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Linking an ecosystem model and a landscape model to study forest species response to climate warming

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Abstract

No single model can address forest change from single tree to regional scales. We discuss a framework linking an ecosystem process model (LINKAGES) with a spatial landscape model (LANDIS) to examine forest species responses to climate warming for a large, heterogeneous landscape in northern Wisconsin, USA. Individual species response at the ecosystem scale was simulated with LINKAGES, which integrates soil, climate and species data, stratified by ecoregions. Individual species biomass results, simulated by LINKAGES at year 10, were quantified using an empirical equation as species establishment coefficients (0.0-1.0). These coefficients were used to parameterize LANDIS, thus integrating ecosystem dynamics with large-scale landscape processes such as seed dispersal and fire disturbance. Species response to climate warming at the landscape scale was simulated with LANDIS. LANDIS was parameterized with information derived from a species level, forest classification map, and inventory data. This incorporates spatially-explicit seed source distributions. A standard LANDIS run with natural fire disturbance regime and current climate was conducted for 400 years. To simulate the effects of climate change, the differences in species establishment coefficients from current and warmer climates were linearly interpolated over the first 100 years assuming climate warming will occur gradually over the next century. The model was then run for another 300 years to examine the consequences after warming. Across the landscape, the decline of boreal species and the increases of temperate species were observed in the simulation. The responses of northern temperate hardwood species vary among ecoregions depending on soil nutrient and water regimes. Simulation results indicate that boreal species disappear from the landscape in 200-300 years and approximately same amount of time for a southern species to become common. Warming can accelerate the re-colonization process for current species such as found for eastern hemlock, where moisture does not become limiting. However, the re-colonization is strongly affected by available seed source explicitly described on the landscape. These phenomena cannot be simulated with most gap models, which assume a random seed rain. © 1999 Published by Elsevier Science B.V. All rights reserved.

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1. Introduction

Forests are expected to change at several scales as a result of climate warming induced by increasing CO₂ and other greenhouse gases (Richie, 1986; Manabe and Wetherall, 1987; Roberts, 1989; Gates, 1990; Foley et al., 1994; Shugart 1996; Sykes and Prentice 1996). Climate warming directly affects tree ecophysiology (Prentice et al., 1992) as well as water availability (Bazzaz et al., 1996; Heal et al., 1996). Increased temperature can also alter ecosystem processes such as soil nutrient regimes by affecting organic matter mineralization dynamics (Pastor and Post, 1986; Running and Nemani, 1991). New combinations of climate variables, soil processes, and individual species responses may result in forest successional paths different from those observed today (Davis and Botkin, 1985; Zabinski and Davis, 1989; Guetter and Kutzbach, 1990; Pastor and Mladenoff, 1992). The rate and magnitude of these changes are often examined with forest ecosystem models or gap models (Shugart et al., 1992; Shugart, 1997). Climate variables, a group of driving factors in gap models, can be flexibly changed to reflect various climate change scenarios (e.g. Pastor and Post, 1988; Botkin and Nisbet, 1992). Projections using gap models have been made for various forest types across a wide geographic range (Botkin et al., 1989; Dale and Franklin, 1989; Bonan et al., 1990; Smith and Shugart, 1996).

At landscape scales, more indirect effects such as climatically induced changes in disturbance regimes (Flannigan and Van Wagner, 1991; Gardner et al., 1996; Loehle and LeBlanc, 1996) and new species migration patterns affected by both current spatial configuration of vegetation and warmer climate (Davis et al., 1991; Leishman et al., 1992; Pitelka et al., 1997) can further alter vegetation dynamics. These cumulative changes can alter landscape patterns and structure defined

by forest patch composition, size, shape, and spatial associations with other types (Mladenoff et al., 1993). However, these potential changes often cannot be simulated with gap models because gap models do not simulate ecological processes that are based on large spatial extents. Rather, these changes can be investigated by spatially explicit landscape models. Forest landscape modeling is a recent endeavor (e.g. Green, 1989; Baker et al., 1991; Urban et al., 1991; Gustafson and Crow, 1994; Turner et al., 1994; Gardner et al., 1996; Keane et al., 1996; Mladenoff et al., 1996; Roberts, 1996; Mladenoff and Baker, in press) often assisted by the development of spatial information capture and processing ability in remote sensing and geographical information systems (GIS). An advantage of applying spatial models to simulate forest landscape (> 10⁴ ha) change is that ecological processes occurring at larger spatial extents (such as wind and fire disturbances, and seed dispersal) and influenced by landscape heterogeneity, can be simulated. Therefore, landscape patterns and the rate of vegetation change in a region can be more realistically simulated over time using these models (Mladenoff and He, in press).

Landscape modeling can be conceived as running gap models simultaneously on multiple sites while incorporating spatial interactions between these sites and larger-scale processes. The computational load of landscape modeling, if interpreted as $m \times n$, where m is the minimum number of computation steps at a single site required for a gap model, and n is the total number of sites of the map, can be substantial. One approach in landscape modeling is the spatial application of gap models (Acevedo et al., 1995; Keane et al., 1996). Computationally, these models cannot be applied to large areas while carrying all the information of a gap model because of the greater m . To compensate, spatially inexplicit scaling-up is one compromise approach. Another approach of

landscape modeling is to reduce the number of computation steps (decreasing m) by integrating or simplifying ecological processes at the site level. In some of these landscape models, ecological processes at individual sites are completely replaced by landscape processes. For example, stand ages are represented as the time since last disturbance (e.g. Baker et al., 1991; Gardner et al., 1996; Li et al., 1997), or vegetation as fire susceptibility classes (Turner et al., 1994). Such models are effective in investigating the interactions of disturbances such as fire and landscape patterns across large regions. However, species-level dynamics that become increasingly important in ecosystem management (Mladenoff and Pastor, 1993) are generally not simulated. Recent development in landscape modeling incorporates forest succession modules that track the presence or absence of species age classes (Mladenoff et al., 1996; Roberts, 1996; Mladenoff and He, in press). Models of this approach allow explicit simulation of seed dispersal on landscapes, as well as successional dynamics on each site at the species level. However, since only species age cohort presence or absence is recorded, not individual trees nor forest density, site specific ecosystem-level processes such as species recruitment or establishment cannot be mechanistically simulated with these models. Species establishment will be altered under climate warming (Davis et al., 1991; Leishman et al., 1992), and will further affect seed migration patterns (Pitelka et al., 1997). Species response to climate warming can be more accurately examined by gap models that mechanistically simulate the interactions between environmental variables and individual trees than landscape models themselves.

Thus, the objective of this study is to present a framework for linking an ecosystem process model (LINKAGES) and a spatially explicit landscape model (LANDIS) to examine the magnitude of forest landscape responses to CO₂-induced climate warming. LINKAGES is used to synthesize individual species response to the climate warming. The synthesized results represented as species establishment coefficients (see later discussion) are used to parameterize LANDIS to integrate ecosystem processes with large-scale landscape processes.

2. Materials and methods

2.1. Ecosystem process model—LINKAGES

The LINKAGES model (Pastor and Post, 1985, 1986) is a derivative of the JABOWA/FORET class of models (Botkin et al., 1972, Shugart, 1984). The model has been extensively described and validated against independent data on species composition, biomass, net primary productivity, soil organic matter, and soil nitrogen availability in many different areas (Pastor and Post, 1986; Pastor et al., 1987; Mladenoff and Stearns, 1993; Post and Pastor, 1996). LINKAGES differs from many other gap models in that it includes explicit decomposition, mineralization, and soil moisture subroutines, allowing soil water and nutrients cycling to interact with species succession. These particular subroutines have been adopted and modified by other recent gap models (e.g. Martin, 1992, Bugmann, 1996). A modified version (Mladenoff and Stearns, 1993) allows output of dead wood pools as well as living biomass, and includes three light response functions instead of two. 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 and Post, 1985). Microbial processes and demographic processes are simulated monthly and ecosystem feedbacks and tree growth are measured annually (Post and Pastor, 1996). The primary outputs include species biomass, basal area, number of trees, carbon and nitrogen pools, nitrogen mineralization, snags, leaf litter, and soil organic matter.

