamea*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), and red pine (*P. resinosa*). North temperate species ("northern hardwoods") include sugar maple (*Acer saccharum*), red maple (*A. rubrum*), white pine (*Pinus strobus*), northern red oak (*Quercus rubra*), yellow birch (*Betula alleghaniensis*), and eastern hemlock (*Tsuga canadensis*). South temperate species ("southern hardwood") include sparsely distributed white oak (*Q. alba*), bur oak (*Q. macrocarpa*), bitternut hickory (Carya cordiformis), and white ash (*Fraxinus americana*). In the barrens ecoregion, tree species are relatively simple including red pine and jack pine, while northern red oak, northern pin oak (Q. *ellipsoidalis*), paper birch, red maple, and aspen present in a minor amount.

Forests in this area underwent extensive forest cutting in the past, and are largely composed of young, secondary forests (Mladenoff and Pastor 1993). Natural disturbance incidence for these young forests is low relative to historic disturbance regimes in this region. Forest management plans are often made based on the assumption of no disturbance or for some areas only small disturbances. However, fire disturbance probabilities will increase as forests age (He and Mladenoff 1999). Furthermore, years of fire suppression may have increased the probability of large, catastrophic fires, as reported elsewhere (McCullough et al. 1998, Baker 1992). Such large disturbance events, should they occur, may profoundly change the forest landscapes for which the forest management plans were made. Therefore, when examining long-term forest composition, age structure, and landscape pattern under

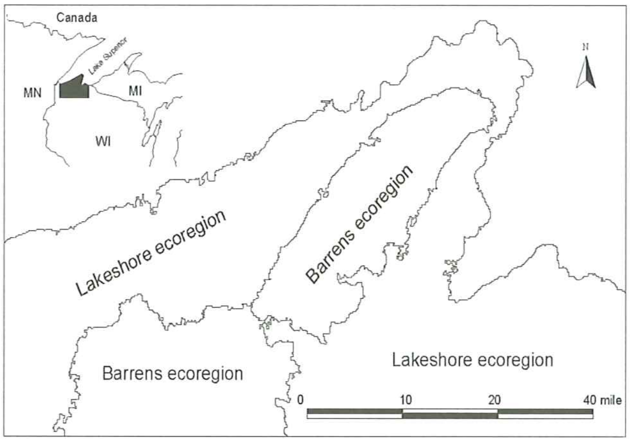

Figure 1. The study area is stratified into two distinct ecoregions.

climate warming, it is important to incorporate fire disturbance in this area (He et al. 2002).

LANDIS model

In LANDIS a landscape is organized as a grid of cells, with vegetation information as attributes for each cell (Figure 2) (Mladenoff et al. 1996, Mladenoff and He 1999, He et al. 1999a). At each cell or site, the model tracks a matrix containing a list of species by rows and the age cohorts at 10-year intervals by columns. The model does not track individual trees, but the species and age cohorts present on each cell. The contents of this species/age cohort matrix varies among sites (cells) depending on what species and age cohorts occur on a given site. The initial distribution of species and age class information can be derived from existing vegetation maps or a classified satellite image combined with forest inventory data. Seed dispersal, fire, windthrow, and harvesting are simulated as spatial processes, which interact with species information stored at each site. Non-spatial processes such as succession and establishment are simulated independently at each site. They also interact with spatial processes such as seed dispersal, and environment variables.

Heterogeneous landscapes can be stratified into ecoregions or landtypes, which are generated from GIS layers such as climate, soil, or digital elevation models (DEM). Assumptions are made about ecological characteristics and are assigned to each ecoregion in LANDIS. Within an ecoregion, similar environments in terms of species establishment and disturbance characteristics such as fire return interval and fuel decomposition rate are assumed (He and Mladenoff 1999). These assumptions have been validated by numerous studies. For example, fires are found to be more frequent and have shorter mean return intervals on xeric ecoregions than mesic ecoregions (e.g., Kauffman et al., 1988); and excessively drained sandy ecoregions may favor one group of species over those found on poorly drained clay ecoregions (Keys et al. 1995).

The most recent developments of LANDIS include a forest harvest module (Gustafson et al. 2000). The harvest module has spatial, temporal, and species age-cohort removal components. The spatial component determines how harvest activity observes stand boundaries and adjacency constraints while the temporal component allows simulation of iterative harvesting rotations and multiple-entry silvicultural treatments. The species age-cohort component allows users to specify the age cohorts removed by specific harvest methods (e.g., clearcutting, selection cutting, and shelter-wood cutting). Because these harvesting components are independent, almost any harvest prescriptions can be simulated by combinations of these three components (Gustafson et al. 2000).

LINKAGES model

LANDIS does not incorporate climate variables and therefore does not simulate effects of climate change directly. Individual tree species response to climate warming was determined from simulations of a gap model, LINKAGES (Pastor and Post 1985) that simulates ecosystem processes (soil water and nutrient dynamics, decomposition, and mineralization) based on soil data and climate input. This was done for 23 tree species on both ecoregions (He et al. 1999b). LINKAGES integrates climate, soil, and species attribute data and derived biomass for current and warming climate (Post and Pastor 1996). To incorporate climate-warming factors in LINKAGES, we used a scenario of a linear annual temperature increase over the next 100 years to a total increase of 5°C in annual mean (Schlesinger and Mitchell 1987, Pastor and Post 1988). This scenario did not predict precipitation changes for northern Wisconsin, but the temperature increase affects soil moisture dynamics.

