

A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA

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Abstract

In the coming century, forecast climate changes caused by increasing greenhouse gases may produce dramatic shifts in tree species distributions and the rates at which individual tree species sequester carbon or release carbon back to the atmosphere. The species composition and carbon storage capacity of northern Wisconsin (USA) forests are expected to change significantly as a result. Projected temperature changes are relatively large (up to a 5.8 °C increase in mean annual temperature) and these forests encompass a broad ecotone that may be particularly sensitive to climate change. Our objective was to estimate the combined effects of climate change, common disturbances, and species migrations on regional forests using spatially interactive simulations. Multiple scenarios were simulated for 200 years to estimate aboveground live biomass and tree species composition. We used a spatially interactive forest landscape model (LANDIS-II) that includes individual tree species, biomass accumulation and decomposition, windthrow, harvesting, and seed dispersal. We used data from two global circulation models, the Hadley Climate Centre (version 2) and the Canadian Climate Center (version 1) to generate transient growth and decomposition parameters for 23 species. The two climate change scenarios were compared with a control scenario of continuing current climate conditions. The results demonstrate how important spatially interactive processes will affect the aboveground live biomass and species composition of northern Wisconsin forests. Forest composition, including species richness, is strongly affected by harvesting, windthrow, and climate change, although five northern species (*Abies balsamea*, *Betula papyrifera*, *Picea glauca*, *Pinus banksiana*, *P. resinosa*) are lost in both climate scenarios regardless of disturbance scenario. Changes in aboveground live biomass over time are nonlinear and vary among ecoregions. Aboveground live biomass will be significantly reduced because of species dispersal and migration limitations. The expected shift towards southern oaks and hickory is delayed because of seed dispersal limitations.

Keywords: biomass accumulation, climate change, harvesting, seed dispersal, tree species migration, windthrow, Wisconsin (USA)

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Introduction

Projected changes in global climate because of increasing greenhouse gas concentrations will have significant effects on terrestrial biomes, particularly forests (Saxe *et al.*, 2001). Both local ecosystem processes (Jenkins *et al.*, 2000; Mickler *et al.*, 2002) and broad-scale

processes, including disturbance regimes (Dale *et al.*, 2001; Flannigan *et al.*, 2001; Lenihan *et al.*, 2003) and species dispersal and migration (Davis, 1989; Pitelka *et al.*, 1997; Hansen *et al.*, 2001; Iverson & Prasad, 2001; Walker *et al.*, 2002; Iverson *et al.*, 2005), will be altered by climate change.

Spatially interactive processes (Reiners & Driese, 2001), including seed dispersal and disturbances, may determine the landscape response to climate change.

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Seed dispersal is a critical link between climate change and species distributions. Because of the rapid rate of climate change predicted, seed dispersal may create a significant lag between species' realized and fundamental niches (Davis, 1989). Seed dispersal may also be limited by land-use fragmentation (Pitelka *et al.*, 1997; Iverson *et al.*, 1999, 2005), disturbance (Pitelka *et al.*, 1997), competition, or restrictions to immigration caused by 'emigration delays' (Kirilenko & Solomon, 1998) of pre-existing species (Davis, 1989; Walker *et al.*, 2002). The proposed dispersal lag may limit increases in carbon storage (Smith & Shugart, 1993; Solomon & Kirilenko, 1997) and/or create depauperate forests with fewer species (Solomon & Kirilenko, 1997; Iverson & Prasad, 2001).

The effects of disturbance on biomass, including the loss of biomass because of fire (Flannigan *et al.*, 2001; Korner, 2003b) and harvesting (Schimel *et al.*, 2000), are often as important as changes in productivity caused by climate change (Li *et al.*, 2000; Korner, 2003b). Disturbance may also modify the effects of climate change on tree species composition (He *et al.*, 1998a). To date, most climate change research that has explored the additional consequences of disturbance has focused on fire at continental or regional scales (Lenihan *et al.*, 1998; Flannigan *et al.*, 2001; Lenihan *et al.*, 2003).

Because of these climatically driven changes in forest dynamics the species composition and carbon storage capacity of northern Wisconsin forests will likely change significantly (He *et al.*, 1998a; Walker *et al.*, 2002). Estimated temperature changes are relatively large (3.8–5.8 °C) for northern Wisconsin (Kittel *et al.*, 2001) and these forests encompass a broad ecotone that may be particularly sensitive to climate change (Hansen & di Castri, 1992; Loehle, 2000).

Understanding the processes that affect aboveground live biomass will be critical if future management goals include carbon sequestration. At a fine scale (0.1 ha), Pastor & Post (1988) estimated that climate change would reduce aboveground biomass by 44–96% in northern Wisconsin, dependent upon soil water-holding capacity. A very coarse continental-scale estimate of aboveground biomass after climate change found either an increase (1–25%) or both increases and decreases (–50% to +50%) for northern Wisconsin, dependent upon the global circulation model (GCM) data, soils, and major vegetation type (Aber *et al.*, 2001; Bachelet *et al.*, 2001). These and other regional projections assume that seeds for all species are universally available. Others have assumed that increased productivity will necessarily result in increased aboveground biomass without considering disturbance, migration, or succession (Mickler *et al.*, 2002).

The Mapped Atmosphere–Plant–Soil System model of vegetation types ('biomes') (Neilson, 1995) found a shift from 'conifer' forest toward the 'north-east mixed' forest in northern Wisconsin under two GCM climate scenarios (Bachelet *et al.*, 2001). However, such continental-scale biogeographical models do not consider initial conditions (northern Wisconsin is not currently dominated by conifer species) or the compounding effects of seed dispersal limitations, individual species response to disturbance, or harvesting (Bachelet *et al.*, 2001; Cramer *et al.*, 2001).

Based on changes in species' fundamental niches across North America, the DISTRIB statistical model found a shift toward oak-hickory forests in northern Wisconsin in four of five scenarios of climate change (Iverson & Prasad, 2001). These results and results from paleoecological data from the Holocene warming (Davis, 1981; Webb, 1981) demonstrate that existing aggregations of species ('communities') probably will not survive climate change intact (Aber *et al.*, 2001). In addition, many important species, particularly northern pines (*Pinus* spp.) and spruces (*Picea* spp.), may be extirpated from the area because of climate change (Walker *et al.*, 2002). Tree species richness in northern Wisconsin may also decline (Iverson & Prasad, 2001).

Evaluating climate change effects on forest ecosystems requires a comprehensive approach that includes shifts in species distributions, disturbance, changes in ecosystem process rates, and the interactions between these processes (Turner *et al.*, 1995; Loehle & LeBlanc, 1996; Tilman, 1998; Aber *et al.*, 2001). Our objective was to examine the regional interactions among climate change, species composition, disturbance, seed dispersal, and ecosystem processes on tree species composition and aboveground live biomass in the forests of northwestern Wisconsin (USA).

Before European settlement (ca. late 1800s), the principal disturbance agents in northern Wisconsin were wind-throw across the region and fire that was locally important (Schulte & Mladenoff, 2005). Fire increased and became more widespread during the logging and postlogging period (mid-1800s–1930s) (Curtis, 1959). However, because of fire suppression since the mid-20th century (Cardille *et al.*, 2001), the principal disturbance agent in the Great Lakes forests today is harvesting (Mladenoff & Pastor, 1993). Therefore, we excluded fire from our simulations.