2.2. Spatially explicit landscape model—LANDIS

2.2.1. Overall model structure

LANDIS is a spatially explicit model designed to simulate forest change over large, heterogeneous landscapes, and over long time-scales (Mladenoff et al., 1996; Mladenoff and He, in press). The major modules of the LANDIS model are forest succession, seed dispersal, wind and fire disturbances, and harvesting (Fig. 1). LANDIS is a

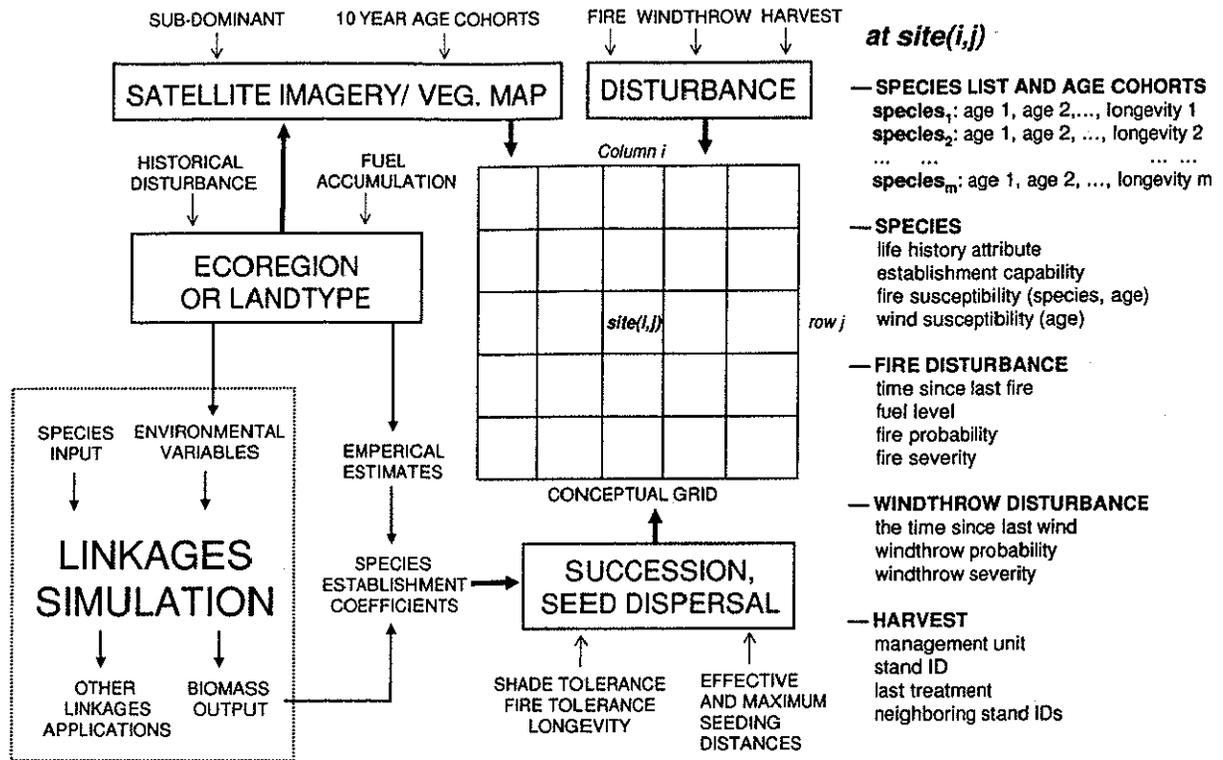


Fig. 1. Specifications in LANDIS model design and the link with LINKAGES. In LANDIS, a landscape divided into equal-sized individual cells or sites. Each site (*i, j*) on a certain landtype, records a unique species list and age cohorts of species. These species data change via establishment, succession, and seed dispersal, and interact with disturbances. Species establishment coefficients can be derived from LINKAGES which synthesizes individual species response to various environments. They can be further used to parameterize LANDIS.

raster-based model in which each cell contains unique species, age cohort, environment, and time since last disturbance information. LANDIS simulates at 10 year time steps for each site; species are recorded as the presence or absence of 10 year age cohorts, not as individual trees. For each site, species birth, growth, death, regeneration, background mortality, and vegetative reproduction are simulated each iteration. At landscape scales, seed dispersal and disturbances are simulated each iteration. To simulate heterogeneous landscapes, land-types, or ecoregions at large scales, are processed from other GIS data layers to stratify the landscape (He et al., 1996; He et al., in press). Within each ecoregion, environmental variables such as climate and soils are by definition assumed homogeneous, as are some characteristics

of disturbance and species establishment (Mladenoff and He, in press). Ecoregion boundaries are static throughout a simulation, but their effect on species establishment can change under changed climate scenarios.

2.3. Seed dispersal and seedling establishment

In LANDIS, the mechanisms of seeding and seedling establishment are simulated differently from those in gap models. In most gap models, seed availability is a completely stochastic process simulated with random seed rain, and seedling establishment is a deterministic process (Shugart, 1984; Leishman et al., 1992). A series of factors determines the establishment of seed on a site, including light levels, temperature, and moisture.

The range of factors varies for different gap models, depending on what is judged to be important for that particular community. In LANDIS, however, the available seed source is spatially explicit. The seed dispersal process comprises three distinct steps: seed travel, on-site checking, and seedling establishment (Mladenoff and He, in press).

First, seed travel distance is a function of the effective and maximum seeding distances of a given species. Seed has a higher probability of reaching a site within the species effective seeding distance than beyond this distance. When seed successfully arrives at a given site, the on-site checking procedure is called to determine whether the species is able to seed-in based on what other species occur on the site and the shade tolerance rank of the seeding species relative to the existing species. For example, aspen cannot seed into a site where sugar maple is established. Secondly, once a species is allowed to seed into the site, it may or may not establish depending on the environmental conditions of the site. All sites on the landscape are stratified by different ecoregions which may favor certain species over others. The species establishment coefficient, a number from 0 to 1, reflects in a relative sense how different environmental conditions favor a particular species in terms of its establishment (Mladenoff et al., 1996). LANDIS does not mechanistically model the species establishment coefficient; rather the coefficients are provided as input to the model. They can be derived either empirically or from the simulation results of an ecosystem process model such as LINKAGES. Thirdly, following dispersal, a uniform random number from 0 to 1 is then drawn to check against the species establishment coefficient to decide if seed can establish. A species can establish only when its establishment coefficient > the random number drawn. Therefore, species with high establishment coefficients have higher probabilities of establishment (Mladenoff and He, in press).

2.4. Disturbance

LANDIS simulates disturbance in combination with the simulational of succession dynamics, dif-

fering from most landscape models except Roberts (1996). Fire, for example, is a stochastic process based on historical data, the distribution of mean fire sizes and mean fire return intervals characterized by ecoregions (He et al., in press). Ecoregions that are sandy and dry are more fire prone than more mesic ecoregions. Fire is simulated as a bottom-up disturbance with small, young trees more vulnerable than large, old trees. Fire effects are also species specific, and species fire tolerance varies. Fire impact is the interaction of species age-classes, species fire tolerance, and fire severity determined by the amount of fuel.

2.5. Study region

Our study region in northwestern Wisconsin, USA (45.5°N 90.5°W to 47.0°N 92.0°W; Fig. 2), comprises about 1.5 million hectares, and falls in the transitional zone between boreal forest to the north and temperate forests to the south (Curtis, 1959; Pastor and Mladenoff, 1992). The region is quantitatively classified into ten ecoregions (Host et al., 1996, Fig. 2). The area is largely forested in the north, including much of the Chequamegon National Forest, and extends into more agricultural areas in the south. Quaternary geology and mesoclimatic gradients are the greatest determinants of environmental variation in the region, leading to very well-drained sandy soil in ecoregions 5 and 9, moderate to well-drained silty-clay in ecoregion 8, moderate to well-drained silt in ecoregion 2, well-drained loamy soil in ecoregions 4 and 7, and loam to silty-loam soil in ecoregions 10 and 11. Summers in the area are short and mild (July mean 18°C), and winter are cold (January mean -10°C) with snow cover from November to April. Annual precipitation is \approx 80 cm. These climatic variables are used in greater detail in the ecoregion classification (Host et al., 1996). The region underwent extensive forest cutting in the past, and is largely composed of young, secondary forests (Mladenoff and Pastor, 1993). Characteristic north temperate species ('northern hardwoods') here include sugar maple (*Acer saccharum*), red maple (*A. rubra*), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*),

northern red oak (*Quercus rubra*), basswood (*Tilia americana*), and yellow birch (*Betula alleghaniensis*). Boreal species include balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), big-toothed aspen (*P. grandidentata*), paper birch (*B. papyrifera*), jack pine (*P. banksiana*), and red pine (*P. resinosa*). Species of more southern distribution are rare including sparsely distributed white oak (*Q. alba*), black oak (*Q. velutina*), bur oak (*Q. macrocarpa*), white ash (*Fraxinus americana*), and hickory (*Carya cordiformis*).