LINKAGES input data include twelve-month mean temperature and precipitation, and their standard deviations, growing season degree-days, soil organic matter (total C), soil nitrogen (total N), and soil moisture including wilting point and field water capacity (Pastor & Post, 1985). Microbial processes and demographic processes are simulated monthly and ecosystem feedbacks and tree growth are measured annually (Post & Pastor, 1996). The primary outputs include species

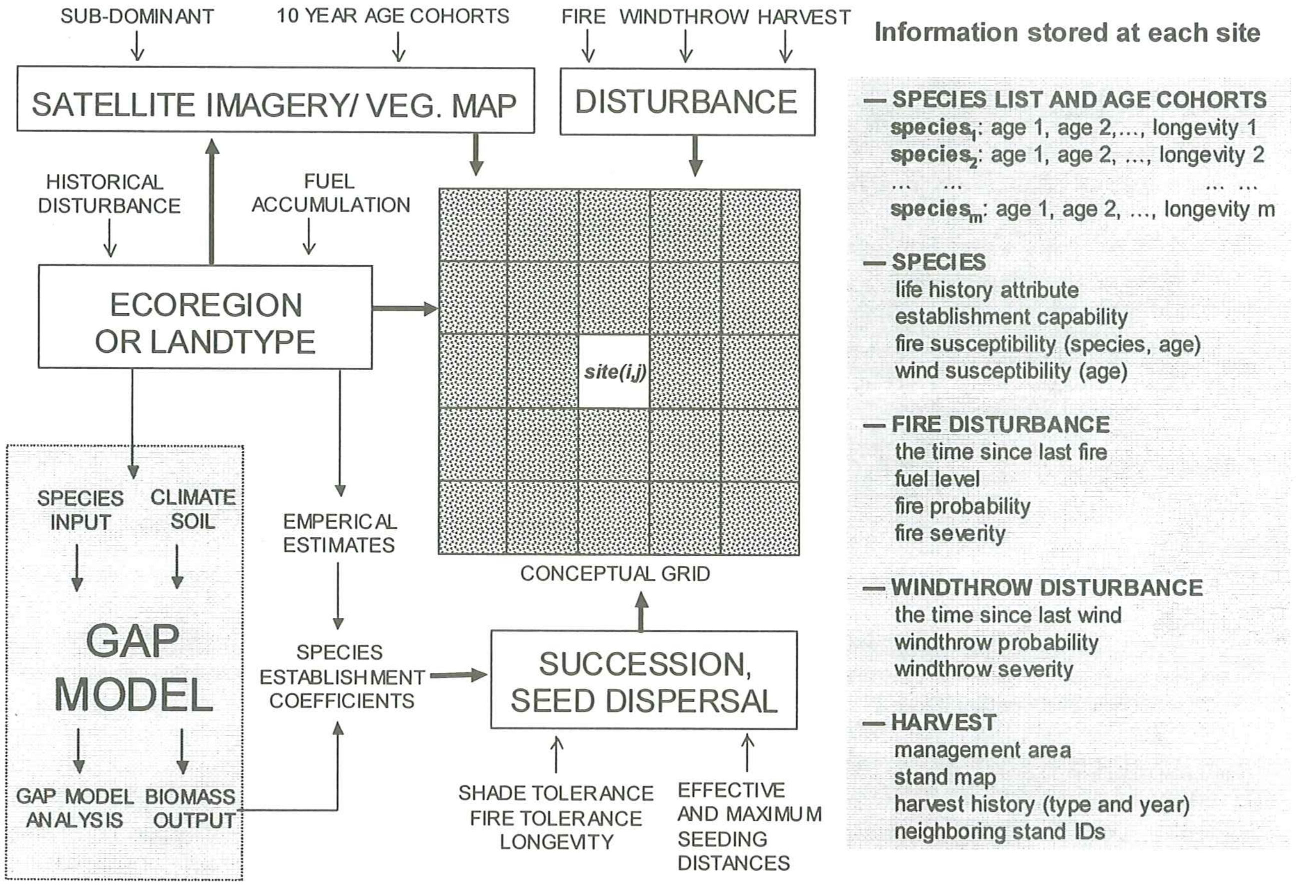

Figure 2. LANDIS model structure and the link with a gap model. In LANDIS, a landscape is divided into equal-sized individual cells or sites. Each *site* (*i, j*) resides on a certain landtype and records a unique species list and age cohorts of species. The species/age cohorts information varies via establishment, succession, and seed dispersal, and interact with disturbances. Species establishment coefficients can be derived from a gap model that synthesizes individual species response to various environments. They can be further used to parameterize LANDIS.

biomass, basal area, number of trees, carbon and nitrogen pools, nitrogen mineralization, snags, leaf litter, and soil organic matter. Biomass simulated for each species was quantified as species establishment coefficient, a parameter used by LANDIS (He et al. 1999b).

Input data

To derive forest compositions (species age-cohorts) as LANDIS input for this large landscape, we developed a GIS processing approach (He et al. 1998) that integrates a species level Landsat TM satellite imagery (Wolter et al. 1995), a quantitative ecoregions classification (Host et al. 1996), and sub-canopy and age class information from a regional forest inventory database (FIA) (Hansen et al. 1992). Fire disturbance regimes are distinctly different between the lakeshore and barrens ecoregions. Mean fire return intervals were estimated empirically at 100 years in the barrens and 800 years in the lakeshore ecoregions, based on the literature on historical data (Heinselman 1973, 1981, Lorimer and Gough 1988, Frelich and Lorimer 1991). Forest management is very different between these two ecoregions (Wisconsin Department of Natural Resources 1990) and therefore, each is treated as a distinct management area. Stand boundaries were derived by classifying current species age class data into dominant forest types, using the LANDIS reclassification algorithm (He et al. 1999a), and delineating contiguous patches (stands) of forest types.