We used a forest landscape simulation model, LANDIS-II, to simulate multiple spatially interactive processes (processes that spread and are dependent upon location and landscape configuration), including wind, harvesting, climate, and seed dispersal (Scheller & Mladenoff, 2004). Other important drivers of ecological change that were not considered include deer

browsing, land-use change, ozone (Ollinger *et al.*, 2002), climate-caused changes in storm frequency (Dale *et al.*, 2001) or changes in harvest rate (Dale *et al.*, 2001). However, by focusing on a limited set of parameters, we were able to isolate the potential effects of the processes of interest: climate change, wind and harvesting disturbance, and species migration.

Our analysis focused on two integrating properties of forests: species composition and aboveground live biomass. Specific research questions included: Under projected climate change scenarios, do seed dispersal and limits to migration affect aboveground live biomass? Will disturbance (harvesting and wind) modify the effects of seed dispersal limitations? How will disturbance and climate change interact and alter forest tree species composition and aboveground live biomass?

Methods

Study area

Our study landscape (~1.5 million ha) currently contains mesic northern hardwood forests, pine barrens, and some boreal forest species (Fig. 1). The area is

dominated by second-growth forest resulting from heavy logging in the late 19th and early 20th centuries and logging continues to be the dominant disturbance throughout our study area (Curtis, 1959; Mladenoff & Pastor, 1993). We simulated 23 common upland tree species (Table 1). A significant portion of the landscape is wetlands, water, or otherwise nonforested. These nonforested areas are important features as they may limit seed dispersal and (or) disturbance. Fragmentation is caused primarily by human land use, largely agriculture.

The climate is continental with cold winters (mean January temperature -12.5°C) and mild summers (mean July temperature 20.0°C). Precipitation is fairly evenly distributed throughout the year and averages 90 cm annually. Soils vary from sandy outwash plains, clayey areas bordering Lake Superior that were former glacial lake bed, and silty or loamy upland forests (STATSGO, 1994). Available soil water-holding capacity (1 m depth), averaged over entire ecoregions, ranges from 8 to 14 cm (Table 2).

LANDIS-II description

We used a spatially explicit and interactive landscape simulation model, LANDIS-II that includes a succession module that simulates growth, decomposition, and biomass accumulation (Scheller & Mladenoff, 2004). LANDIS-II is an extension of LANDIS, which has been extensively tested and applied in northern Wisconsin forests (He & Mladenoff, 1999; Gustafson *et al.*, 2000; Mladenoff, 2004). LANDIS-II can simulate wind, harvesting, and fire. LANDIS-II is composed of a grid of interacting cells, similar to a cellular automaton model. Each grid cell exists within an ecoregion with homogeneous soil and climate properties. All cells can contain multiple species-age cohorts with associated age and aboveground biomass data. Each cohort can be independently killed as a consequence of disturbance or age-related mortality.

Cohort establishment following a reproduction event (seed dispersal, planting, or resprouting) depends on light availability (Scheller & Mladenoff, 2004) and a species establishment probability dependent upon soil and climate (Scheller *et al.*, 2005). The establishment probability was calculated at 10-year intervals. Each species establishment probability varies spatially because of differences in soil properties and temporally because of changing climate (Scheller *et al.*, 2005). LANDIS-II does not currently have a dynamic soils compartment. However, because species establishment probabilities are calculated using a gap model with dynamic soil pools these probabilities reflect climatic changes in soil carbon and nitrogen not directly modeled within LANDIS-II.

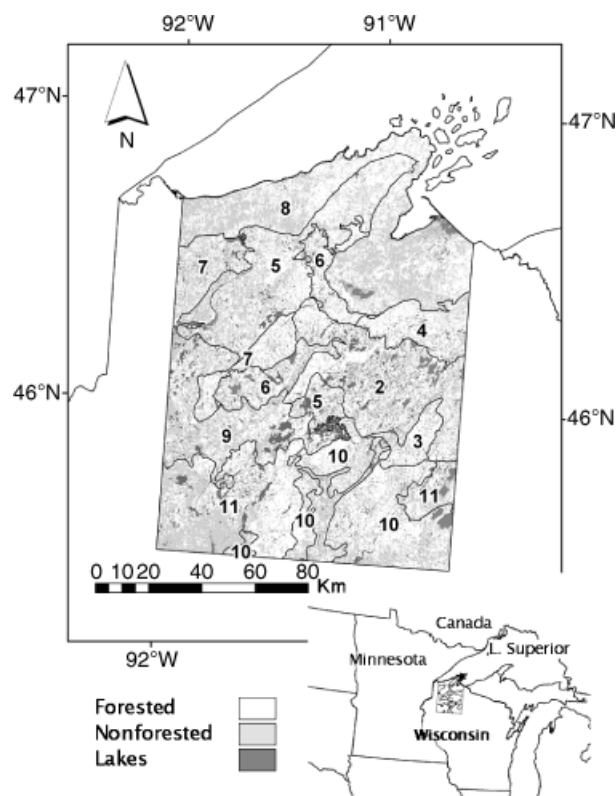


Fig. 1 Study area with 10 ecoregions.

Table 1 Input data for 23 species typical of northern Wisconsin upland forests

Species	Foliar nitrogen (%)	Maximum LMA (g m^{-2})	Leaf retention (years)	Maximum age (years)	Age of maturity (years)	Shade tolerance (no units)	Maximum seed dispersal (m)	Maximum number of growing degree days*
<i>Abies balsamea</i>	1.6	204	4.0	150	25	5	160	2386
<i>Acer rubrum</i>	2.4	75	1.0	150	10	3	200	6600
<i>Acer saccharum</i>	2.5	85	1.0	300	40	5	200	3200
<i>Betula alleghaniensis</i>	2.4	66	1.0	300	40	4	400	2500
<i>Betula papyrifera</i>	2.3	100	1.0	120	30	2	5000	2036
<i>Carya cordiformis</i>	2.3 [†]	111 [†]	1.0	300	30	4	1000	5076
<i>Fraxinus americana</i>	2.1	76	1.0	200	30	4	140	5993
<i>Picea glauca</i>	1.5	286	4.0	200	25	3	200	1911
<i>Pinus banksiana</i>	1.6	244	2.3	70	15	1	60	2216
<i>Pinus resinosa</i>	1.5	250	2.3	250	35	2	275	2035
<i>Pinus strobus</i>	2.2	175	3.0	400	15	3	250	3165
<i>Populus grandidentata</i>	2.5	80	1.0	90	20	1	5000	3169
<i>Populus tremuloides</i>	2.5	83	1.0	90	15	1	5000	2900
<i>Prunus pensylvanica</i>	2.9	53	1.0	30	10	1	3000	2500
<i>Prunus serotina</i>	2.7	101	1.0	200	20	3	3000	5993
<i>Quercus alba</i>	2.5	88	1.0	400	40	3	1000	5537
<i>Quercus ellipsoidalis</i>	2.3	54	1.0	200	35	2	1000	2234
<i>Quercus macrocarpa</i>	2.3	88	1.0	300	30	2	1000	5153
<i>Quercus rubra</i>	2.5	79	1.0	250	25	3	1000	3471
<i>Quercus velutina</i>	2.4 [†]	98 [†]	1.0	300	30	2	1000	5076
<i>Thuja occidentalis</i>	1.3	222	2.0	350	30	2	60	2188
<i>Tilia americana</i>	2.8	46	1.0	250	15	4	120	3137
<i>Tsuga canadensis</i>	1.2	170	3.0	450	60	5	100	3800

All other values from Scheller & Mladenoff (2004), unless otherwise noted.

