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RESEARCH ARTICLE

The formulations of site-scale processes affect landscape-scale forest change predictions: a comparison between LANDIS PRO and LANDIS-II forest landscape models

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Abstract
Context Forest landscape models (FLMs) are important tools for simulating forest changes over broad spatial and temporal scales. The ability of FLMs to accurately predict forest changes may be significantly influenced by the formulations of site-scale processes including seedling establishment, tree growth, competition, and mortality.
Objective The objectives of this study were to investigate the effects of site-scale processes and interaction effects of site-scale processes and harvest on landscape-scale forest change predictions.
Methods We compared the differences in species' distribution (quantified by species' percent area), total aboveground biomass, and species' biomass derived from two FLMs: (1) a model that explicitly incorporates stand density and size for each species age cohort (LANDIS PRO), and (2) a model that explicitly tracks biomass for each species age cohort (LANDIS-II with biomass succession extension), which are variants from the LANDIS FLM family with different formulations of site-scale processes.
Results For early successional species, the differences in simulated distribution and biomass were small (mostly less than 5 %). For mid- to late-successional species, the differences in simulated distribution and biomass were relatively large (10–30 %). The differences in species' biomass predictions were generally larger than those for species' distribution predictions. Harvest mediated the differences on landscape-scale predictions.
Conclusions The effects of site-scale processes on landscape-scale forest change predictions are dependent on species' ecological traits such as shade tolerance, seed dispersal, and growth rates.

Keywords Site-scale processes · LANDIS PRO · LANDIS-II · Species' distribution · Species' biomass · Harvest · Small Khingan Mountains

Introduction

Forest landscape dynamics are affected by site-scale processes (e.g., establishment, growth, mortality, and competition) and landscape-scales processes (such as

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seed dispersal and disturbance) (Oliver and Larson 1996). Because the interactions of these multi-scale processes are complex, forest landscape models (FLMs) have emerged as valuable tools for predicting forest dynamics over large spatial–temporal scales (Keane et al. 2004; Perry and Enright 2006; Scheller and Mladenoff 2007; He 2008; Taylor et al. 2009). FLMs usually treat the simulated landscape as raster cells (or sites). Site-scale processes are simulated in each cell whereas forest landscape processes are simulated across the study region. Because computation load increases with the complexity of site-scale processes (e.g., more species or more detailed quantitative information), FLMs typically sacrifice the realism of site-scale processes to make landscape-scale simulation feasible (He 2008; Wang et al. 2013).

Recent FLMs attempt to improve simulation realism with various designs to represent site-scale dynamics, and these designs vary greatly (Lischke et al. 2006; Scheller et al. 2007; Seidl et al. 2012; Wang et al. 2013). For example, TreeMig (Lischke et al. 2006) tracks horizontal and vertical stand structure in a cell and accounts for seed production, seed dispersal, seed bank dynamics, germination, and sapling development. LANDCLIM (Schumacher et al. 2004) tracks numbers of trees and biomass by species' age cohort; simulates the effects of abiotic factors (terrain, soil, and climate) on tree size, density, and biomass and simulates the resource competition-caused mortality driven by maximum stand biomass. LANDIS-II with its biomass succession module tracks biomass by species' age cohort and uses a ratio of actual biomass to potential biomass to quantify resource availability at each cell, assuming age-cohort biomass by species incorporates stand density information (Scheller et al. 2007, 2011). LANDIS PRO (Wang et al. 2014a) tracks number of trees and diameter at breast height (DBH) by species' age cohort; quantifies growing space using the stand density index within each cell; and simulates resource competition and stand development using theories of stand dynamics.

Different formulations of site-scale processes in FLMs may lead to differing simulation results (Elkin et al. 2012; Liang et al. 2015). For example, species relative abundance simulated by a FLM with detailed site-scale processes based on stand density was generally larger than that simulated by a model with simplified site-scale processes (Liang et al. 2015). Different tree growth formulations affected species composition associated with elevation and species-specific biomass (Elkin et al. 2012). Another study on the effect of dynamic stand structure on succession showed that using mean stand structures instead of their horizontal and vertical distributions yielded different transient and equilibrium species biomasses (Löffler and Lischke 2001). FLMs long-term simulations that did not explicitly include tree growth and inter-species competition, resulted in long lived, shade tolerant species (Schumacher et al. 2004). Some studies also showed that FLMs with relatively simple site-scale processes may have simulation results similar to models with detailed site-scale processes, because site-scale processes were frequently overridden by landscape-scale processes in these landscapes (e.g., clear-cut harvest or stand-replacing fire) (Romme et al. 1998; Schumacher et al. 2004; Turner 2010). However, these simple FLMs may produce biased predictions for forest landscapes where disturbance is infrequent and site-scale processes largely drive forest landscape dynamics (Moorcroft et al. 2001; Schumacher et al. 2004; Elkin et al. 2012; Wang et al. 2013).