LINKAGES climate input was derived from 30-year (1960-1990) mean, high-resolution raster format (1 × 1 km) climatic data. These include monthly mean precipitation and temperature, and their associated standard deviations, for a total of 48 climatic data layers. Soil texture, soil organic matter, and total nitrogen were interpreted from the state geographic soil database (STATSGO), incorporating a polygon coverage and hierarchical relational database (Soil Survey Staff, 1992). For climate warming, we used a scenario of 5°C of gradual annual-temperature increase over 100 years and no obvious precipitation changes (Schlesinger & Mitchell, 1987). Temperature increase was evenly redistributed to each month. Other climate change scenarios such as those with detailed monthly temperature and precipitation predictions can be used as alternatives.

Simulation scenarios

Three LANDIS simulation scenarios were used in this study: current climate with existing harvest regime (CH), warming climate with existing harvest regime (WH), and warming climate with selection harvest regime (WHs). The current climate with selection harvest (CHs) is also a legitimate scenario because the comparison of CH and CHs can show the impacts of harvesting under current climate. However since this focus of this research is the impacts of harvesting under warming climate, we did not include CHs scenario.

For the existing harvest regime, approximately 30% of the management area in the barrens ecoregion is considered for clearcutting at a 40-year rotation on stands with a minimum age of 50 years (He et al. 2002). Stands in this ecoregion are relatively homogeneous and therefore they are randomly selected for harvest (Table 1) in LANDIS. Harvest of individual species in LANDIS is simulated using an age-cohort mask, a binary format with "1" indicating removal of a given age cohorts (Table 2). In the lakeshore ecoregion, 75% of the stands in the management area are considered for harvesting every decade under the group selection method (Table 1). However, for all the stands selected, group selection only removes approximately 10% of the area within each stand and creates small openings in the stand. Stands in the lakeshore ecoregion are highly homogeneous, and therefore the oldest stands are harvested first (Gustafson et al. 2000).

For the selection harvest regime, we kept the general harvest regime unchanged, including cutting size and rotation, but selectively target certain species for cutting (Table 1). In the barrens ecoregion we harvest all species except the predominant red pine and jack pine in order to reduce competitions by other species. Red pine and jack pine are assumed to be under stress due to climate warming. In other words, all age cohorts of jack pine and red pine in the removal mask for the barrens ecoregion are set to 0, while the age cohorts of the remaining species are set to 1 (Table 2) (Gustafson et al. 2000). In the lakeshore ecoregion, we harvest sugar maple, the shade tolerant species, to create openings for shade intolerant, mid-successional northern hardwood species to establish.

We used LANDIS to simulate all three scenarios for 300 years from the same starting conditions. For the warming climate with existing harvest and warming climate with selection harvest scenarios, differences between species establishment coefficients for current and warming climate were linearly interpolated for each decade (one model iteration) over the first 100 years, assuming that the warming occurs during the first 100 years. The model was then run for the remaining 200 years without further climate change to examine post-warming landscape responses. All simulations were calibrated following an approach proposed in He and Mladenoff (1999), to ensure that simulated fire disturbances match the distributions of natural fire regimes.

Individual trajectories of species abundance under the current climate with existing harvest scenario were completed in a previous study (He et al. 2002) for all 23-tree species. They served as baselines to compare with the simulations of the warming climate with existing harvest and warming climate with selection harvest scenarios in this study. Our comparisons for different simulation scenarios are limited to those species that dominant in the landscape. We did not separate species trajectories by the two ecoregions under various simulation scenarios, since 90% of jack pine and red pine occur in the barrens ecoregion, while 90% of the remaining species occur in the lakeshore ecoregion.

III. RESULTS

Tree species responses under the warming climate with existing harvest scenario

Under the warming climate with existing harvest Scenario, boreal tree species including quaking aspen, paper birch, balsam fir, jack pine, and red pine had the most dramatic decreases

Table 1. General forest harvesting regime for current climate with existing harvest, warming climate with existing harvest, and warming climate with selection harvest scenarios

	Lakeshore ecoregion	Barrens ecoregion
harvesting methods	Group selection	Clearcutting
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 of the ecoregion[1])	75%	30%
stand proportion	10%	100%
mean group size (cells) [2]	20	N/A
standard deviation (cells	10	N/A

[1] Proportion of forest stands in ecoregion subject to harvest.
[2] Cells are 60´ 60-m.