*Data from Pastor & Post (1986) and Bolster *et al.* (1996).

[†]Data from Fownes (1985).

Table 2 Ecoregion soil parameters for PnET-II input

Ecoregion	Field capacity (cm m^{-1})	Wilting point (cm m^{-1})
2	21.2	9.6
3	24.9	10.7
4	20.9	10.1
5	15.5	7.5
6	17.9	8.5
7	20.2	10.2
8	34.7	22.2
9	14.5	6.7
10	24.9	10.6
11	20.4	9.2

The succession module with biomass simulates cohort growth, competition, mortality, and dead biomass decay. Four biomass pools are calculated: live wood and foliage for each cohort and dead wood and litter for each cell. The biomass module requires maximum aboveground net primary productivity

(ANPP) input data to calculate aboveground live biomass accumulation (Scheller & Mladenoff, 2004). Maximum ANPP varied dependent upon soils, climate (including transient climate change), and individual species data. Actual ANPP varied dependent upon cohort age and competition (Scheller & Mladenoff, 2004).

Model initialization

We divided our study area into 10 ecoregions (Host *et al.*, 1996) that are based on relatively homogeneous soils and climate within each (Fig. 1, Table 2). An initial vegetation map, including species and age information, was derived from a satellite forest classification (Wolter *et al.*, 1995) and Forest Inventory and Analysis data (He *et al.*, 1998b). The satellite classification also delineated nonforested areas that resulted from historic land-use change. Nonforested areas remained nonforested during model execution. Simulation resolution was 200 m (4 ha).

In order to simulate harvesting across the landscape, it was necessary to define harvest stand boundaries. We were limited to 65 000 stands as input because of the 16-bit input files. Our method for parsing the landscape began with the original satellite classification data (Wolter *et al.*, 1995). First, individual 30 m \times 30 m pixels from the satellite data were filtered and clumped into polygons using a 3 \times 3 majority filter. The data were then intersected with TIGER road, rivers, and railroad data (US Census Bureau, 2002) to further divide the data into logical parcels. Lastly, the data were aggregated to the simulation resolution and synchronized with the land type boundaries used to divide the total landscape into homogeneous ecoregions. This procedure produced 52 188 individual stands. The mean size of stands eligible for harvesting was 24 ha, the median was 8 ha.

Experimental design

We simulated forest change across northwestern Wisconsin using three climate scenarios and two disturbance scenarios. The three climate scenarios included two GCMs projections and a continuation of current climate conditions (no climate change). Our original experimental design treated wind as a separate factor. However, preliminary model runs indicated that wind alone was not sufficiently different from our control (no disturbance) scenario to merit further analysis. Therefore, only two disturbance scenarios were included in the final analysis: (1) no disturbance; and (2) harvesting and wind combined. All scenarios were simulated at 10-year time steps over 200 years.

Wind was parameterized to approximate historic rotation periods, where heavy windthrow (>62% canopy removal, based on the median density of trees removed) had a rotation period of approximately 1300 years (Schulte & Mladenoff, 2005), without harvesting. Rotation periods were designated for the entire landscape; individual disturbances occurred stochastically. Our model also simulated light or medium (<62% canopy removal) windthrow. The total wind regime, including light or medium windthrow, had a rotation period of approximately 200 years.

Harvesting was parameterized using a combination of clearcuts, heavy thinning, and selective cutting (Gustafson *et al.*, 2000). The same harvesting prescription was applied to all ecoregions and all climate scenarios although implementation of a harvesting prescription is dependent upon the availability of the target species and ages. Clear-cutting removed all cohorts, preferentially occurred on sites dominated by shade-intolerant species (e.g. *Populus* spp., *Pinus banksiana*), and harvested up to 5% of all harvest stands in

each ecoregion at each decade. Heavy thinning removed all cohorts older than an approximate merchantable age, preferentially occurred on sites dominated by mid-successional species (e.g. *Pinus* spp., *Quercus* spp.), and harvested up to 5% of all harvest stands in each ecoregion at each decade. Selective harvesting preferentially harvested late-successional stands (dominated by very shade-tolerant species). Selective harvesting removed one-fourth of all mid- or late-successional cohorts (randomly selected by age) and occurred on up to 10% of all stands in each ecoregion at each decade. We assumed that harvesting removed all of the bole wood, 50% of branch biomass (10% of the total, Jenkins *et al.*, 2003), and left all foliage on site.

We used a seed dispersal probability distribution that follows a negative exponential curve for both the effective and maximum seeding distances with 95% of the distribution assigned to the effective distance (Ward, 2004). The algorithm approximates leptokurtotic distributions (Clark *et al.*, 1998) and is robust to changes in grid cell size (Ward, 2004). The effect of seed dispersal and species migration was tested by simulating two alternate seed dispersal assumptions. The first assumption was that migration was limited by the maximum seed dispersal distance as derived from the literature (He & Mladenoff, 1999). Therefore, distance to favorable sites, landscape configuration, and fragmentation limit species movement in these scenarios, along with the normal successional processes (e.g. shade exclusion). LANDIS-II incorporates all these processes when species migration is limited by species dispersal. The alternate assumption was that the seeds of all species were universally available, i.e. there were no limitations to seed dispersal and species migration except for successional processes and the ability to establish given climatic conditions and soils.

Several other assumptions were made in all of our scenarios. We assumed that all soil properties remained constant across time, including water-holding capacity and carbon content. Currently, LANDIS-II does not include a dynamic soil compartment. We also assumed that there was no CO₂ fertilization effect on aboveground productivity. A consistent or sustained productivity increase in response to increased CO₂ has not been demonstrated (Calfapietra *et al.*, 2003; Korner, 2003a) and modeling productivity with CO₂ fertilization across large landscapes awaits further ecosystem model developments (Karnosky, 2003).

GCMs

For our control scenario (no climate change), temperature and precipitation data were compiled from 30-year