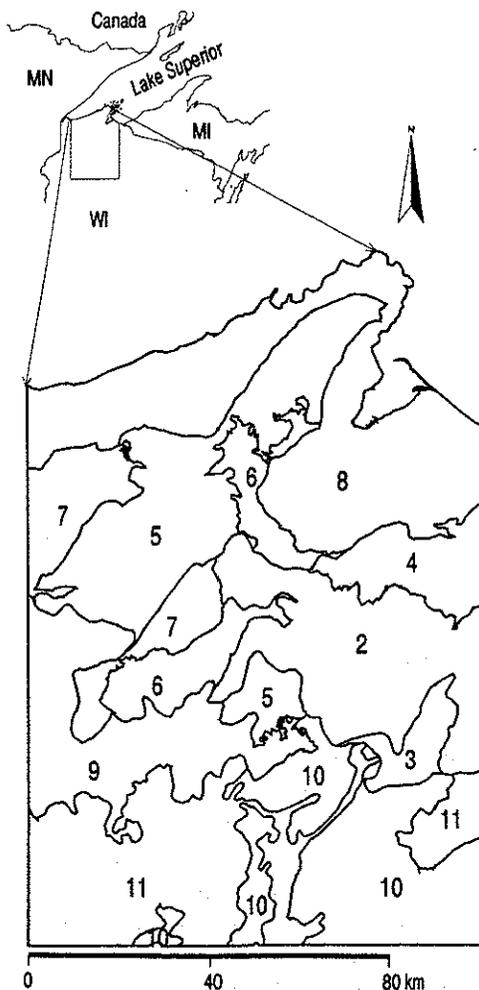


Fig. 2. Study region and the ecoregions within the study area.

2.6. Use of the ecosystem model, LINKAGES

2.6.1. Input data

LINKAGES climate input was derived from 30 year (1960–1990) mean, high-resolution raster format (1×1 km) climatic data (ZedX, 1994). 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 and 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. Soil polygons were rasterized at 30×30 m resolution which preserves the details of the STATSGO data (Soil Survey Staff, 1992). Soil texture was then used to further interpolate wilt point and field capacity (Hillel, 1980). Growing season degree-days were digitized from an existing map (Wisconsin Agricultural Statistics Service, 1987), and spatial interpolation was made by using Arc/Info TIN (ESRI, 1996). Growing season was also rasterized as Arc/Info grid format at 1×1 km resolution due to its coarse scale.

To automate input of spatial environmental data sets required by LINKAGES, an Arc/Info AML (Arc Macro Language) program was written to assist in locating sample points. Sampling was stratified by ecoregions. A total of 30–100 samples were randomly selected within each ecoregion depending on its size, and the program then calculated the means of all the climatic and soil variables to represent the ecoregion. These means were used as LINKAGES environmental input variables for every ecoregion (Table 1).

2.6.2. Simulation scenarios

To examine differences in species establishment by ecoregion we simulated one species at a time in LINKAGES, planting the same number of trees

Table 1
LINKAGES environment input parameters for ecoregions

	Eco 2	Eco 3	Eco 4	Eco 5	Eco 6	Eco 7	Eco 8	Eco 9	Eco 10	Eco 11
Latitude	-90.8	-90.9	-90.5	-91.4	-91.6	-91.8	-90.9	-91.1	-90.7	-90.9
Longitude	46.1	45.8	46.3	46.2	46.2	46.2	46.6	46.0	45.3	45.5
Growing season	151.1	139.4	148.1	144.0	146.5	149.1	153.7	145.4	141.1	139.6
Total C (%)	98.3	98.3	83.4	73.5	81.9	100.0	84.6	85.8	111.9	94.8
Total N (%)	7.0	6.6	5.9	5.2	7.0	5.9	7.0	5.2	6.6	5.9
Field capacity	39.2	35.8	30.0	10.3	39.2	30.0	39.2	10.6	35.8	30.0
Wilting point	23.3	16.7	13.3	3.6	24.3	13.3	23.4	3.6	16.7	13.3
Jan_T	-12.5	-12.1	-12.7	-12.5	-12.5	-12.6	-12.5	-12.4	-11.4	-11.7
Feb_T	-10.2	-9.7	-10.5	-10.0	-10.0	-10.0	-10.1	-10.0	-9.1	-9.3
Mar_T	-3.6	-3.2	-3.9	-3.4	-3.4	-3.4	-3.5	-3.4	-2.6	-2.8
Apr_T	4.8	5.2	4.6	5.1	5.2	5.2	5.1	5.1	5.7	5.5
May_T	11.9	12.2	11.7	12.1	12.2	12.2	12.0	12.1	12.6	12.4
Jun_T	17.1	17.4	16.9	17.3	17.4	17.5	17.3	17.3	17.7	17.6
Jul_T	20.0	20.3	19.8	20.3	20.4	20.4	20.2	20.2	20.6	20.5
Aug_T	18.5	18.8	18.4	18.8	19.0	19.0	18.9	18.8	19.2	19.1
Sep_T	13.4	13.8	13.2	13.7	13.8	13.8	13.9	13.7	14.2	14.0
Oct_T	7.3	7.6	7.1	7.6	7.7	7.7	7.8	7.6	8.0	7.9
Nov_T	-1.2	-0.8	-1.4	-1.0	-0.9	-1.0	-0.7	-1.0	-0.3	-0.5
Dec_T	-9.3	-8.9	-9.6	-9.3	-9.3	-9.3	-9.1	-9.2	-8.3	-8.6
Jan_P	2.4	1.6	2.4	2.3	2.4	2.3	2.7	2.4	2.6	2.5
Feb_P	1.9	1.5	1.9	1.8	1.8	1.8	2.1	1.9	2.2	2.1
Mar_P	3.4	2.4	3.4	3.5	3.5	3.5	3.7	3.5	4.0	3.8
Apr_P	5.4	2.9	5.3	5.5	5.6	5.6	5.7	5.6	5.9	5.8
May_P	7.6	3.6	7.5	7.5	7.4	7.5	7.0	7.6	8.0	7.9
Jun_P	9.8	5.0	9.7	9.7	9.5	9.7	8.9	9.8	9.9	9.9
Jul_P	8.6	4.4	8.5	8.6	8.6	8.6	8.5	8.6	8.7	8.7
Aug_P	9.3	5.3	9.3	9.1	9.0	9.1	8.7	9.2	9.3	9.3
Sep_P	8.6	5.2	8.5	8.6	8.5	8.6	8.4	8.6	8.6	8.6
Oct_P	5.5	3.5	5.5	5.6	5.6	5.6	5.7	5.6	5.7	5.7
Nov_P	3.8	2.6	3.8	3.8	3.9	3.8	4.3	3.8	4.2	4.1
Dec_P	2.6	1.5	2.6	2.6	2.7	2.6	3.2	2.6	3.0	2.9

Eco = ecoregion.

T = temperatures in °C.

P = precipitation in cm, growing season in days; field capacity and wilt point in cm.

Monthly S.D.s of temperature and precipitation are omitted.

(200 saplings/ha) for each ecoregion environment. The model was first iterated to generate a forest floor with the environmental and species inputs for each ecoregion. When carbon and nitrogen in the forest floor reached steady state, we run the model to 50 iterations (years). Individual runs were conducted for each of the 23 species \times 10 ecoregions \times 20 replications. Without counting replications, there were 230 independent scenarios. The parallel set of 230 \times 20 LINKAGES runs was conducted under the warmer climate scenario.

2.7. Species establishment coefficient

As described above, the species establishment coefficient is a LANDIS input parameter and reflects the species establishment probability on a given ecoregion. The coefficients can be difficult to estimate based on limited literature and expert knowledge, especially for multiple species and ecoregions (23 \times 10 in our case). This difficulty is increased when deriving species establishment coefficients for changed climate scenarios. Using modeling results from LINKAGES minimizes the

subjectivity of establishment coefficient estimates and synthesizes individual species response to different environments including the warmer climate. Biomass output from LINKAGES, an indicator of species productivity, was used in calculating the species establishment coefficient using an empirical method:

$$e_{ij} = b_{ij} / \max \left\{ \sqrt{\sum_{j=2}^{11} b_{ij}}, \sqrt{\sum_{j=2}^{11} b'_{ij}} \right\} \quad (1)$$

Where b_{ij} and b'_{ij} are the biomass of species i on ecoregion j under current and warmer climate respectively, e_{ij} is the establishment coefficient of species i on ecoregion j under current climate, $\sum_{j=2}^{11} b_{ij}$ is the sum of the biomass of species i on all ecoregions. e_{ij} is then scaled to 0–1. j starts from 2 since there are ten ecoregions (2–11) in our study area (Fig. 2). Dividing by the square sum makes e_{ij} comparable among different ecoregions. The square root makes e_{ij} comparable by relativizing the biomass differences due to species physiological differences. The max operation ensures that species e_{ij} is comparable between current climate and climate warming conditions. We used the LINKAGES output from the first 10 years to examine species establishment. The output indicates that each species either completely disappears or reaches a stable trend within 10 years.