Table 2. Removal mask in LANDIS harvest module

Species	Age cohorts at 10-year interval
Balsam fir	000000000000000
Red maple	000000000000000
Sugar maple	111111111111111111111111111111
Yellow birch	000000000000000000000000000000
Paper birch	000000000000
Bitternut hickory	000000000000000000000000000000
White ash	00000000000000000000
White spruce	00000000000000000000
Jack pine	0000000
Red pine	0000000000000000000000000
White pine	0000000000000000000000000000000000000000
Big toothed aspen	000000000
Quaking aspen	000000000
Pin cherry	000
Black cherry	00000000000000000000
White oak	0000000000000000000000000000000000000000
Pin oak	00000000000000000000
Bur oak	000000000000000000000000000000
Red oak	0000000000000000000000000
Black oak	000000000000000000000000000000
White cedar	00000000000000000000000000000000000
American basswood	0000000000000000000000000
Eastern hemlock	000000000000000000000000000000000000000000000

Harvest on individual species in LANDIS is simulated using this age-cohort mask, a binary format with "1" indicating removal of a given age cohorts. Setting all age cohort of sugar maple to 1 (the above example) simulates the selection cutting in the lakeshore ecoregion, while setting all age cohorts of jack pine and red pine to 0 and rest of the species age cohorts to 1 simulates the selection cutting in the barren ecoregion. The length of each binary string represents the longevity of the corresponding species at 10-year interval

under a warming climate due to the unfavorable environment for seedling establishment, as found elsewhere (He et al. 1999b). Quaking aspen abundance decreased to 15% of the landscape at year 50, after the first generation aspen reached its longevity and died (Figure 3a). A second generation remained on 15% of the landscape for about another 50 years and declined linearly after year 100. By year 150, quaking aspen decreased to about 3% of the landscape. Paper birch had a brief increase between year 10 and 50, corresponding to the decline of quaking aspen (Figure 3b). It started to decrease in abundance 50 years into the warming period and declined more quickly within the warming period than after warming. Paper birch abundance decreased to less than 2% of the landscape after year 150 (Figure 3b). Similar to paper birch, the abundance of balsam fir increased during the first 50 years because the recovery process was more dominant than the negative effects on the species induced by warming. As a shade tolerant and competitive species, its declining process took about 150 years, longer than aspen and paper birch, even though they have similar longevity (Figure 3e).

Jack pine, primarily occurring in the barrens ecoregion, initially benefited from the clearcutting regime. Clearcutting removed jack pine along with other species from the stands selected for harvesting. However, jack pine, an early successional shade intolerant species, can establish faster than other species in this ecoregion. Decreases of northern hardwood species under warming climate further reduced competition against jack pine. Therefore, jack pine had higher abundance in the warming climate with existing harvest scenario than in the current climate with existing harvest scenario for the first 80 years before unfavorable warming conditions became a dominant factor that eventually drove the decline of jack pine. It decreased to about 2% of the landscape by year 150. Red pine showed stronger resistance to the effects of warming than jack pine. It did not increase in abundance as in the current climate conditions, but its declining process did not occur for the first 80 years (Figure 3d). Red pine abundance declined after year 80 and down to about 3% of the landscape at year 250 (Figure 3d).

By year 300, northern hardwood species had experienced substantial declines, but not as significant as those for boreal species. Sugar maple, the most shade tolerant species, declined from 30% to 12% of the landscape by year 300 (Figure 3f). Similarly, yellow birch experienced a decline in abundance under warming climate. It began with a low percent cover on these two ecoregions, and its abundance decreased to 1% of the landscape at year 300 (Figure 3g). The declining process for white pine was longer than most other species, partly due to