Understanding the effects of site-scale processes is important for reducing uncertainties in forest change predictions. Despite many prior attempts, comparing FLMs predictions remains challenging because differences in FLM designs and formulation make it difficult to identify and separate the effects of site-scale processes. Comparing models with the same modeling framework but different site-scale process formulations can overcome some of these problems.

In this study, we evaluated two widely used FLMs, variants from the LANDIS FLM family with different formulations of site-scale processes, to investigate the effects of site-scale processes on landscape-scale forest change predictions: (1) a model that explicitly incorporates stand density and size for trees of each species by age cohort (LANDIS PRO), and (2) a model that explicitly tracks biomass for each species age cohort (LANDIS-II with biomass succession extension; but note that the biomass extension is one of several available succession extensions for LANDIS-II). Both LANDIS PRO and LANDIS-II models are spatially explicit, raster-based landscape models, which are used to simulate forest succession, seed dispersal, wind, fire, biological disturbance, and harvest over large spatial (e.g., $>10^6$ ha) and temporal (e.g., >10^2 years) scales with flexible spatial (30–500 m pixel size) and temporal (1–10 years) resolutions (Scheller and Mladenoff 2005; Gustafson et al. 2010; Luo et al. 2014; Wang et al. 2015a, b, 2016). Specifically, we examined the differences in species' distribution (quantified by species' percent area), total aboveground biomass (AGB), and species' biomass between the two models at the short-, medium-, and long-term, respectively. We also investigated how landscape processes (harvest in this study) interacted with site-scale processes and influenced landscape-scale predictions.

Methods

Case study landscape

Our study area (1.8 million ha) was located in Small Khingan Mountains region of northeastern China (Fig. 1). The topography is rolling with elevations ranging from 139 to 1141 m. Climate is continental, with long and cold winters (mean January temperature, −1 °C) and short, but warm and humid summers (mean July temperature, 21 °C). The annual precipitation increases gradually from 485 mm in the north to 694 mm in the south. The area is dominated by brown coniferous forest soils. The area is characterized as mixed coniferous and broadleaved forests dominated by Korean pine (*Pinus koraiensis*), spruce (*Picea koraiensis* and *Picea jezoensis*), fir (*Abies nephrolepis*), larch (*Larix gmelinii*), oak (*Quercus mongolica*), elm (*Ulmus japonica*), maple (*Acer mono*), ash (*Fraxinus mandshurica*), walnut (*Juglans mandshurica*), amur corktree (*Phellodendron amurense*), ribbed birch (*Betula costata*), dahur birch (*Betula davurica*), basswood (*Tilia amurensis*), white birch (*Betula platyphylla*), and poplar (*Populous davidiana*). Because of extensive timber harvest (clear-cut) in the 1970–1980s (Feng et al. 1999; Bu et al. 2008), the age of early successional species typically ranges from 30 to 40 years (even aged).