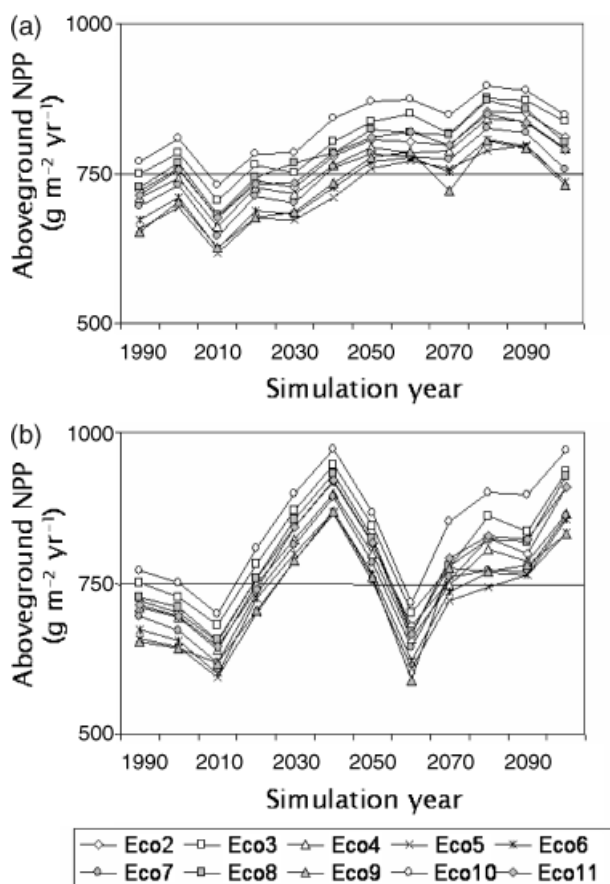


Fig. 2 Estimated mean aboveground net primary productivity (NPP) calculated from a modified version of PnET-II from 1990 to 2100. For each 10-year average, species with establishment coefficients = 0 were assumed to stop accruing biomass and are excluded. (a) Climate projections from the Hadley Climate Centre (v. 1) global circulation model (GCM). (b) Climate projections from the Canadian Climate Centre (v.2) GCM. 1990 values calculated from the 30-year climate means, 1960–1990.

(1960–1990) averages (ZedX, 1995). Current day surface solar irradiance (SSI) was set equal to the 1991 values (NASA Langley Atmospheric Sciences Data Center, 2000).

Data from two ocean–atmosphere GCMs were used in our climate change scenarios: the Canadian Climate Centre (CCC) model v.1 (Flato *et al.*, 2000) and the Hadley Climate Centre (HAD) model v.2 (Johns *et al.*, 1997). Both models predict transient changes in maximum temperature, minimum temperature, precipitation, and mean daily irradiance from current day conditions to 2100. The GCMs both use IPCC projections of a ‘business as usual’ build-up of CO₂ (IS92a), reaching 712 ppm at year 2190 (Intergovernmental Panel on Climate Change, 2001) and incorporate the effects of sulphate aerosols. GCM data were obtained from the VEMAP phase two transient climate dataset

(Kittel *et al.*, 2001). The data are available as a gridded dataset with a 0.5° latitude and longitude resolution. The Hadley GCM predicted a 3.8 °C increase in mean annual temperature and a 38 cm increase in annual precipitation at year 2100, from the 30-year averages, averaged across our study area. The Canadian GCM predicted a 5.8 °C increase in mean annual temperature and a 20 cm increase in annual precipitation at year 2100.

For the climate change scenarios, we began with current climate for year 1990 and used a 10-year mean of the VEMAP data (consistent with our 10-year time steps) for each subsequent decade (e.g. year 2100 climate was estimated as the mean of years 2006–2015) from year 2000 to 2100. Both temperature data and SSI were calculated as the predicted change from year 2000 (the first climate change year) plus the current day climate values. Using the change in temperature and SSI eliminated GCM projection errors for current day climate (Jenkins *et al.*, 2000). For simulation years after 2100, we used the mean climate data from the 10-year average for 2100. Therefore, our estimates after 2100 are conservative, in that most greenhouse gas emission scenarios predict that CO₂ will continue to rise after 2100 (Intergovernmental Panel on Climate Change, 2001). However, this does increase the uncertainty in our model estimates beyond the first 100 years.

The species establishment probabilities were estimated for every 10-year interval prior to model execution using these climate data, initial soils data from STATSGO (STATSGO, 1994), and the LINKAGES gap model (Pastor & Post, 1986) for each of the 10 ecoregions (He *et al.*, 1998a; Scheller *et al.*, 2005). We used LINKAGES because it incorporates species climatic tolerances (Table 1) when calculating growth and hence, establishment probability. Soil water-holding capacity and input carbon and nitrogen values were held constant throughout our simulations. However, the initial forest floor was generated iteratively using the 10-year climate averages and the leaf litter of that species (Pastor & Post, 1986).

GCM climate data were also used to calculate maximum ANPP for each species and ecoregion combination, a required model input parameter. A generalized ecosystem process model, PnET-II (Aber *et al.*, 1995), was used to estimate maximum ANPP (estimated from wood and foliage NPP) for every 10-year interval for every species taking into account ecoregional differences in soils. PnET-II was modified to more explicitly model the effects of leaf mass area on photosynthesis (Scheller & Mladenoff, 2004) and validated against empirical data from northern Wisconsin (Fassnacht & Gower, 1997; Scheller & Mladenoff,

2004). PnET-II requires only one soil parameter, soil water-holding capacity, that varied between ecoregions but was held constant over time. Maximum ANPP generally increased over time, although there was large variation between decades (Fig. 2). Estimates of ANPP highlight the differences because of soils where ecoregions 5 and 9 had the lowest soil water-holding capacity and ecoregion 10 the highest (Fig. 2).

Data analysis

Multiple model runs with unique random number sequences ('replications') are often used to assess model uncertainty. However, replications may not be useful for estimating differences among scenarios if the inherent or stochastic variability is low. Also, the use of replication to assess differences can be biased by increasing the number of replications and subsequently shrinking the standard error of the results. To assess stochastic variation, we replicated one scenario four times. At the scale of the total landscape, the mean aboveground live biomass of the four replications had a standard error of less than 1 Mg ha^{-1} , averaged across all decades and therefore replication did not appear to provide a good estimate of significant differences among scenarios. As an alternative, we regressed aboveground live biomass (Mg ha^{-1}) against climate using a mixed model in SAS (Littell *et al.*, 1999). Climate scenarios were compared separately for each disturbance scenario. An autoregressive (order one) and an unstructured covariance structure were modeled with decadal biomass as the sampling unit (Littell *et al.*, 1999). Because of the small sample size (< 50), a robust standard error (Huber-White) was used (Littell *et al.*, 1999; Maas & Hox, 2004). The statistical model with the lowest Bayesian Information Criterion was subsequently used to test for differences among scenarios. An *F*-test was conducted to estimate differences (Tukey's, $\alpha = 0.05$) among adjusted biomass means for each climate scenario (Littell *et al.*, 1999).

Differences in forest composition among scenarios and across time (initial conditions and year 2190) was evaluated using nonmetric multidimensional scaling with relative Sørensen's distance metric (McCune & Mefford, 1999). A species by ecoregion matrix was created for each climate and disturbance scenario at two time points: initial conditions and at year 2190. The species by ecoregion matrix consisted of the aboveground live biomass for each tree species, averaged by ecoregion. One ordination was conducted using all six scenarios and both time periods. Nonforested sites were excluded. Each ecoregion represents a single community. Communities close together in ordination space have relatively equal (as defined by Sørensen's

distance metric (McCune & Mefford, 1999)) distributions of species biomass. Conversely, two species close together in ordination space have a relatively equal distribution of aboveground live biomass values across communities. Although two species may have relatively equivalent biomass distributions across communities, e.g. higher or lower biomass in the same communities, the absolute biomass values may differ substantially between the two species.