2.8. Use of the landscape model

2.8.1. Input data layers

The forest composition map for LANDIS input is a species-level forest classification map created by Wolter et al. (1995), using differences in tree species phenology captured in a series of Landsat TM and MSS satellite images from throughout the growing season. The map contains dominant canopy species but not age classes, nor the associated secondary species and their age classes, which comprise important seed source information. Secondary species and age class information were derived by integrating the TM classification with forest inventory plot data (Hansen, 1992), stratified by landtypes (He et al., in press). A total of 134 unique (species \times age \times ecoregion) site combinations resulted on the input map. These spatially explicit species and age-class data

provide a reasonable approximation of forest composition at large scales and allow mapping of available seed sources. All species life history attributes used by LANDIS were taken from the literature as reported elsewhere (Mladenoff and He (in press)). The final landscape input map contained 462000 cells (840 \times 550) with a 200 \times 200 m cell size.

2.8.2. Simulation scenario

LANDIS runs were conducted for the entire study area starting with current tree species and age-class distributions. 400 year LANDIS runs were conducted for both current and the warming climates with species establishment coefficients derived under both regimes from LINKAGES. For the warming climate run, differences between establishment coefficients for current and warming climate were linearly interpolated for each decade (LANDIS iteration) over the first 100 years reflecting a 5°C temperature increase scenario (Schlesinger and Mitchell, 1987). The model was then run for another 200 years to examine the landscape consequences of the warmed climate. A natural fire regime for this region was simulated. Historical fire data were interpreted from empirical studies in the region (Heinselman, 1973, 1981; Canham and Loucks, 1984; Frelich and Lorimer, 1991). Mean fire return interval varies among ecoregions from 200 (ecoregions 5, 9), to 500 years (ecoregions 3, 11), to 800 (ecoregion 10), and 1000 years (ecoregions 2, 6). Model results validation and model calibration were performed with the routine represented elsewhere, and will be omitted here.

3. Results

3.1. Individual species response to the climate warming—LINKAGES simulation

Under current climate all boreal and most northern hardwood species examined had stable or steadily increasing biomass within the first 10 years. Early successional species such as aspen and jack pine (Fig. 3a–c), are able to gain biomass quickly. These early successional species

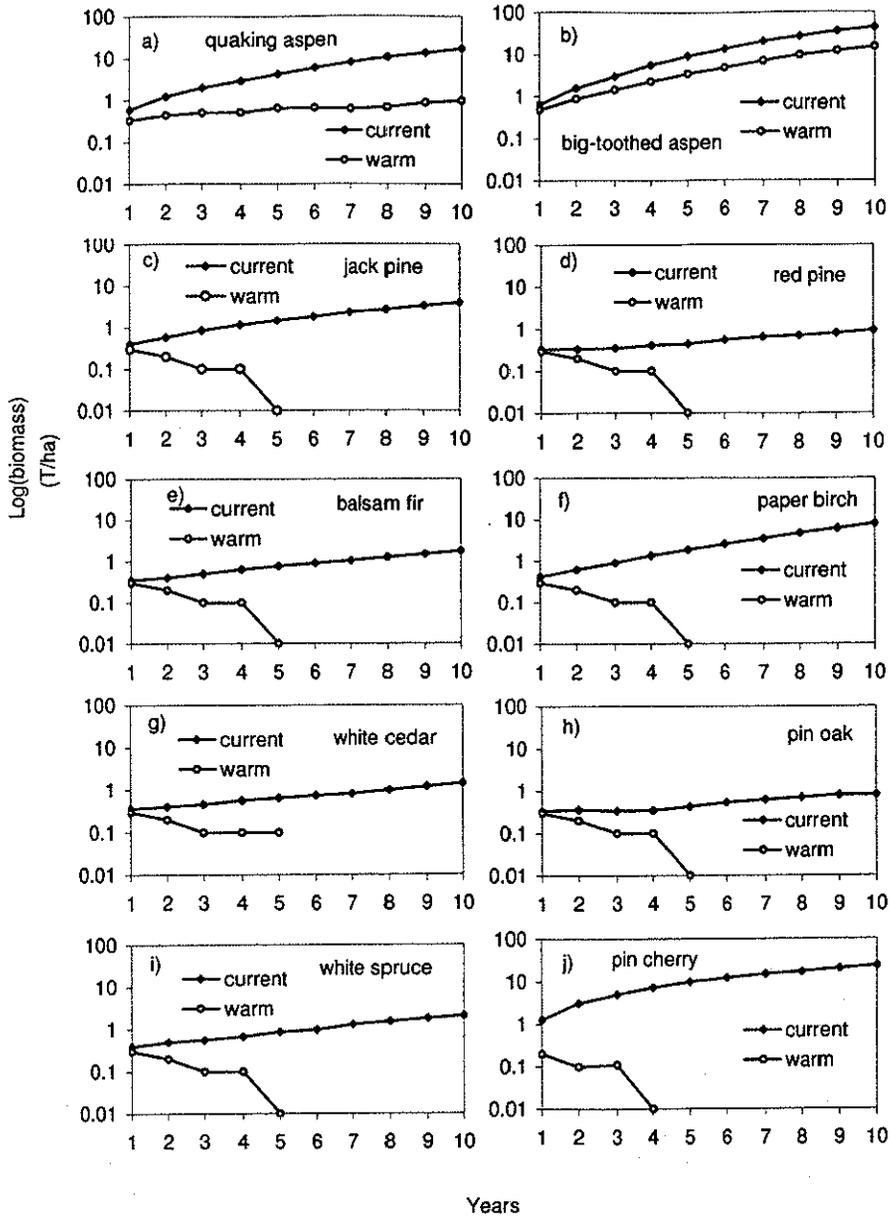


Fig. 3. Semi-log plot of LINKAGES biomass output for ten boreal species from years 0 to 10.

are currently among the most adapted species in the study region. Under the 5°C temperature increase scenario, the biomass of all boreal species and some northern hardwood species decreases. Starting with approximately equal biomass, jack pine, red pine, balsam fir, paper birch, white

cedar, northern pin oak, white spruce, and pin cherry decreased below 0.01 T/ha after the first four iterations (Fig. 3c–j, respectively). These species are not able to establish under the warmer conditions even with 200 saplings of each species planted at year 0. Quaking aspen and big-toothed

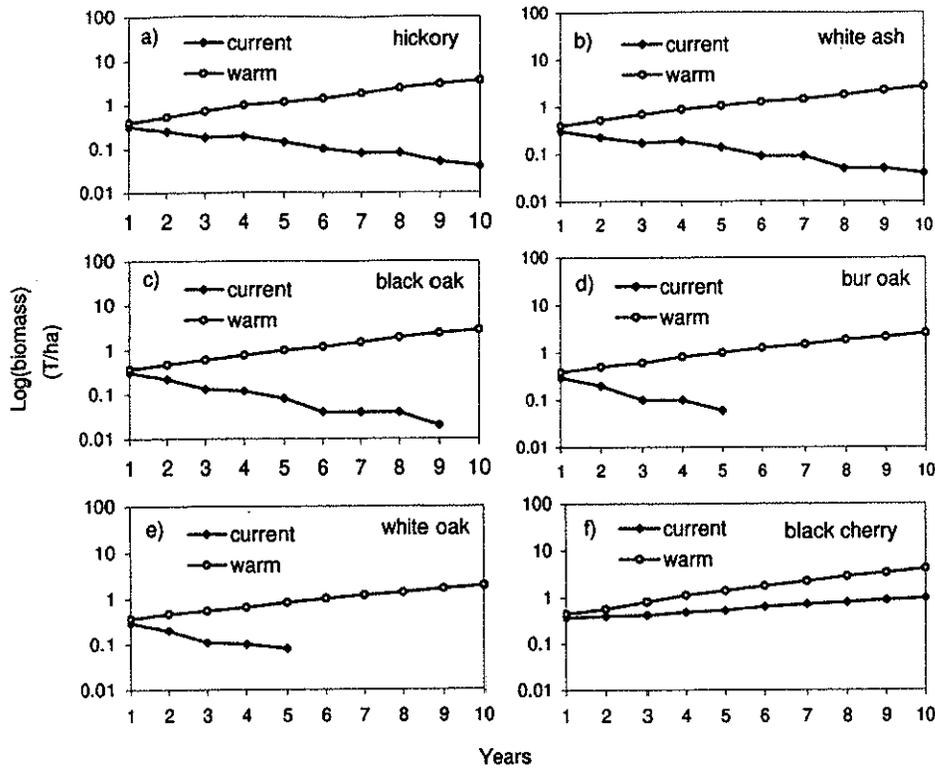


Fig. 4. Semi-log plot of LINKAGES biomass output for six southern species from years 0 to 10.

aspen (Fig. 3a, b), two widely established northern species, show decreases in biomass compared with current temperature runs, especially quaking aspen.