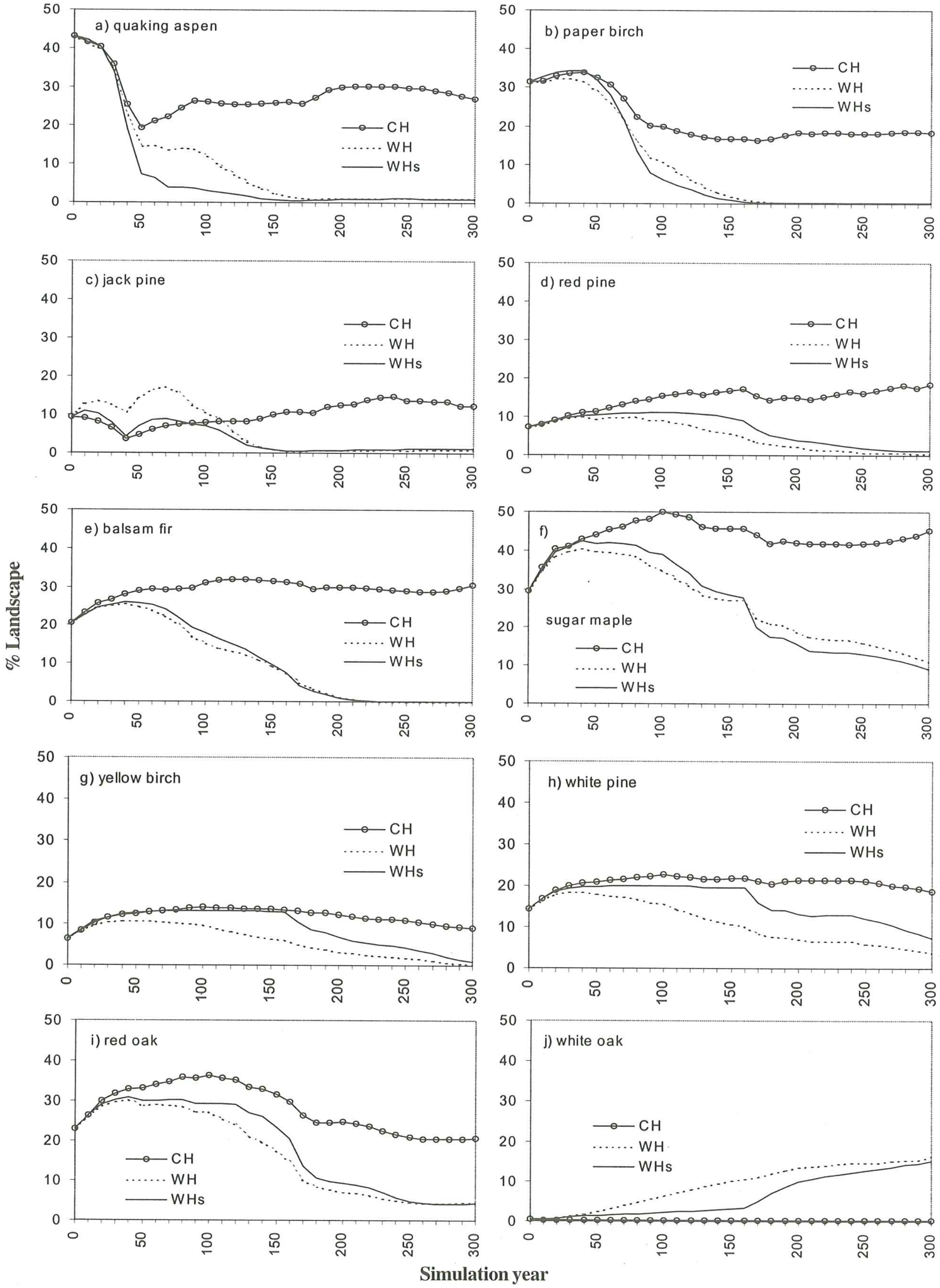

Figure 3. Figures a)-n) represents trajectories of 14 selected tree species simulated with LANDIS over 300 years under the current climate with existing harvest (CH), warming climate with existing harvest (WH), and warming climate with selection harvest (WHs) scenarios.

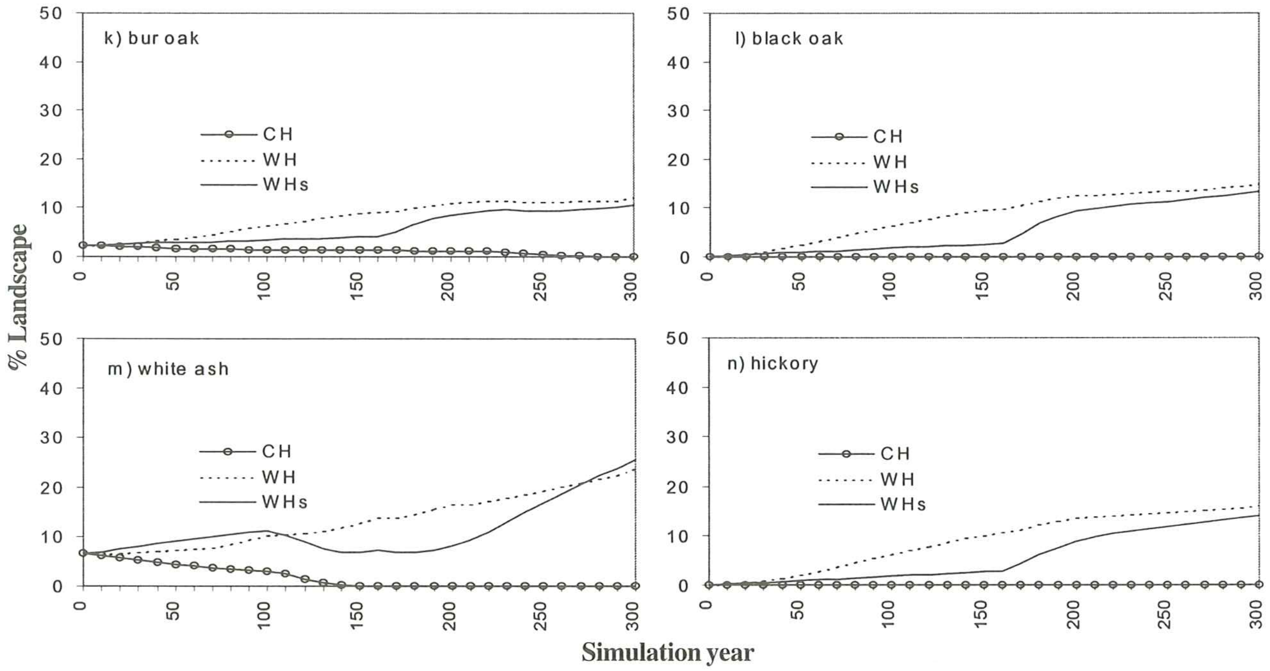

Figure 3. Cont'd

decline at year 50 and its abundances stabilized after year 200, remaining on about 5% of the landscape (Figure 3h). Red oak started to decline 80 years into the warming. From year 90 to 190 red oak decreased linearly and stabilized at about 8% of the landscape for the remaining period of simulation (Figure 3i).

A warming climate created favorable environments for the southern hardwood species. Unable to establish under current climate, these species had very low abundance (<1%) at year 0. Under warming climate, their abundances increased to 15%-30% of the landscape by year 300. Similar patterns of increase in abundances were found for all southern hardwood species, including white oak (Figure 3j), bur oak (Figure 3k), black oak (Figure 3l), white ash (Figure 3m), and hickory (Figure 3n).

Tree species responses under the warming climate with selection harvest scenario

In examining individual species response to different harvest regimes, we compared species trajectories between the warming climate with existing harvest and warming climate with selection harvest scenarios. In the warming climate with selection harvest scenario, selection cutting was designed to reduce competition against species already under stresses due to warming. In the barrens ecoregion, selection cutting of all hardwood species except red pine and jack pine was implemented. In the lakeshore ecoregion, selection cutting of only sugar maple was implemented to reduce competition against boreal and hardwood species under a warming climate.