We calculated the combined effect of seed dispersal limitations and climate change by subtracting the landscape mean aboveground biomass with seed dispersal limitations from the aboveground biomass without seed limitations (the 'seed dispersal difference') for the control (no climate change) scenario and the two climate change scenarios. We then subtracted the control scenario seed dispersal difference from the seed dispersal difference for each of our climate change scenarios. The final outcome represents the potential loss of aboveground biomass because of the inability of species to migrate rapidly to their optimal spatial distribution. Communities generated under the universal seed assumption were not ordinated as these simulations were only intended to test a single hypothesis and should not be confused with our other scenarios that represent potential communities.

Results

Aboveground live biomass

Spatial heterogeneity because of harvesting and wind is apparent from maps of initial aboveground live biomass and biomass at year 2190 (Fig. 3). Our initial landscape under-represents landscape heterogeneity because of the random assignment of community types within each ecoregion, i.e. disturbances were not clustered when the age classes were initially assigned (He *et al.*, 1998b).

Regardless of whether harvesting and wind were simulated, climate changes significantly increased aboveground live biomass for both the Hadley and Canadian climate change scenarios (Fig. 4). All scenarios were significantly different either with or without disturbance ($P < 0.001$). With our simulated disturbances, aboveground biomass initially decreases in the first 20 years (Fig. 4b). Both harvesting and wind reduced aboveground biomass (Fig. 5), although harvesting removed greater than three times as much biomass.

A comparison of mean aboveground live biomass at the beginning and the conclusion of our simulations demonstrates which species exhibited the greatest change over time. Five northern species were extirpated

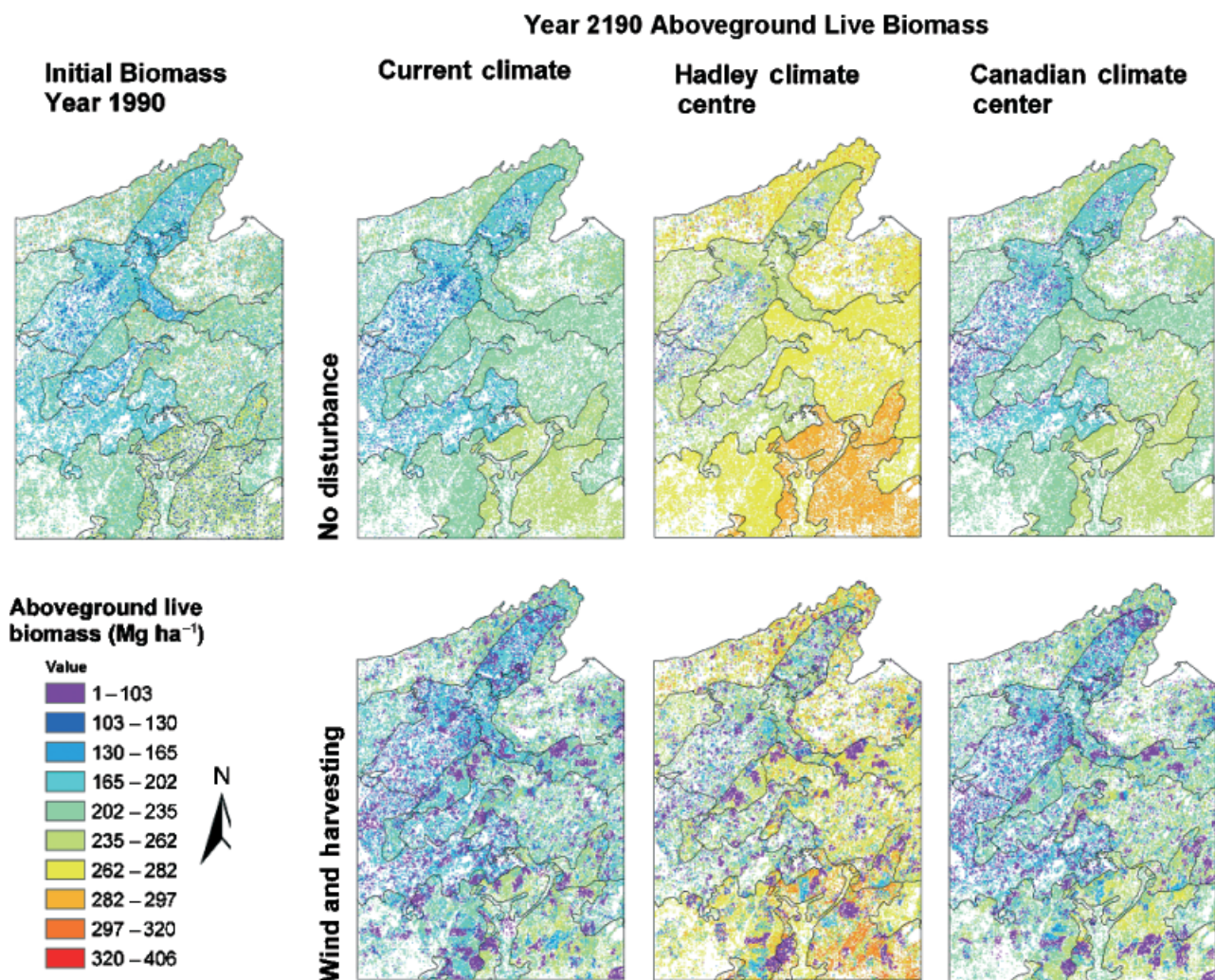


Fig. 3 Maps of aboveground live biomass at year 1990 and from three climate scenarios at year 2190 (30-year climate average, Hadley Climate Centre, Canadian Climate Centre) and two disturbance scenarios (no disturbance and simulated wind and harvesting).

from the landscape (mean aboveground biomass at or near zero for every ecoregion) during both climate change scenarios and regardless of disturbance scenario because of low or near zero species establishment coefficients: balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), white spruce (*Picea glauca*), jack pine (*P. banksiana*), and red pine (*P. resinosa*) (Table 3). Pin cherry (*Prunus pensylvanica*) was extirpated under all scenarios and was excluded from further analysis.

Without disturbance, sugar maple (*Acer saccharum*), a very shade-tolerant and widely dispersed species, gained the most biomass, dependent upon climate scenario (52, 150, and 115 Mg ha^{-1} for the control, Hadley, and Canadian climate scenarios, respectively). Balsam fir gained biomass (50 Mg ha^{-1}) only when climate was held constant. Eastern hemlock (*Tsuga canadensis*) had large biomass gains ($12\text{--}14 \text{ Mg ha}^{-1}$)

only within the climate change scenarios without disturbance (Table 3). Not including the extirpated species, aspen (*Populus* spp. combined) biomass declined the most ($34\text{--}36 \text{ Mg ha}^{-1}$) without disturbance, followed by red maple (*A. rubrum*) and red oak (*Q. rubrum*) (Table 3). With harvesting and wind, basswood (*Tilia americana*) gained biomass under all climate scenarios. With disturbance, biomass gains or losses were more evenly distributed across species at the end of our simulations (Table 3).

Forest composition

Our ordination of tree species biomass in ecoregion space generated two axes. Axis one explained 69.0% of the total variance in the community data, axis two explained 13.8% of the total variance (Fig. 6).