Southern species on the other hand show positive responses with warming, with biomass gains from < 1.0 T/ha under current temperature to > 10 T/ha under climate warming (Fig. 4a–f). Hickory and white ash, uncommon species under current climate, both show a steady increase under warming conditions (Fig. 4a, b). Black oak, bur oak, and white oak, are not able to establish under current climate with their biomass decreasing below 0.1 T/ha within the first 10 years. These southern oaks show steady increases under warming conditions (Fig. 4c–e). The biomass of black cherry increases under both climate conditions for the first 10 years, but it increases more under the warmer climate condition (Fig. 4f).

Warming-induced biomass changes of most northern hardwood species varies among ecoregions. Species establishment ability decreases for all species on ecoregions where soil water holding capacity and soil nutrients are limiting; e.g. for sugar maple (Fig. 5a) and red maple (Fig. 5c) on ecoregion 5 (Table 1). While on ecoregions with more suitable water and nutrient regimes, a biomass increase is observed; e.g. sugar maple on ecoregion 7 (Fig. 5b) and red maple on ecoregion 10 (Fig. 5d). On ecoregion 7, red oak biomass is slightly lower under warming conditions (Fig. 5e). On ecoregion 4, similar to ecoregion 7 but with more precipitation from June to August (Table 1), a positive red oak biomass response to warming was observed (Fig. 5f). For the remaining northern hardwood species on ecoregions other than 5, the temperature threshold is still an important factor affecting species biomass fluctuation. Red maple increases

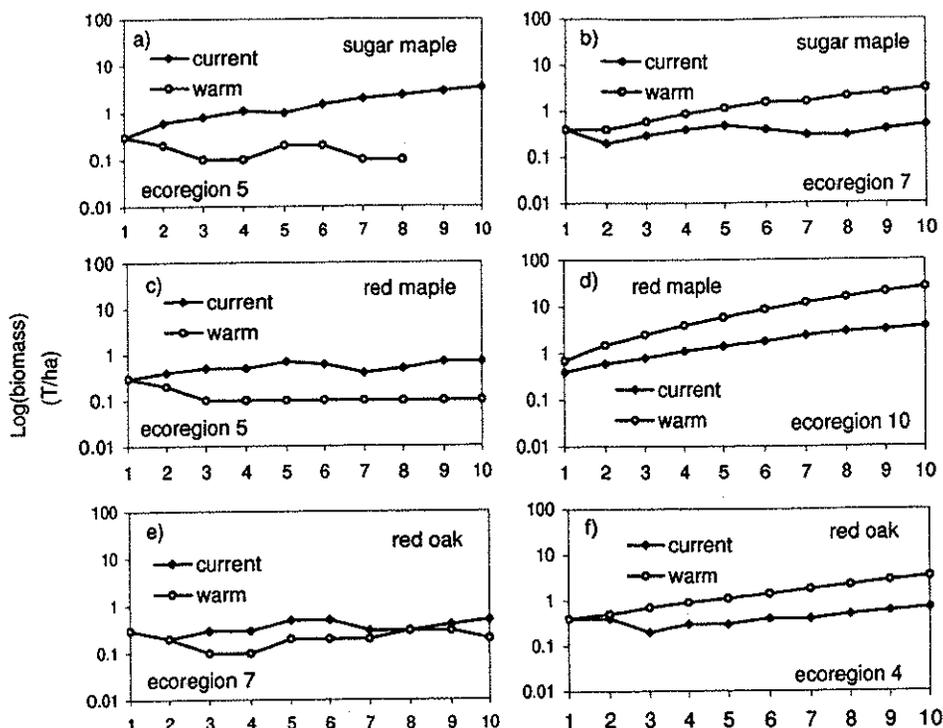


Fig. 5. Semi-log plot of LINKAGES biomass output for three northern hardwood species from years 0–10 for different ecoregions.

in biomass on all ecoregions except 5 (Table 2). Yellow birch increases only on ecoregion 9, white pine and white oak on ecoregion 4 (Table 2). These LINKAGES simulations are more detailed results based on a finer classification of the environment, that are similar to generalized LINKAGES results shown previously for the region (Pastor and Post, 1988).

3.2. Species establishment coefficients

Biomass output from LINKAGES at year 10 was used to calculate species establishment coefficients (Eq. (1)), since linear correlation was found among the biomass outputs projected from year 0 to 50. The derived coefficients (Table 3) reasonably relativize species performance in terms of establishment coefficients among both species and ecoregions. For example, the biomass of big-toothed aspen reaches 80.70 T/ha on ecoregion 10 under current climate, the largest biomass among all ecoregions under both current and warmer

climate (Table 2). The establishment coefficient of the species on ecoregion 10 is calculated as 1.00 (Eq. 1, Table 3), the largest number possible. On ecoregion 8 the biomass of big-toothed aspen is simulated as 38.90 T/ha, about half of the amount simulated for ecoregion 10, its establishment coefficient on ecoregion 8 is calculated as 0.48 (Eq. (1), Table 3). As another example, on ecoregion 6 the biomass of big-toothed reached 37.70 T/ha under current climate, much higher than that of paper birch, 14.70 T/ha (Table 2). However, similar establishment coefficients are calculated (Eq. 1, Table 3), 0.47 for the aspen and 0.43 for the paper birch, because physiologically, aspen biomass accumulates more quickly than that of paper birch.

3.3. Forest landscape response to climate warming—LANDIS simulation

3.3.1. Impact of seed dispersal

Ecological processes at landscape scales such as seed dispersal are simulated in a spatially explicit

Table 2
LINKAGES simulated biomass at year 10 under current and warmer climate

	Eco 2	Eco 3	Eco 4	Eco 5	Eco 6	Eco 7	Eco 8	Eco 9	Eco 10	Eco 11
<i>A. balsamea</i>	2.50	2.80	1.80	0.00	2.30	2.50	2.00	0.00	1.20	2.50
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>A. rubrum</i>	1.80	2.70	1.10	0.70	1.90	2.90	3.20	0.30	3.70	2.80
(w)	10.60	18.70	4.90	0.20	2.20	6.50	11.50	0.50	25.80	14.90
<i>A. saccharum</i>	5.00	4.70	4.10	0.10	5.00	0.50	10.60	0.00	0.50	9.00
(w)	1.30	2.20	1.60	0.00	0.10	3.10	0.30	0.00	0.80	0.80
<i>B. papyrifera</i>	13.60	5.60	14.50	1.70	14.70	6.10	8.90	1.60	5.00	7.30
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>B. alleghaniensis</i>	3.90	4.10	3.10	0.00	2.10	2.30	1.70	0.00	6.60	1.40
(w)	0.10	0.10	1.00	0.00	0.10	0.60	0.00	0.20	0.00	0.80
<i>C. cordiformis</i>	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.10
(w)	3.90	6.10	5.10	0.00	2.00	5.50	3.60	0.00	6.00	3.60
<i>F. americana</i>	0.00	0.10	0.00	0.00	0.00	0.20	0.00	0.00	0.10	0.00
(w)	3.40	4.90	3.90	0.00	0.30	4.40	2.40	0.30	3.90	3.60
<i>P. glauca</i>	5.90	2.60	3.60	0.40	1.40	2.30	2.60	1.60	0.20	0.30
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. strobus</i>	2.10	0.10	0.00	0.00	0.00	2.80	2.80	0.70	3.80	3.70
(w)	0.90	0.00	1.10	0.00	0.00	0.00	0.10	0.00	0.00	0.00
<i>P. banksiana</i>	4.00	4.50	4.40	2.50	4.60	4.00	4.70	2.70	4.00	3.90
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. resinosa</i>	1.70	2.30	2.50	0.10	0.40	0.10	1.20	0.50	0.00	0.60
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. grandidentata</i>	41.20	54.90	66.70	13.10	37.70	53.30	38.90	8.80	80.70	43.80
(w)	20.60	31.00	39.70	0.30	5.20	5.70	35.00	0.20	7.90	2.10
<i>P. tremuloides</i>	24.50	29.90	10.10	4.10	5.10	29.30	20.50	2.90	34.90	9.50
(w)	4.10	1.30	3.20	0.10	0.20	0.10	0.50	0.10	0.00	0.10
<i>P. serotina</i>	0.80	1.60	0.70	0.00	0.70	1.30	0.40	0.00	2.20	2.00
(w)	6.10	6.10	5.20	0.00	4.60	4.60	5.90	0.00	5.90	3.70
<i>P. pensylvanica</i>	32.20	30.40	23.60	0.90	25.40	34.70	19.90	5.10	33.60	30.60
(w)	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Q. ellipsoidalis</i>	0.20	0.40	0.70	0.20	0.90	0.20	1.30	0.00	2.90	1.30
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Q. alba</i>	0.00	0.00	0.00	0.00	0.10	0.10	0.00	0.00	0.00	0.00
(w)	2.60	3.40	2.60	0.00	0.20	1.80	2.60	0.00	3.70	2.20
<i>Q. ruba</i>	2.30	2.40	0.00	0.00	2.60	2.20	2.80	0.00	3.10	3.10
(w)	1.60	1.10	2.30	0.00	0.20	0.30	0.70	0.00	1.70	0.30
<i>Q. velutina</i>	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.10	0.20
(w)	3.00	5.90	3.80	0.00	0.20	3.80	3.20	0.10	6.50	1.90
<i>Q. macrocarpa</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(w)	2.90	3.30	3.90	0.00	2.60	3.70	2.40	0.00	3.30	4.00
<i>T. occidentalis</i>	1.70	2.30	1.90	0.00	1.90	2.00	2.20	0.00	0.90	1.60
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>T. americana</i>	3.00	1.90	4.20	0.00	7.10	0.00	10.00	0.00	2.00	3.20
(w)	1.60	8.20	6.40	0.00	0.00	2.70	0.60	0.00	5.10	7.70
<i>T. canadensis</i>	0.10	0.70	0.00	0.00	0.30	1.60	0.20	0.00	1.10	1.40
(w)	0.30	1.40	2.30	0.00	0.00	1.50	0.10	0.00	1.10	0.10