We anticipated sugar maple trajectory under the warming climate with selection harvest scenario to be the same as that under the warming climate with existing harvest scenario since both scenarios remove sugar maple. However, our results indicate that the warming climate with selection harvest scenario would lead to higher sugar maple abundance for about the first half of the simulation (year 20-160) and lower sugar maple abundance for the remaining years (170-300) (Figure 3f). This is because sugar maple seedlings can establish under the shade of early and mid successional forests. In the lakeshore ecoregion, group selection harvest in the warming climate with existing harvest scenario removed sugar maple along with all other species. This created small openings in stands that were harvested, and competition in these openings prevented sugar maple from establishing until other species have established. In fact, group selection in the warming climate with existing harvest scenario further limited sugar maple abundance. For the warming climate with selection harvest scenario, however, since selection cutting removed only sugar maple and left all other species unchanged, no openings were created. Sugar maple could seed back and establish in the stands immediately following a harvest. Therefore, compared with the warming climate with existing harvest scenario, the abundance of sugar maple actually increased in the warming climate with selection harvest scenario before year 160 (Figure 3f). Since the warming climate with selection harvest scenario did not remove tree species other than sugar maple, stands of these remaining species aged with increasing simulation years. Therefore, these stands were ranked high priority for harvesting under the "oldest first" ranking method (Table 1), and the sugar maple sub-canopy and understory in these stands were also harvested. After year 160 unfavorable warming conditions decreased the amount of sugar maple that seed back to the harvested stands. With continuing harvesting, sugar maple abundance in the warming climate with selection harvest scenario became lower than that in the warming climate with existing harvest scenario (Figure 3f).

Species responses to the selection cutting of sugar maple in the lakeshore ecoregion reveal complicated interactions of succession, establishment, and competition among them. Mid- to shade tolerant species including yellow brich, white pine, and red oak benefited from the selection cutting, resulting in higher abundances in the warming climate with selection harvest than that in the warming climate with existing harvest scenario (Figure 3g, 3h, and 3i). Under the warming climate with selection harvest scenario, yellow birch abundance was about 50% higher than that under the warming climate with existing harvest scenario. It was able to maintain the level seen under current climate and was little affected by warming until year 160. As previously discussed, fire probabilities increase with increasing forest age. Large fires did not occur before year 160, but did occur after that time. These fires had catastrophic impacts on many boreal and northern hardwood species including yellow birch, which were already under stress due to climate warming. Although yellow birch abundance was about 10% higher than the warming climate with existing harvest scenario, it was never able to recover after fire to its previous level under warming conditions (Figure 3g). Similar patterns were also found for white pine (Figure 3h), which resisted climate warming until 160, but decreased under both fire disturbance and unfavorable establishment conditions, and maintained a 20% higher abundance than under the warming climate with existing harvest scenario.

Selection cutting of sugar maple did not benefit early successional species such as aspen and paper birch. The increases in abundances of mid-shade tolerant species made the abundances of aspen and paper birch lower in the warming climate with selection harvest scenarios than that in the warming climate with existing harvest scenario (Figure 3a-b).

In the barrens ecoregion, a positive response of jack pine and red pine to selection cutting of hardwoods was found. Compared to the warming climate with existing harvest scenario, the warming climate with selection harvest scenario increased jack pine abundance by an average of 40-50% during the warming period (Figure 3c). After warming, jack pine declined and the trajectories of jack pine under warming climate with selection harvest and warming climate with existing harvest scenarios eventually converged at year 150 (Figure 3c). In the warming climate with selection harvest scenario, red pine did not decline under climate warming. It was able to maintain its abundance until year 160 and was then removed in significant proportions by fires. Although red pine abundance in the warming climate with selection harvest scenario stayed higher throughout the simulation than that in the warming climate with existing harvest scenario, it never recovered to its current abundance level due to the combined effects of warming and fire disturbance (Figure 3d).

Forest landscape responses

Compared to the current climate with existing harvest scenario, we examined how forest landscape responded to climate warming under the two harvest scenarios. Under the current climate with existing harvest scenario, northern hardwoods and boreal forests completely dominated the lakeshore ecoregion at year 0 (Figure 4a). This situation persisted to the end of the simulation, except that the initially fine-grained distribution pattern of northern hardwood and boreal forest evolved to patchy distributions under natural fire regimes (Figure 4b-d). In the barrens ecoregion, jack pine and red pine dominated, especially in the central part at year 0 (Figure 4a). However, since human disturbance resulted in a low fire frequency compared to the historical regimes in this ecoregion, boreal and northern hardwood species established in the northern barrens, where pine was formerly common (Figure 4a). With simulation of a natural fire regime under the current climate with existing harvest scenario, recovery of jack pine and red pine occurred with their abundances gradually increasing to become completely dominant in the barrens ecoregion by year 300 (Figure 4d).

Under climate warming, boreal forests gradually declined in the lakeshore ecoregion. They were replaced initially by northern hardwoods, as seen in a snapshot at year 100 (Figure 4e and 4h). Northern hardwoods neither experienced a significant decline nor increased in abundance during the first 100 years, while the warming occurred. The warming climate with selection harvest scenario preserved more boreal forests than the warming climate with existing harvest scenario (Figure 4e and 4h). In the barrens ecoregion for the first 100 years, a decline of pine forest was observed (Figure 4e and 4h). This was largely due to the decline of red pine found in the species trajectories under warming conditions (Figure 3d). The decline of pine benefited northern hardwoods, primarily red oak, which became dominant, especially in the northern barrens at year 100.