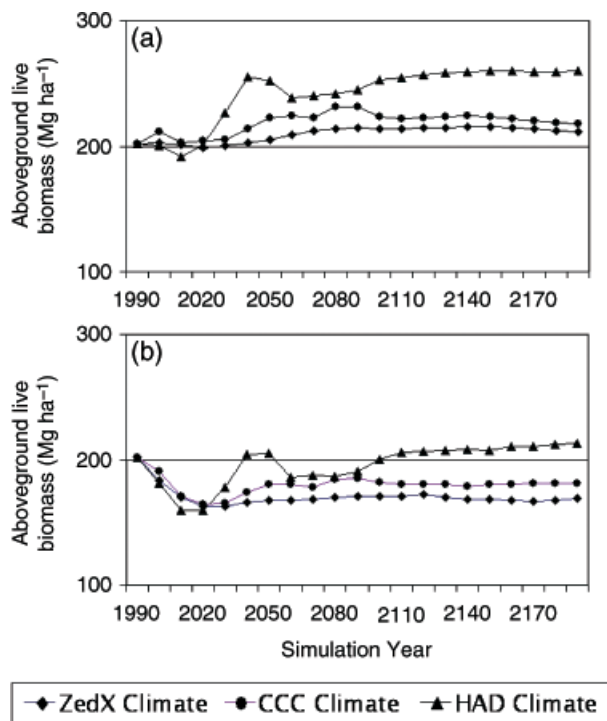


Fig. 4 Total landscape mean aboveground live biomass estimates from three climate scenarios (30-year climate average, Hadley Climate Centre (HAD), Canadian Climate Centre (CCC)). (a) Aboveground live biomass from scenarios without disturbance. (b) Aboveground live biomass from scenarios with simulated wind and harvesting. Nonforested sites excluded from calculations.

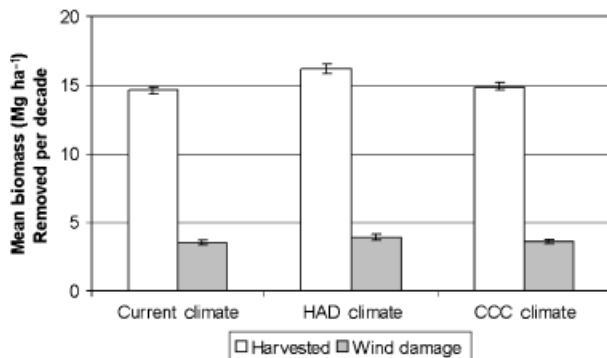


Fig. 5 Mean aboveground biomass killed because of either simulated harvesting or wind for three climate scenarios (30-year climate average, Hadley Climate Centre (HAD), Canadian Climate Centre (CCC)).

The position of communities in ordination space reflected the distribution of species biomass (Fig. 6a). In the control climate scenario with disturbance, communities generally have lower second axis scores than the initial communities (Fig. 6a), suggesting that axis two is disturbance controlled. Communities in the

control climate scenario with disturbance shifted the least over the course of the simulation and ecoregions became more similar than were the initial ecoregions, notably ecoregions 6 and 11 (Fig. 6a). The control climate scenario without disturbance was associated with typical shade-tolerant species, including sugar maple, eastern hemlock, balsam fir, and yellow birch (*B. alleghaniensis*).

The two climate change scenarios, with and without disturbance, resulted in communities with higher axis one values and variable increases in axis two values. This represents an increase in biomass of more southern species, bitternut hickory (*Carya cordiformis*), bur oak (*Q. macrocarpa*), white oak (*Q. alba*), and black cherry (*P. serotina*) (Fig. 6b). However, with climate change and disturbance, axis one values were reduced and axis two scores increased, indicating a shift away from the most shade-tolerant species (Fig. 6b).

The position of species along axis one was associated with climate tolerance (Fig. 6b). The northern pines (jack pine and red pine), paper birch and other associated northern species had lower axis one scores. Species that increased with climate change had higher axis one scores (Fig. 6b). The second axis was associated with shade tolerance, with more shade-tolerant species having lower axis two scores.

The mean number of species lost per ecoregion was significantly larger when disturbance was excluded compared with scenarios with disturbance for the control and the Hadley climate scenarios (Fig. 7). The mean number of species lost per ecoregion was highest for the two Canadian climate scenarios. The number of species lost was lowest (0.3 species per ecoregion) under the scenario with disturbance and current climate. For a given climate scenario, the mean number of species gained per ecoregion was greater when disturbance was included, although the differences were not significant (Fig. 7). The Canadian climate scenarios resulted in a net loss of species with or without disturbance (1.5 and 2.3 species per ecoregion, respectively).

Seed dispersal limitations

Without disturbance, aboveground live biomass increased by up to 9.1 Mg ha^{-1} if seed availability was unlimited (Fig. 8a). The effect of seed dispersal limitations peaked near year 2060, after which time the seed dispersal effect declined for the Hadley climate and held constant near 5 Mg ha^{-1} for the Canadian scenario. Because the absence of disturbance generally excluded less shade-tolerant species (Fig. 6), including the more southern oaks, the difference in biomass is

Table 3 Changes in aboveground live biomass (Mg ha^{-1}) between years 1990 and 2190 for 17 species as simulated by LANDIS-II under three different climate scenarios and two disturbance scenarios

Species	No disturbance			Wind and harvesting		
	Current climate	HAD	CCC	Current climate	HAD	CCC
<i>Abies balsamea</i>	49.8	-15.6	-15.8	6.3	-15.7	-15.8
<i>Acer rubrum</i>	-15.7	-15.5	-14.8	-7.5	-6.9	-7.1
<i>Acer saccharum</i>	52.3	149.8	115.0	-4.0	38.2	21.7
<i>Betula alleghaniensis</i>	-1.4	1.5	-6.5	1.3	4.1	-8.7
<i>Betula papyrifera</i>	-8.0	-10.5	-10.5	4.3	-10.5	-10.5
<i>Carya cordiformis</i>	-0.1	0.2	0.7	-0.1	3.0	4.0
<i>Fraxinus americana</i>	-4.3	-3.2	-3.0	-4.2	-0.9	-0.3
<i>Pinus banksiana</i>	-5.5	-5.5	-5.5	-2.9	-5.5	-5.5
<i>Pinus resinosa</i>	-1.8	-2.5	-2.5	-0.8	-2.5	-2.5
<i>Populus grandidentata</i>	-9.9	-9.6	-8.6	2.9	3.8	4.3
<i>Populus tremuloides</i>	-25.5	-25.2	-25.2	-13.3	-12.0	-16.6
<i>Prunus serotina</i>	-1.5	-1.2	-0.9	0.6	5.7	5.0
<i>Quercus alba</i>	-0.4	0.4	0.7	-0.9	1.7	2.4
<i>Quercus macrocarpa</i>	0.6	2.6	3.1	0.7	3.5	3.4
<i>Quercus rubra</i>	-14.4	-12.5	-13.7	-13.6	-8.7	-9.1
<i>Tilia americana</i>	0.5	-4.9	-2.5	5.8	18.6	20.7
<i>Tsuga canadensis</i>	1.5	13.8	12.4	-0.9	2.2	1.9

HAD, Hadley Climate Centre; CCC, Canadian Climate Centre.