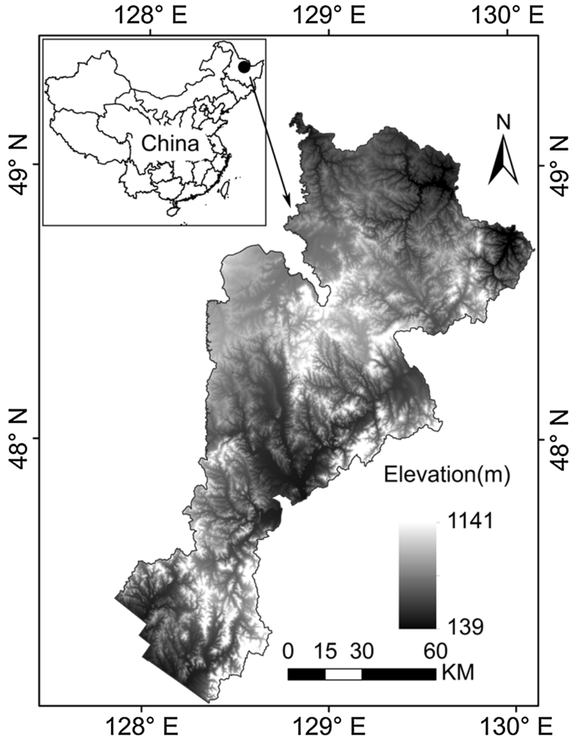


Fig. 1 The geographic location of the study area

Model description

Both LANDIS PRO and LANDIS-II models stratify heterogeneous landscapes into relatively homogeneous land types (also called ecoregions) based on climate, soil, or terrain attributes (e.g., slope, aspect, and elevation). Each land type is assigned unique attributes, such as the probability that a species can successfully become established in the absence of competition (species establishment probability, SEP). However, the fundamental difference in the philosophy of these two models is that LANDIS PRO models stand dynamics by density and size of species age classes for each cell and then calculates biomass based on allometric equations (e.g., Jenkins et al. 2004); In contrast, LANDIS-II models total biomass production for each cell and then partitions it into components by species and age class (Scheller and Mladenoff 2004). Because of the different designs in these two models, site-scale information is tracked differently, which results in different formulations of site-scale processes, including establishment, tree growth, competition, and mortality.

LANDIS PRO

The LANDIS PRO model (http://landis.missouri.edu/landispro70.php) explicitly simulates species-level processes and inter- and intra-specific competition and stand development by incorporating the number of trees and DBH for each age cohort in each cell (Wang et al.

2013). Since stand parameters including species density and basal area at each cell are compatible with forest inventory data, LANDIS PRO can directly utilize forest inventory data for model initialization, calibration, and validation without a spin-up process, which allocates initial biomass from all the cohorts to specified age at the start of the simulation (Wang et al. 2014b).

Growth

Tree growth is simulated as age and DBH increment by species age cohort (Fig. 2). Age increment is determined by the model time step. DBH increment is achieved by species' specific age-DBH relationship customized for each land type (Murphy and Graney 1998; Loewenstein et al. 2000; Condit et al. 2006), which can account for the effects of site quality on tree growth. Generally, for shade-intolerant, early successional species, DBH reaches maximum at a faster rate, whereas for shade-tolerant, mid- to late-successional species, DBH increases at a slower rate.

Establishment

Seedling establishment is regulated by the seed dispersal, number of potential germination seeds per mature tree (NPGS), proportion of total growing space occupied (GSO), species shade tolerance, and species establishment probability. Seed dispersal is modeled as a function of species effective and maximum seeding distances (He and Mladenoff 1999). The number of seeds reaching a cell is determined by NPGS and dispersal distance. The total NPGS for each species is accumulated from all available parent trees within the dispersal kernel. For the seed estimated to arrive on the cell, GSO is checked to determine whether there is enough space for establishment. On an open growing cell, the stand dynamics are characterized by extensive seedlings establishment of various species except for the most shade tolerant species, because that the most shade tolerant species needs a relative shading environment to establish and geminate. As the growing space is gradually occupied (stand reaches crown closure), only seedlings of shade tolerant species can establish (Fig. 2). Once a seed is determined eligible, SEP as a surrogate of environmental suitability is used to determine the probability for this seedling to become established by comparing the species establishment probability with a uniformly drawn random number (0–1). This procedure captures the stochasticity of species establishment and ensures that species with high species establishment probability have higher probabilities of establishment (Mladenoff and He 1999).