At year 150, landscapes from both the warming climate with existing harvest and warming climate with selection harvest scenarios diverge further from the landscape under the current climate with existing harvest scenario (Figure 4b, 4e, and 4h). In the barrens ecoregion under warming, the initial patch structure disappeared completely, leaving red pine and jack pine in a highly dispersed distribution (Figure 4f and 4i). The abundance of both pine and northern hardwoods in the barrens ecoregion declined under both scenarios. However, with selection cutting, the warming climate with selection harvest scenario maintained more pine forests than the warming climate with existing harvest scenario (Figure 4f and 4i). At year 150 under the warming climate with existing harvest scenario, migration of southern hardwood species was seen in many places where boreal forests used to be (Figure 4f). Northern hardwood forests also shrank in their distribution, replaced also by southern hardwood forests (Figure 4f). Under the

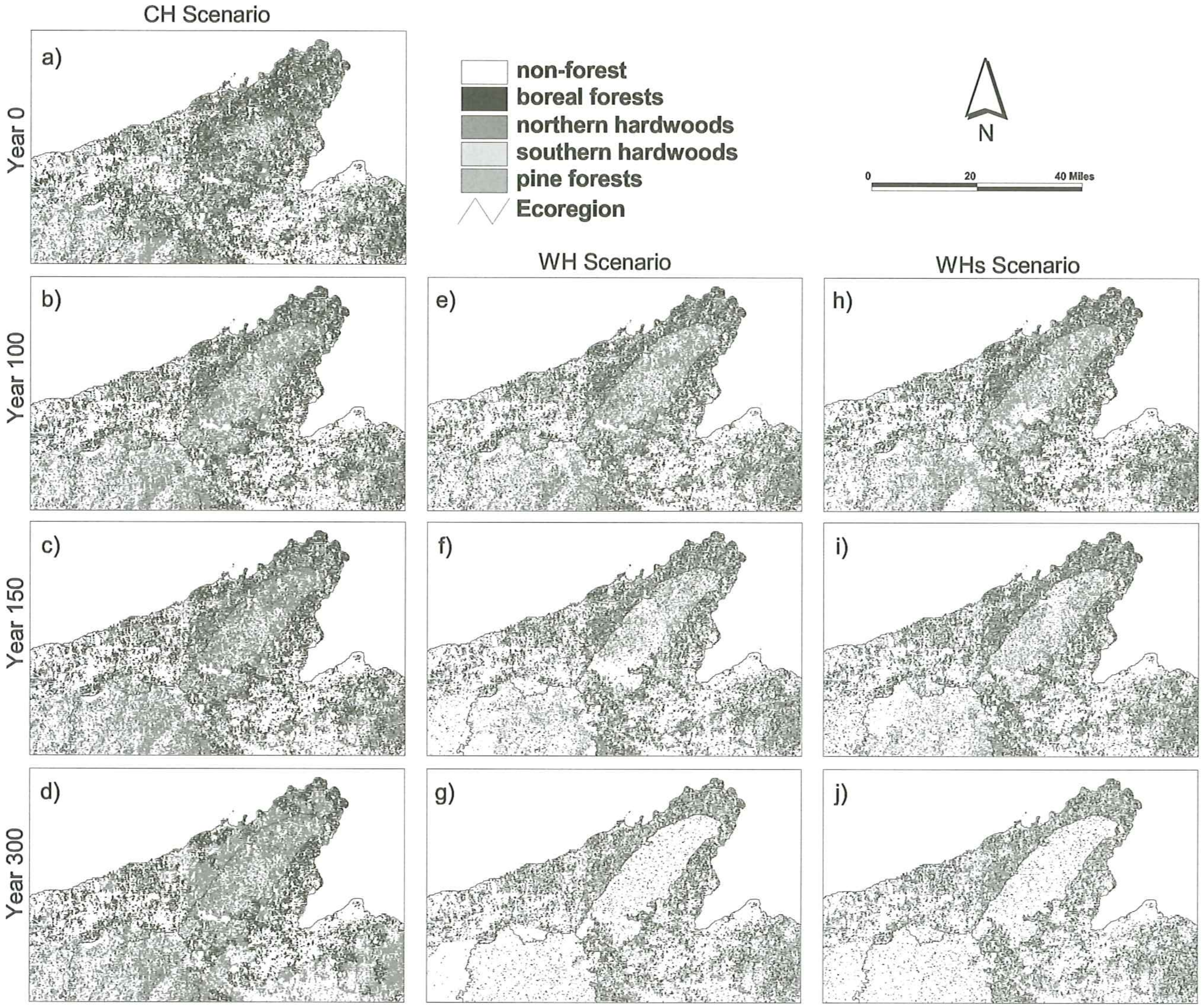

Figure 4. Figures a)-j) shows forest landscape succession under the current climate with existing harvest (CH), warming climate with existing harvest (WH), and warming climate with selection harvest (WHs) scenarios at year 0, 100, 150, and 300 years, respectively.

warming climate with selection harvest scenario, however, the migration north of southern hardwood species was seen, but they were dispersed in the ecoregion still dominated by northern hardwood forest (Figure 4i). At year 150, landscapes under the warming climate with existing harvest and warming climate with selection harvest scenarios showed the greatest differences in the lakeshore ecoregion. This indicates that forest harvesting played an important role in delaying the declining process of boreal forests and northern hardwoods.