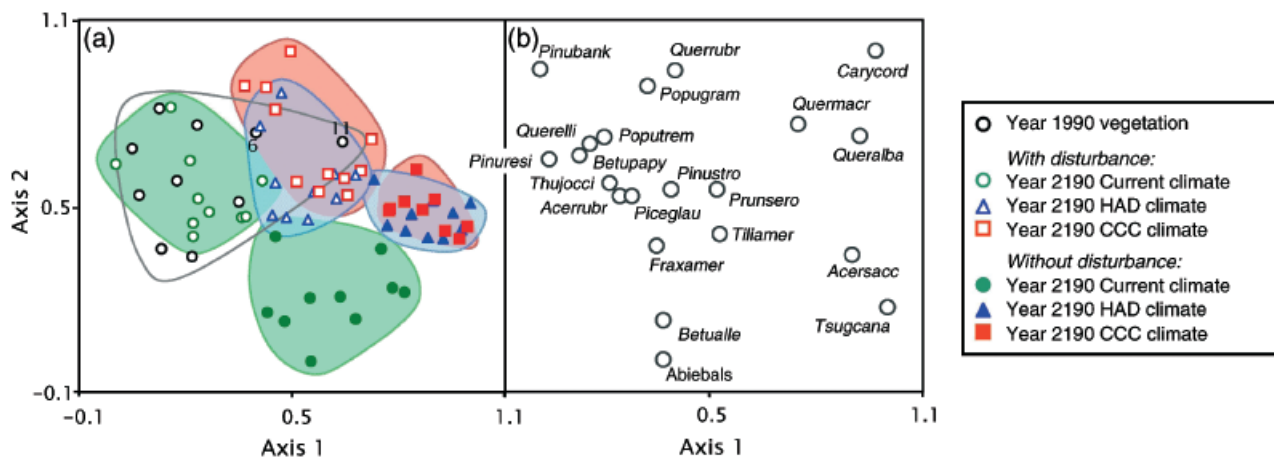


Fig. 6 Nonmetric dimensional scaling ordination of community aboveground biomass data. Communities were ordinated using and Sorenson's dissimilarity measure. (a) Distribution of 10 ecoregions at years 1990 and 2190. The range of communities at year 1990 is approximated with a clear irregular ellipse. Colored ellipses approximate the community range of each climate scenario at year 2190. (b) Distribution of 22 tree species in ordination space. Distance indicates dissimilarity between relative biomass distribution across ecoregions. Species codes are derived from the first four letters of the generic name plus the first four letters of the specific name (Table 1). Data were drawn from three climate scenarios (30-year climate average, Hadley Climate Centre (HAD) (v.1), Canadian Climate Centre (CCC) (v.2)) and two disturbance scenarios (no disturbance and both wind and harvesting). Axes are unit less.

due primarily to the expansion of the spatial distribution of eastern hemlock.

In scenarios with wind and harvesting, aboveground biomass generally increased more than scenarios without disturbance if seed availability was unlimited and declined after year 2090 (Fig. 8). We decomposed

the effect of seed dispersal limitations by species at year 2190 for the climate change scenarios with disturbance (Fig. 9). The largest increases in aboveground biomass when seed dispersal was unlimited were because of bitternut hickory. An increase in hemlock aboveground biomass contributed the second most biomass. Other

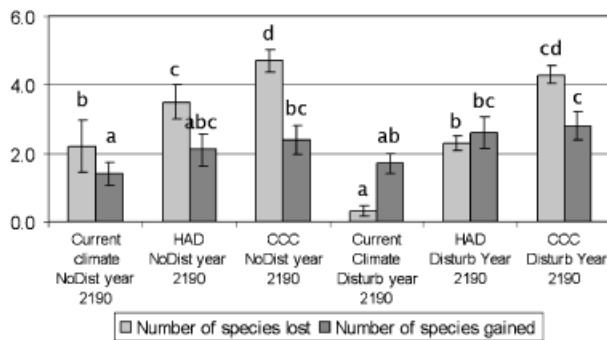


Fig. 7 The number of species lost or gained (out of 22 species total) averaged across 10 ecoregions; the error bar represents \pm one standard error, $N = 10$. Model output at year 2190 for three climate scenarios (current climate, 30 years mean climate; HAD, Hadley Climate Centre GCM; CCC, Canadian Climate Centre GCM; GCM, global circulation model) and two disturbance scenarios (NoDist, no disturbance; Disturb, wind and harvesting simulated). Different letters indicate significant differences ($\alpha = 0.10$) among scenarios in the number of species lost or gained.

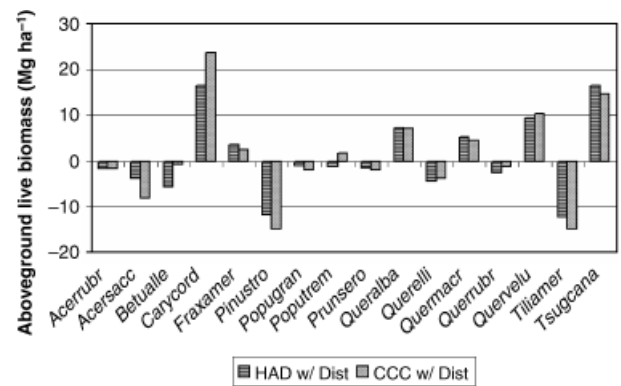


Fig. 9 The difference between scenarios with unlimited seed dispersal and scenarios with limited seed dispersal at year 2190 for 16 species and two climate scenarios, Hadley Climate Centre (HAD), Canadian Climate Centre (CCC). Only the scenarios with disturbance are depicted. Species codes are derived from the first four letters of the generic name plus the first four letters of the specific name (Table 1).

more southern species, including white ash (*Fraxinus americana*), black oak (*Q. velutina*), white oak, and bur oak also contributed to seed dispersal limitations. Some species decreased in biomass when seed dispersal was unlimited, including sugar maple, yellow birch, white pine, and basswood (Fig. 9).

Discussion

Our simulations project that climate change may significantly increase aboveground live biomass (carbon storage capacity), dependent upon the projected climate scenario. Given the assumptions made for our model, the climate scenarios without harvesting and wind may be regarded as the maximum possible carbon storage for a given climate scenario. Our simulations without disturbance indicate a potential increase in aboveground live biomass from 5% to 29% (the CCC and HAD climate projections, respectively, at year 2190). Our simulation results are difficult to compare with other models that simulated biomass change without explicitly considering landscape interactions, simulated biomass change at different scales (Pastor & Post, 1988; Aber *et al.*, 2001) and (or) used different GCMs (Pastor & Post, 1988).