Fig. 2 Comparison of LANDIS PRO succession and LANDIS-II biomass succession ▶

Competition

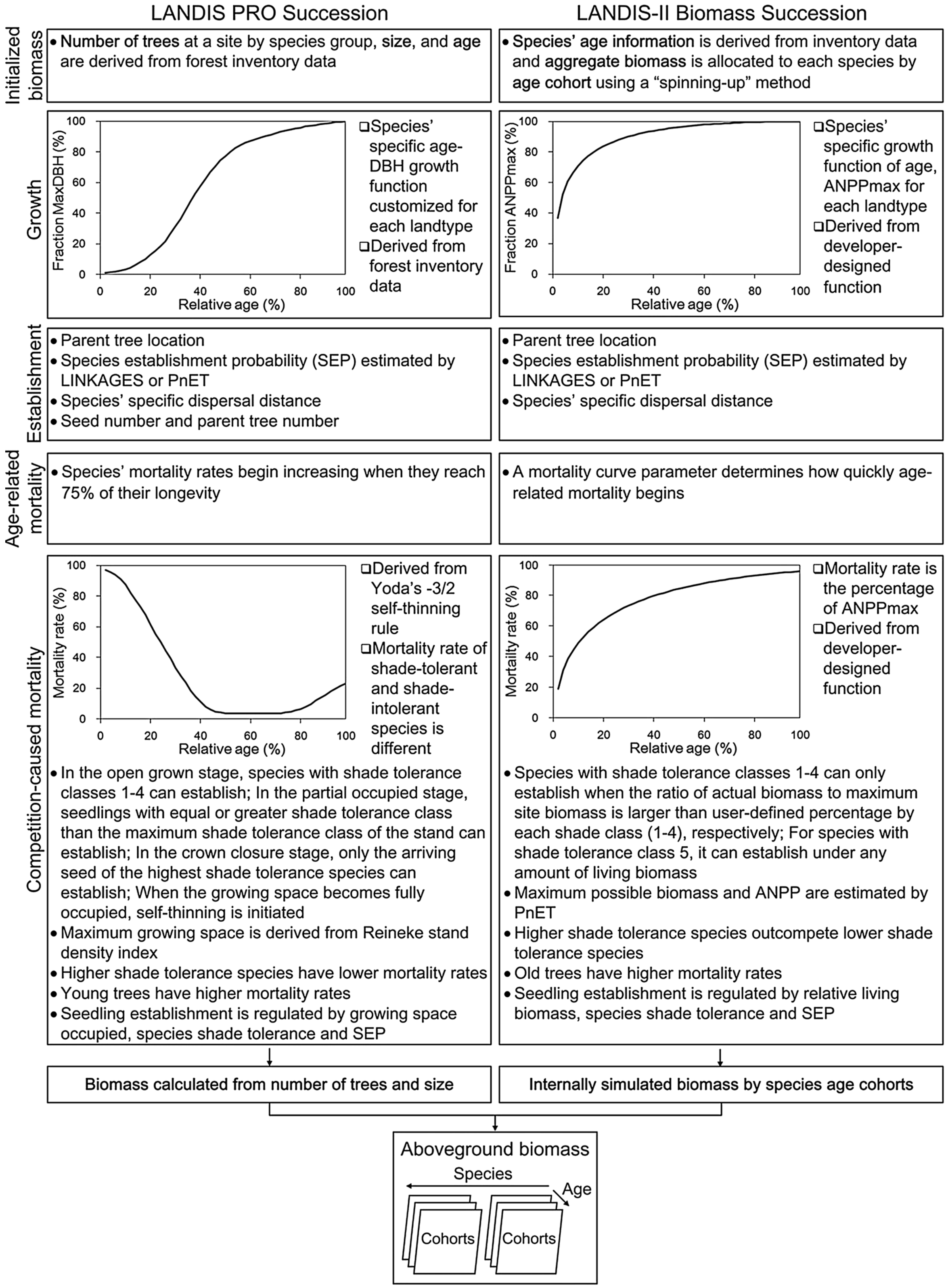
The competition intensity is regulated by the amount of GSO within each cell. GSO is defined as the percentage of the total physical growing space occupied by the trees in each cell and is derived from Reineke's stand density index (Reineke 1933; Wang et al. 2013). Resource availability varies among different stand development stages because of the dynamics of establishment and mortality. Four GSO govern progression through the stages of stand development described by (Oliver and Larson 1996; Wang et al. 2013). Seedlings can establish depending on species' shade tolerance and species establishment probability at the stand initiation stage. Once stands become fully occupied, competition-caused mortality (self-thinning) is initiated, which follows Yoda's −3/2 self-thinning rule (Yoda et al. 1963). Self-thinning continues to understory reinitiation and old-growth stages if no disturbances occur (Wang et al. 2013).