At year 300, the forest landscape under warm climate completely differed from the landscape under the current climate (Figure 4d, 4g, and 4j). In the lakeshore ecoregion, formerly dominant boreal and northern hardwood forests were replaced largely by southern hardwood forests comprising southern oak species (bur oak, white oak, and black oak), white ash, and hickory, which occurred only in minor amounts under current climates (Figure 4g and 4j). Boreal forests in this ecoregion completely disappear, while northern hardwoods became a minor cover type compared to southern hardwood forests. A more dramatic transformation occurred in the barrens ecoregion. More than 98% of jack pine and red pine forests disappeared. The remaining pines were distributed in a very sparse and random fashion (Figure 4g and 4j). With both pine and southern hardwood species that migrated being unable to reproduce and establish under warming conditions, the barrens ecoregion could transform into an area with only grass and shrub species. The warming climate with existing harvest and warming climate with selection harvest scenarios did not lead to significant difference in the barrens ecoregion.

V. DISCUSSION

We used simulation modeling to examine broad-scale response under climate warming. Our simulation results suggest that forest landscapes in two ecoregions of northern Wisconsin would experience a significant change under climate warming. In the lakeshore ecoregion, with better water and nutrient conditions, currently dominant boreal and northern hardwood forests would transform into southern hardwood forests that are more favored under warming climate. These results are consistent with those simulated for this region using gap models (Pastor and Post 1988). However, our results suggest that landscape transformation and species extinction will not occur as dramatically as predicted from many gap models (see review by Loehle and LeBlanc 1996). On the contrary, incorporating realistic initial seed source distribution and simulating seed dispersal spatially, our results suggest that the landscape transition is gradual and becomes apparent 50-150 years after warming. In contemporary time scales and assuming warming occurs from the beginning of this century, landscape transformations would probably be seen during 2150-2300.

In a spatially explicit manner, our simulation results further suggest that the landscape transition would occur in the following three stages. 1) Initially, during the first 100 years while the warming occurs, the proportions of boreal forest in the landscape decrease substantially, while northern hardwoods stay relatively stable. Boreal forests are intolerant to the warmer and drier climate, and they disappear from the landscape around year 150. 2) From 100 to 200 years, the landscape transforms to an intermediate status co-dominated by both northern and southern hardwood forests. Boreal forests are replaced by northern hardwood forests, the most common forest cover under the current climate. Although northern hardwood forests are also affected by warming, for the first 150 years under warming climates, they experience neither substantial declines, nor increases in abundance as they do under the current climate scenario. This is due to their high abundance and relatively better temperature and drought tolerance than boreal forests. However, after year 150, declines of northern hardwoods are shown as many species reach their longevity and new seedlings are unable to establish under warming climate. 3) Finally, from year 200 to 300, southern hardwood forests replace northern hardwoods and become the dominant. The transition of the landscape from the one dominated by northern hardwoods and boreal forest to one dominated by southern species takes about 200 years. In the barrens ecoregion under warming conditions, northern hardwoods replace boreal forests in the northern area. Because red pine, jack pine, northern hardwoods and new southern species are unable to establish under the warmer and drier conditions, the remainder of this ecoregion would transform into a region with only grass and shrub species by year 250.

Our results indicate that species respond to climate warming individually and the responses are from the combined effects of species current age, longevity, competition, and environmental suitability (He et al. 1999b). A species may not respond to climate warming immediately, as adult trees are generally tolerant to changing environments (Loehle and LeBlanc 1996). Once established and mature, they will stay on the landscape unless removed by harvest and fire. Boreal and northern hardwood species that have long longevity and high drought tolerance can delay the impacts of climate warming by about 100 years as shown for red oak, sugar maple, yellow birch, and white pine. Over large time scales however, global warming will eventually represent a major force in transforming landscapes. At broad scales, species response to warming can be further complicated by landscape processes. As we have demonstrated, fire disturbance can accelerate the decline of boreal and northern hardwood species such as yellow birch (Figure 3g) and white pine (Figure 3h). Disturbance also makes the northerly migration of southern hardwood species relatively easy (He et al. 2002).

Unlike fire disturbance, forest harvesting changes species composition and age structure in a systematic way throughout the simulation. Our results suggest that a selection cutting scenario that preserves boreal and northern hardwood species can play an important role in delaying landscape transitions to southern hardwood forests. As shown at year 150, southern hardwood forests are sparse and dispersed as simulated under selection cutting scenarios (Figure 4i), while they are seen replacing boreal forests and occurring in small patches under existing forest harvest scenarios (Figure 4f). This result confirms what we have previously speculated about the roles of forest harvesting (He et al. 2002). However, the proportions of various cover types simulated under both the warming climate with existing harvest and warming climate with selection harvest scenarios at year 300 are very similar. This suggests that the different harvest regimes do not alter the long-term impacts of climate warming.

We have presented a modeling framework that links an ecosystem model with a spatial landscape model. Individual species response at the ecosystem scale to climate warming is simulated with a gap model that integrates climate, soil, and species data (He et al. 1999b). The simulation results, in the form of biomass for each tree species, are quantified as input to the landscape model, which integrates the climate-warming response of individual species with large-scale, landscape processes including fire and harvest. This allows us to examine spatially explicit responses at landscape scales and succession trajectories under different management scenarios. Results from such an approach are more realistic than those derived from gap or simple landscape transition models alone. Furthermore, this approach presents a viable solution to examining large-scale and long-term issues such as landscape response to climate warming at species level and yet in a spatially explicit manner.

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