Simulated aboveground live biomass exhibited limited sensitivity to temporal variation in ANPP. Particularly under the Hadley climate scenario, the decadal variation in ANPP (Fig. 3) did not produce equally large variation in aboveground live biomass (Fig. 4). Given that biomass is regulated by many processes, including dispersal, establishment, competition, and mortality, this result was not unexpected. Simulated aboveground live biomass initially decreases with

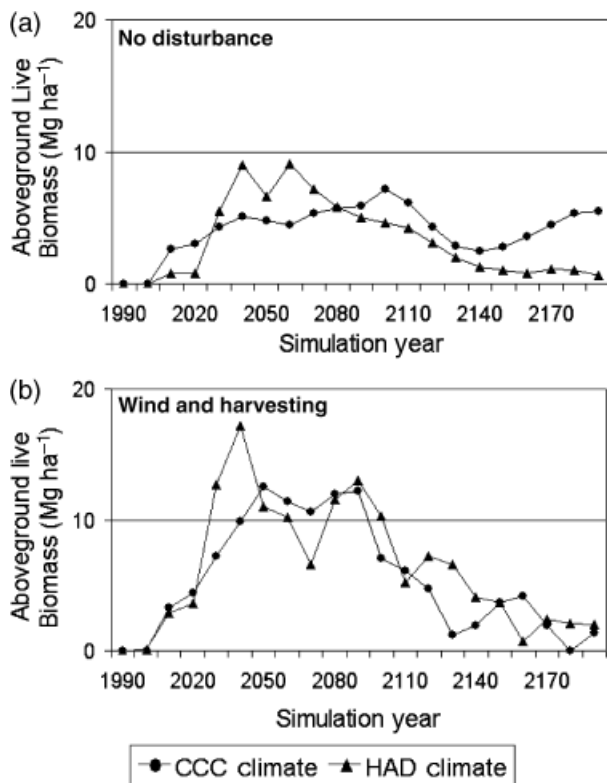


Fig. 8 The difference between scenarios with unlimited seed dispersal and scenarios with limited seed dispersal for two climate scenarios, Hadley Climate Centre (HAD), Canadian Climate Centre (CCC) and two disturbance scenarios (no disturbance and both wind and harvesting).

disturbance, suggesting an initial overestimate of biomass because of recent partial harvests and (or) a simulated harvesting prescription that overestimated biomass removal.

Consideration of disturbance is important to understanding the effects of climate change effects on forest composition. In all climate scenarios, changes in forest composition were on average larger when disturbance was excluded (Fig. 6). Many northern species are shade intolerant (e.g. jack pine, red pine, paper birch) and even without climate change, these species are almost completely extirpated if adequate light for germination is absent. A model simulation of southern boreal forests in northeast Minnesota also found that disturbance was essential for conserving many existing species (Scheller *et al.*, 2005). Even though some form of disturbance may initially allow for regeneration and establishment, five species (balsam fir, paper birch, white spruce, jack pine, red pine) will nonetheless be extirpated if climate changes as projected (Table 3).

Under our climate change scenarios with disturbance, the Canadian climate projections simulated a larger change in forest composition than the Hadley climate projections, similar to previous research (Walker *et al.*, 2002), although the difference is relatively minor (Fig. 6a) (Iverson & Prasad, 2001). A larger shift toward increased oak and hickory has been predicted (Hansen *et al.*, 2001; Iverson & Prasad, 2001). However, these predictions were deterministic and not spatially interactive and did not take into account the restrictions because of seed dispersal or the interactive effects of disturbance. Our scenarios with disturbance produced a smaller overall change in forest composition than scenarios without disturbance.

Harvesting and wind also influenced changes in tree species richness over time (Fig. 7). Without harvesting and wind, tree species richness declines, similar to previous research (Iverson & Prasad, 2001), because of the combined effects of shade exclusion and, under the two climate change projections, species lost because of climatic shifts. With harvesting and wind, the number of species lost decreased and the number of species gained increased for all three climate scenarios. Nevertheless, only one of our two climate change scenarios had a significant net increase in tree species with disturbance, although temperature and precipitation relationships predict an decrease in tree species richness if climate changes (Currie, 2001). Mean species gain would have been greater if seed dispersal had not limited migration (data not shown).

The effect of seed dispersal limitations was larger with harvesting and wind than without (Fig. 8). Without disturbance, eastern hemlock had the greatest potential for dispersal and (or) migration. In the

presettlement landscape, eastern hemlock was more widely distributed and regionally was the leading dominant (Schulte *et al.*, 2002) and was associated with high aboveground biomass (Crow, 1978). The probability of establishment for hemlock is higher on average under both climate change scenarios (data not shown), although we did not consider the large negative effects of current day deer browsing (Mladenoff & Stearns, 1993). When disturbances were simulated, the removal of local seed sources was an additional limitation to seed dispersal although disturbance did create germination opportunities. Although management, i.e. planting, could offset this seed deficit to some degree, the required effort would be enormous at a regional or state-wide scale. The ultimate cause for the seed dispersal effect on biomass is the lag between fundamental and realized niches (Iverson *et al.*, 2005). Particularly the southern oaks and bitternut hickory, which had relatively large growth rates and the highest establishment probabilities after climate change, were not present at all potentially suitable sites if seed dispersal was distance limited (Iverson *et al.*, 2005). Although the effect of seed dispersal declined after the mid-point of our simulations, we would expect the effect to continue if we had not held climate constant after year 2100.

Validation and other caveats

Our simulations of forest change may be conservative and underestimate the effects of climate change as climate was held constant after the first 100 years. Also, more recent climate projections suggest that temperature changes may be greater than the CCC projections (Gordon *et al.*, 2000; Pope *et al.*, 2000).

Our simulations are limited by the available data used to construct many important relationships. For example, the effects of CO₂ fertilization on ANPP are poorly understood and were not incorporated into these simulations. We also assumed that many potentially important exogenous drivers were minimal and (or) stationary through time, including nitrogen deposition, deer browsing, insect defoliation, and changes in human land use and management. Significant research needs include the incorporation of a better model of soils and nutrient dynamics, particularly as a significant portion of forest carbon is soil organic carbon. Therefore, our simulations should not be used as predictions. Rather they are intended to highlight the relative importance of the different processes simulated, and highlight potential future trends, given the presented suite of assumptions and scenarios.

Strict validation (*sensu* Gardner & Urban, 2003) of long-term predictions is not possible (Rastetter, 1996).

An evaluation of uncertainty is often promoted as an alternative assessment of model validity (Chen *et al.*, 2000; Reilly *et al.*, 2001). Long-term climate and greenhouse gas emission predictions are the largest uncertainty in any climate change simulation (Allen *et al.*, 2000). The large difference between our climate change estimates of aboveground live biomass reflects this large uncertainty. Another potentially significant source of uncertainty is seed dispersal, which is at best poorly understood (Clark *et al.*, 1998; Higgins *et al.*, 2003). Our stochastic model does incorporate some inherent uncertainty although our experience is that inherent uncertainty was small relative to the effects of climate change.

Conclusions

By using a landscape simulation model that includes spatially interactive processes, ecosystem or biogeochemical processes, and individual species attributes, we can assess the important interactions that will drive forest change and the potential consequences of climate change. For example, lags in species migration are a spatial process that could significantly reduce carbon storage potential. However, it is disturbance, in this case harvesting and wind that may serve as critical organizing processes during the forthcoming period of rapid climate change. The effects of disturbance may be as important as the effects of climate change alone on forest composition (Schimel *et al.*, 2000). Although we only tested a single suite of harvesting practices, we conclude that harvesting and wind can influence the strength and duration of seed dispersal effects, the magnitude of forest composition change, and the direction of tree species richness change. Disturbance may accelerate the shift toward more southern species, although the effect is variable across the landscape. Any positive effects of harvesting must be balanced against the loss of carbon storage potential across the landscape.

In conclusion, our model, LANDIS-II, in conjunction with multiple climate and disturbance scenarios provides a useful analytical tool to begin addressing the consequences of climate change and identifying the driving processes at a landscape scale. We anticipate refining and extending our model in order to consider additional dimensions of climate change, including carbon dioxide fertilization, increasing ozone, insect defoliation, and other potentially confounding processes.

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