Mortality

Tree mortality in LANDIS PRO includes: (1) stand-scale resource competition-caused mortality (self-thinning), (2) natural mortality due to reaching longevity, (3) disturbance-caused mortality (Fig. 2). Tree mortality due to self-thinning is characterized by removing trees from small to large size classes and from low to high shade tolerance classes. Thus, higher shade tolerance species have lower mortality rates. This form of mortality is tree-based as opposed to age cohort-based (i.e., rather than modeling the death of an entire age cohort as a single entity, individual trees or subsets of trees within a cohort can die).

Harvest

In LANDIS PRO, the harvest module is developed based on a previous LANDIS model (Gustafson et al.



	LANDIS PRO Succession	LANDIS-II Biomass Succession
Initialized biomass	• **Number of trees** at a site by species group, **size**, and **age** are derived from forest inventory data	• **Species' age information** is derived from inventory data and **aggregate biomass** is allocated to each species by **age cohort** using a "spinning-up" method
Growth	❑Species' specific age-DBH growth function customized for each landtype ❑Derived from forest inventory data	❑Species' specific growth function of age, ANPPmax for each landtype ❑Derived from developer-designed function
Establishment	• Parent tree location • Species establishment probability (SEP) estimated by LINKAGES or PnET • Species' specific dispersal distance • Seed number and parent tree number	• Parent tree location • Species establishment probability (SEP) estimated by LINKAGES or PnET • Species' specific dispersal distance
Age-related mortality	• Species' mortality rates begin increasing when they reach 75% of their longevity	• A mortality curve parameter determines how quickly age-related mortality begins
Competition-caused mortality	❑Derived from Yoda's -3/2 self-thinning rule ❑Mortality rate of shade-tolerant and shade-intolerant species is different • In the open grown stage, species with shade tolerance classes 1-4 can establish; In the partial occupied stage, seedlings with equal or greater shade tolerance class than the maximum shade tolerance class of the stand can establish; In the crown closure stage, only the arriving seed of the highest shade tolerance species can establish; When the growing space becomes fully occupied, self-thinning is initiated • Maximum growing space is derived from Reineke stand density index • Higher shade tolerance species have lower mortality rates • Young trees have higher mortality rates • Seedling establishment is regulated by growing space occupied, species shade tolerance and SEP	❑Mortality rate is the percentage of ANPPmax ❑Derived from developer-designed function • Species with shade tolerance classes 1-4 can only establish when the ratio of actual biomass to maximum site biomass is larger than user-defined percentage by each shade class (1-4), respectively; For species with shade tolerance class 5, it can establish under any amount of living biomass • Maximum possible biomass and ANPP are estimated by PnET • Higher shade tolerance species outcompete lower shade tolerance species • Old trees have higher mortality rates • Seedling establishment is regulated by relative living biomass, species shade tolerance and SEP
	Biomass calculated from number of trees and size	**Internally simulated biomass by species age cohorts**

2000). However, because LANDIS PRO tracks density and basal area by species age cohort, its harvest module can simulate basal area or stocking-level controlled harvest actually used in forest management. It can simulate most silvicultural treatments currently used in forest management including single tree selection, group selection, thinning from below, thinning from above, and clear-cut (Fraser et al. 2013).

LANDIS-II

The LANDIS-II model (LANDIS-II 6.0 using the Biomass Succession module http://www.landis-ii.org/) represents each forest site in terms of aboveground biomass by tree species age cohorts, rather than individual trees (Scheller et al. 2007). The model was developed as a framework to partition externally estimated cell productivity—typically derived from a physiologically-based lumped parameter model (e.g., PnET-II; Aber et al. 1995)—among species age cohorts. AGB for each species at each time step is a function of existing biomass, aboveground net primary productivity (ANPP), and mortality. In LANDIS-II, initial biomass of each species age cohort is calculated by "spin-up" all the cohorts to their specified age at the start of the simulation (Scheller and Mladenoff 2004; Scheller et al. 2007). For example, if one species in a cell has two age-cohorts (e.g., age 20 and 100), the 100-year cohort is modeled to grow without competition for 80 years until the 20-year cohort is added. Then changes in the two cohorts are projected forward for the remaining 20 years with competition between them for growing space. A mortality fraction parameter specifies a constant proportion of total cell biomass to be removed at each time step. Thus, within the spin-up phase, growth and mortality are simulated for the number of years equal to each cohort's current age, and a cell's initial biomass incorporates assumptions about prior competition among existing cohorts.