W = warmer climate.

Eco = ecoregion.

Table 3
Species establishment coefficients under current and warmer temperature

	Eco 2	Eco 3	Eco 4	Eco 5	Eco 6	Eco 7	Eco 8	Eco 9	Eco 10	Eco 11
<i>A. balsamea</i>	0.15	0.17	0.11	0.00	0.14	0.15	0.12	0.00	0.07	0.15
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>A. rubrum</i>	0.05	0.07	0.03	0.02	0.05	0.08	0.08	0.01	0.10	0.07
(w)	0.28	0.50	0.13	0.01	0.06	0.17	0.31	0.01	0.68	0.40
<i>A. saccharum</i>	0.21	0.19	0.17	0.00	0.21	0.02	0.44	0.00	0.02	0.37
(w)	0.05	0.09	0.06	0.00	0.00	0.12	0.01	0.00	0.03	0.03
<i>B. papyrifera</i>	0.40	0.16	0.42	0.05	0.43	0.18	0.26	0.05	0.15	0.21
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>B. alleghaniensis</i>	0.20	0.21	0.16	0.00	0.11	0.12	0.09	0.00	0.34	0.07
(w)	0.01	0.01	0.05	0.00	0.01	0.03	0.00	0.01	0.00	0.04
<i>C. cordiformis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00
(w)	0.17	0.26	0.22	0.00	0.09	0.24	0.16	0.00	0.26	0.16
<i>F. americana</i>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
(w)	0.17	0.24	0.19	0.00	0.01	0.22	0.12	0.01	0.19	0.18
<i>P. glauca</i>	0.34	0.15	0.20	0.02	0.08	0.13	0.15	0.09	0.01	0.02
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. strobus</i>	0.14	0.01	0.00	0.00	0.00	0.18	0.18	0.05	0.25	0.24
(w)	0.06	0.00	0.07	0.00	0.00	0.00	0.01	0.00	0.00	0.00
<i>P. banksiana</i>	0.17	0.19	0.18	0.10	0.19	0.17	0.19	0.11	0.17	0.16
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. resinosa</i>	0.14	0.19	0.21	0.01	0.03	0.01	0.10	0.04	0.00	0.05
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>P. grandidentata</i>	0.51	0.68	0.83	0.16	0.47	0.66	0.48	0.11	1.00	0.54
(w)	0.26	0.38	0.49	0.00	0.06	0.07	0.43	0.00	0.10	0.03
<i>P. tremuloides</i>	0.49	0.59	0.20	0.08	0.10	0.58	0.41	0.06	0.69	0.19
(w)	0.08	0.03	0.06	0.00	0.00	0.00	0.01	0.00	0.00	0.00
<i>P. serotina</i>	0.03	0.06	0.03	0.00	0.03	0.05	0.02	0.00	0.09	0.08
(w)	0.24	0.24	0.21	0.00	0.18	0.18	0.24	0.00	0.24	0.15
<i>P. pensylvanica</i>	0.54	0.51	0.40	0.02	0.43	0.59	0.34	0.09	0.57	0.52
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Q. ellipsoidalis</i>	0.02	0.04	0.06	0.02	0.08	0.02	0.12	0.00	0.26	0.12
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Q. alba</i>	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
(w)	0.15	0.20	0.15	0.00	0.01	0.11	0.15	0.00	0.22	0.13
<i>Q. rubra</i>	0.14	0.14	0.00	0.00	0.16	0.13	0.17	0.00	0.19	0.19
(w)	0.10	0.07	0.14	0.00	0.01	0.02	0.04	0.00	0.10	0.02
<i>Q. velutina</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
(w)	0.15	0.29	0.19	0.00	0.01	0.19	0.16	0.00	0.32	0.09
<i>Q. macrocarpa</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
(w)	0.15	0.17	0.20	0.00	0.13	0.19	0.12	0.00	0.17	0.20
<i>T. occidentalis</i>	0.12	0.16	0.13	0.00	0.13	0.14	0.15	0.00	0.06	0.11
(w)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>T. americana</i>	0.14	0.09	0.19	0.00	0.32	0.00	0.46	0.00	0.09	0.15
(w)	0.07	0.37	0.29	0.00	0.00	0.12	0.03	0.00	0.23	0.35
<i>T. canadensis</i>	0.01	0.07	0.00	0.00	0.03	0.16	0.02	0.00	0.11	0.14
(w)	0.03	0.14	0.23	0.00	0.00	0.15	0.01	0.00	0.11	0.01

W = warmer climate.

Eco = ecoregion.

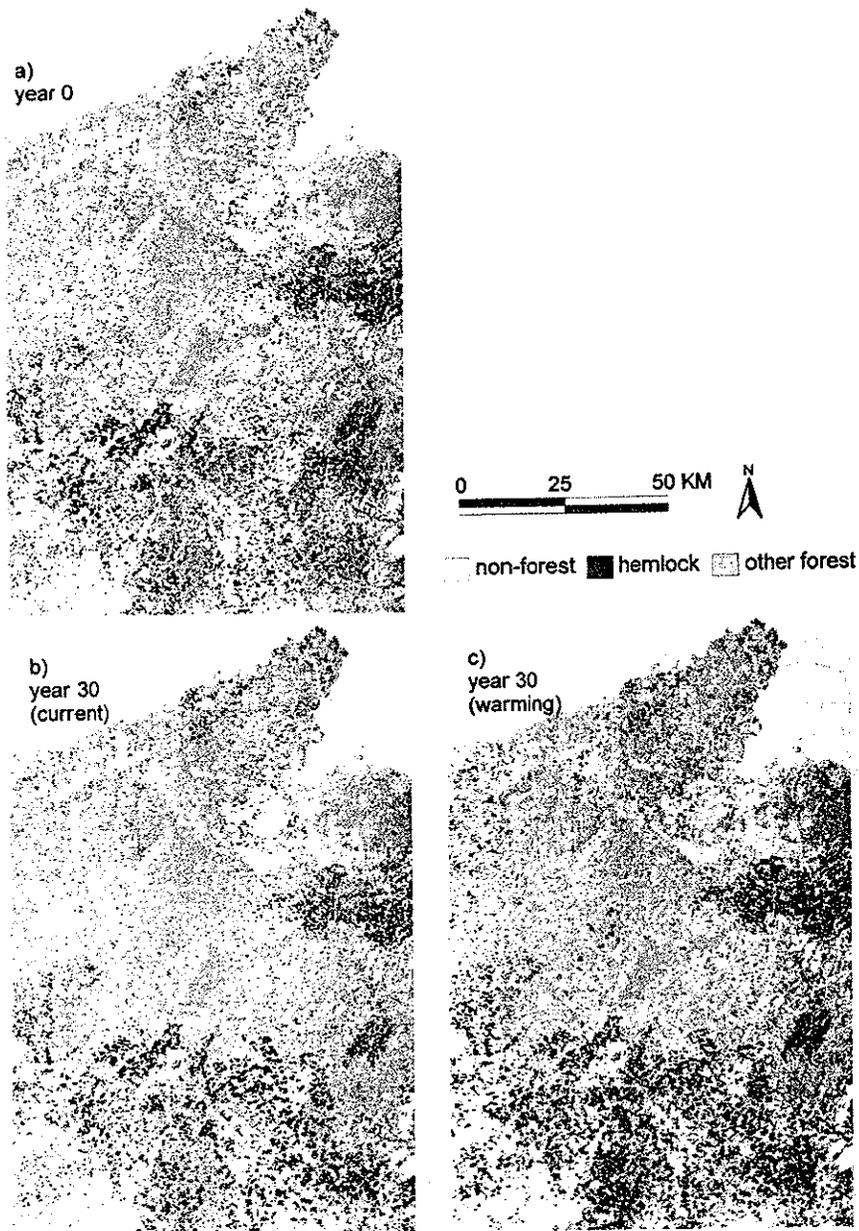


Fig. 6. Snapshots of LANDIS simulations of species spatial distribution for hemlock at year: (a) 0; (b) 30; (d) 60; and (f) 100; under current climate, and for hemlock at year: (c) 30; (e) 60; and (g) 100; under the period of warming.

manner for all species in LANDIS. For example, hemlock, historically a dominant species, is currently uncommon due to wide-spread cutting and fire during the last century and early this century (Mladenoff et al., 1994). Under current climate at

year 0, hemlock patches are small and highly fragmented (Fig. 6a). Small clumps or individual pixels especially for the southeastern area of the landscape are shown as seed sources but are sparse (Fig. 6a). At year 30, due to seed dispersal,

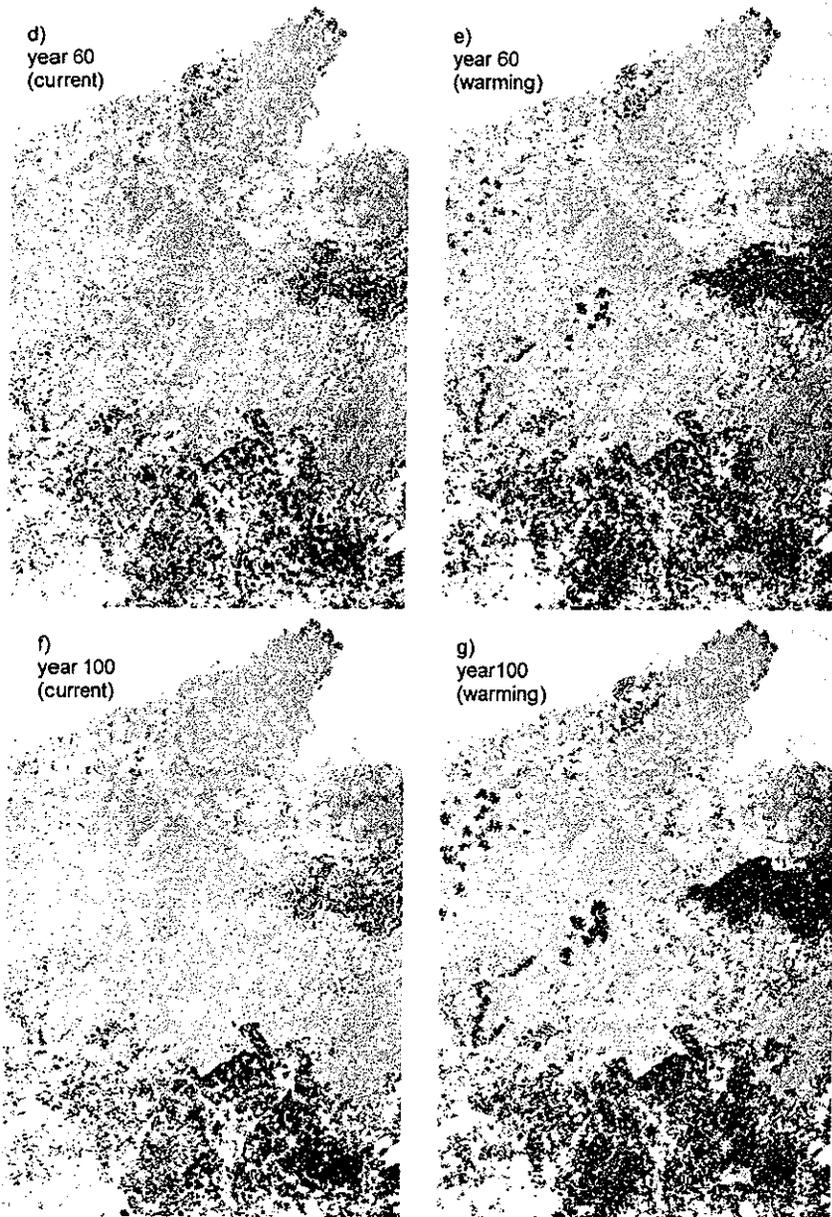


Fig. 6. (Continued)

the formation of small hemlock patches where hemlock seed source present is observed (Fig. 6b). On the other hand, the absence of hemlock from much of the landscape is due to the fire disturbance. Herbivory, which may impact hemlock, is not simulated here. With the low abundance at

the beginning of the simulation, the re-colonization process of hemlock on the landscape is slow and strongly affected by the available seed sources. At year 60, hemlock patches are larger but still fragmented (Fig. 6d). Very dense, large patches of hemlock are formed on the landscape

at around year 100 and they only occur at the places where seed is locally abundant (Fig. 6f). This implies that the encroachment of hemlock into other area may take much longer, since hemlock patches do not occur at sites beyond its seeding range. Patches of any species are based on the interactions of species succession, competition, disturbance, as well as the establishment ability of a species under a given environment. These patterns (Fig. 6a, b, d) cannot be realistically simulated on a large landscape where a random seed rain is assumed.

It is interesting to see that warming can further alter the re-colonization process. At year 30 under warming climate, a noticeable increase of hemlock on the landscape is found (Fig. 6c) compared to the current climate one (Fig. 6b). This trend becomes more evident at year 60 (Fig. 6e), with dense and large hemlock patches found on the landscape. At 100 years into the warming scenario, hemlock patches emerge on various parts of the landscape over a significant proportion of the landscape (Fig. 6g). This may imply accelerated hemlock re-colonization process under warmer climate, at the current northern limit of its range, if moisture remains adequate.

3.3.2. Species abundance on the landscape

LANDIS simulated individual species responses at landscape scale for all 23 species. The species responses to climate warming simulated by LANDIS corresponds to the trends simulated by LINKAGES but with great variations resulting from the interactions of landscape-scale processes such as seed dispersal, disturbance, and variable species establishment by ecoregions. The sum of the areas where a species occurs on the landscape simulated by LANDIS is represented as percent abundance.

The abundance of big-toothed aspen and paper birch, two early successional boreal species, decreases under climate warming with the current fire disturbance regime (Fig. 7a). Starting at about 8% of the landscape, the abundance of big-toothed aspen fluctuates through time and reaches about 12% of the landscape under current climate. Under the warmer climate, its abundance slightly decreases (Fig. 7a). Similar to aspen, paper birch shows a decline under warming but at a different

level. Starting at about 12% of the landscape, paper birch abundance decreases significantly for the first 100 years of climate warming. It continues to decrease on the landscape for another 100 years until its abundance approached 0 (Fig. 7a). Without climate warming, paper birch is able to cover $\approx 12\text{--}17\%$ of the landscape at year 400 under the simulated disturbance regime.

There is no decrease of red oak abundance during the warming period. However, its abundance under warmer climate is about 5% less than that simulated for current climate (Fig. 7b). We are not certain whether this drop is due to direct warming impacts on red oak or indirect impacts from other species due to enhanced competition. This can be examined further by running single species on the landscape, which eliminates competition. However, white oak, a southern species, shows very minor presence under the current climate simulation, but increases substantially under warming (Fig. 7b). At year 400, white oak occurs on nearly 10% of the landscape. The invasion of white oak under climate warming involves interactive processes of fire disturbance, seed dispersal, and species competition. As a mid-shade tolerance species, white oak needs fires to create open space by removing the dominant, shade tolerant sugar maple. Fire along with the warming climate make white oak migration north possible. Similar to white oak, other southern species including black oak, bur oak, hickory, and white ash, which are not able to establish well under current climate, are each able to cover more than 10% of the landscape under warming. Sugar maple, the most dominant species, is affected by warming (Fig. 7c). Under current climate, sugar maple stays around 30% of the landscape for most of the simulation (Fig. 7c). However, about a 10% decrease is simulated by year 400. Yellow birch, another late successional species, is able to maintain on nearly 10% of the landscape under current climate (Fig. 7c). With warming climate its abundance declines to a level of less than 3% of the landscape (Fig. 7c).

For conifer species, white pine begins at a low abundance on the landscape due to historical cutting (Mladenoff and Pastor, 1993). White pine is able to reach 12% of the landscape under

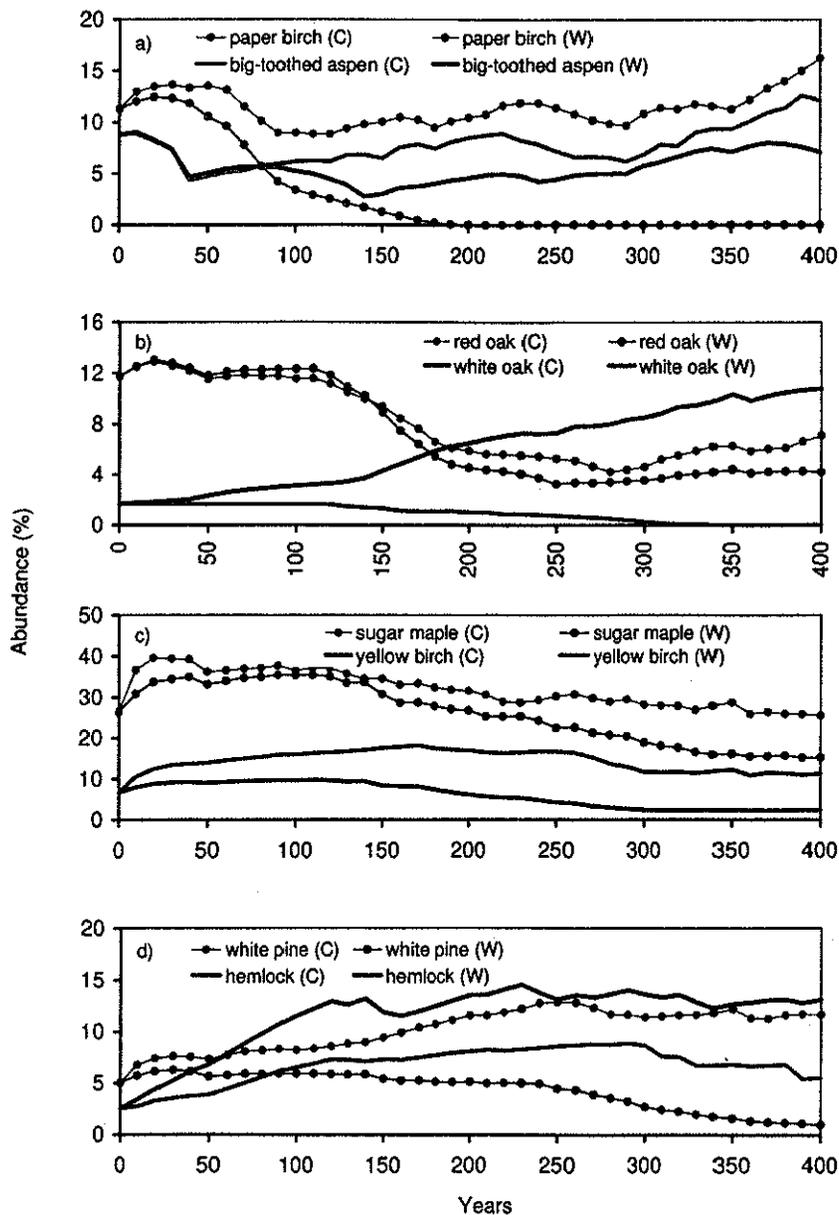


Fig. 7. LANDIS simulated abundance of eight selected species over 400 year under both current climate (c) and warmer climate.

current climate by year 400 (Fig. 7d). Similar to yellow birch, its abundance declines with warming and becomes a minor species by year 400 (Fig. 7d). Eastern hemlock, which also was heavily impacted historically, increases with climate warming by about 10% under warmer climate (Fig. 7d).

4. Discussions

In general, the climate-change scenario results in higher maximum and minimum temperature, and a greater number of growing degree-days. The new values may approach or exceed the maximum thresholds for many boreal species.

This can result in decreasing southern range limits or shifting of these species northward. At the same time, the temperature increase also makes it possible for southern species to establish where minimum temperature and growing degree-days did not meet their minimum requirement under the current climate. This can result in an increase or migration north of the southern species. For many northern hardwood species, 5°C warming is still within their thresholds. Complicated negative feedbacks of temperature and site conditions affect species biomass, resulting in an increase in biomass where soil water is not limiting and nitrogen availability is enhanced, or a decreased biomass where soil water and nitrogen availability become more limiting. This observation is comparable to that found by others (Solomon, 1986; Pastor and Post, 1988). Simulation results of hemlock also suggest that large-scale processes such as species re-colonization can be altered by climate warming.

The significant decreases in biomass were simulated for boreal species with the LINKAGES model under the warming scenario, suggesting the unfavorable environment for the species establishment. However, at landscape scale, with a realistic initial seed source distribution and spatial seed dispersal simulated by LANDIS model, these boreal species persist on the landscape for at least more than 100 years. For example paper birch (Fig. 3f) persists for 200 years on the landscape under the warmer climate. Species with greater longevity, such as white cedar and white spruce, do not disappear from the landscape for at least 300 years. As shown for white pine with 400 years of longevity, the declining process takes much longer than for those boreal species with relatively short longevity.

With the landscape model, species response to climate warming was examined in a spatially explicit manner. The quantitative simulation results for the large study area cannot be achieved otherwise. The abundance information summarized for each species is the interactive result from species succession, competition, disturbance, and variable environments in space and time, as well as the starting spatial distribution of each species. The latter may become less important with an increas-

ing time span. However, it should be pointed out that LANDIS is a semi-quantitative model recording only species age-cohort presence or absence, not individual trees. The exact simulated location of a species at a given year is not deterministic with the stochastic components implemented in seed dispersal, fire disturbance, and the method used for model parameterization [He et al. (in press)]. A particular spatial event should not be considered as a prediction of the model. However, at the ecoregion or entire landscape level, species abundance information generalized from the model simulation has considerable validity as a landscape pattern outcome.

We have presented a modeling framework for evaluating the impact of climate warming on forest species at landscape scales by linking an ecosystem model with a spatial landscape model. These two models, however, were designed to investigate ecological processes that occur at different scales. Explicit and non-explicit assumptions built into the models will affect simulation results. Gap models have been useful over the past two and a half decades in examining interactions between forest species and the environment. Although individual trees are simulated, gap models differ from ecophysiological models (e.g. Keane et al., 1989; Bonan and Sirois, 1992; Prentice et al., 1992; Friend and Shugart, 1993) in the spatial and temporal scales of operation. Mechanisms of species physiological response to environment such as temperature or water measured on the order of days in mechanistic models (e.g. Keane et al., 1989) cannot be directly simulated in gap models, which usually operate at monthly or yearly time steps. Therefore, integration and simplifications of these mechanisms are made as non-explicit assumptions in gap models. As pointed out by others (Fischlin et al., 1995; Bugmann et al., 1996; Loehle and LeBlanc, 1996), since the response function of species growth to temperature in gap models is a parabolic curve, the models predict maximum growth at temperatures found near the north-south midpoint of the geographic range of the species, and the response function of species growth to moisture reflects a linear or curvilinear negative association between tree growth and the number of drought days per

growing season. When temperature approaches the northern or southern range limit of a species, or when drought occurs, minimum growth rates are simulated that can result in the death of the species. Since the range where a species actually grows in presence of competition (the realized niche), instead of the range where a species can grow physiologically (fundamental niche) are used to implement these response functions in gap models, the application of gap model to examination of climate warming can lead to prediction of large forest changes (Loehle and LeBlanc, 1996).

Yet more accurate response functions based on the fundamental niche are not broadly available. To address this concern, others have run gap models with the maximum end of the temperature response function left open, assuming water availability to become the limiting factor [e.g. Urban et al., in press]. In our approach, we used the gap model results from relatively short time periods (year 10). Starting with an adequate amount of biomass, short time simulations de-emphasize the possible dramatic changes that may accumulate through time. On the other hand, long-term changes are simulated with the landscape model, which incorporates the interactions of large-scale ecological processes such as seed dispersal and fire disturbance.

5. Conclusion

It is not our intention here to predict the results of global warming in this abbreviated example. Rather, we present the methodology of linking an ecosystem process model with a spatial landscape model to examine forest landscape response to climate warming. Modeling allows us to examine the consequences under various sets of assumptions; in this study, an annual temperature increase of 5°C for the region. The results from the landscape model reveal the spatial distribution of the species simulated under the examined climate scenario including the effects of spatial processes, and landscape heterogeneity.

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