Growth

Tree growth is simulated as both age and ANPP increment by species age cohort (Fig. 2). This is done through a species- and landtype-specific growth curve parameter, which specifies ANPP as it approaches its maximum (ANPPmax; Fig. 2). A cohort's contribution to ANPP increases with age (the ratio of actual cohort biomass to maximum possible biomass for the cohort), slowing asymptotically as total cell biomass approaches Bmax.

Establishment

Seedling establishment in LANDIS-II is a function of dispersal distance, species shade tolerance, onsite biomass, and species establishment probability (Fig. 2). The probability of seed dispersal is modeled with two negative exponential probability distributions parameterized by the effective and maximum seed dispersal distances of a species (Ward et al. 2005), which is based on a previous dispersal algorithm (He and Mladenoff 1999). Once seed arrives at a given cell, light conditions are determined by comparing the species shade tolerance and relative living biomass (a percentage of actual biomass to maximum cell biomass). Species with shade tolerance classes 1–4 can only establish when the ratio is larger than the user-defined percentages for each shade class (1–4) (Scheller and Mladenoff 2004). Species in shade tolerance class 5 (most tolerance) can establish under any amount of living biomass. After checking light condition, environmental suitability is checked by comparing species establishment probability with a 0–1 random number. Seedlings established in LANDIS-II are assigned a small amount of biomass irrespective of seedling number and parent tree abundance.

Competition

LANDIS-II simulates competition as a function of Bmax, biomass already occupied by species age cohorts and the growth rate specific to each species as determined by the potential ANPP (ANPPpotential) (Fig. 2). The actual ANPP for any species age cohort is dependent upon ANPPpotential, cohort age, and overstory competition. Competition reduces actual cohort ANPP below its potential when canopy-dominant cohorts suppress younger cohort and faster-growing species outcompete slower-growing species. Competition is expressed as measure of cohort biomass compared to other biomass on the cell (Scheller and Miranda 2015).

Mortality

LANDIS-II includes age-related mortality, competition-caused mortality, and disturbance-caused mortality (Fig. 2). Age-related mortality increases nonlinearly with age, and a mortality curve parameter determines how early in a cohort's life span age-related mortality begins. Competition-caused mortality increases also as a function of age, ANPPmax and Bmax. Competition-caused mortality can remove partial cohorts and is relatively low when a cohort is young, accelerates to plateau as the cohort approaches its longevity (Scheller and Miranda 2015).

Harvest

The harvest extension generally follows the previous harvest module as described in Gustafson et al. (2000). Stands are prioritized for harvest using user-defined ranking algorithms (e.g., maximum cohort age) that use biomass criteria related to forest management objectives. For each harvest event, the number of cells to be harvested must be indicated according to the species and age cohort removal rules specified in a prescription (e.g., clear-cut and thinning). Harvest can remove all or a specified percentage of a cohort's biomass.

Model parameterization and calibration

LANDIS PRO and LANDIS-II shared two spatial data inputs (land type map, forest composition map) and other non-spatial parameters (e.g., species' vital attributes, species establishment probability). The land type map in this study was derived from a digital elevation model (DEM), which classified the study area into 8 major land types. We modeled the most prominent 15 tree species. The initial forest composition map at year 2000 including species and age information was generated from forest stand inventory data. Species' vital attributes (Table 1) were estimated based on previous studies and consultations with local forestry experts (He et al. 2005; Yan and Shugart 2005; Bu et al. 2008). Species establishment probability for each species was estimated using a simulation approach that used climate data and measures of species climatic and edaphic tolerances (Gustafson et al. 2010; Thompson et al. 2011). Besides the above shared parameter, each model has its own specific parameters.

Parameters specific to LANDIS PRO included number of trees by species age cohort in each cell, four GSO thresholds for each land type, and additional species‘ vital attributes (e.g., growth rates, maximum stand density index, NPGS, and maximum DBH). We directly derived number of trees by species age cohort at year 2000 from forest inventory data. Maximum stand density index is defined as the maximum number of 10-inch diameter trees per hectare, and has already been reported for many species (Reineke 1933; Long 1985). We derived maximum stand density index and DBH from literature and previous studies and growth rates from forest inventory data (Burns and Honkala 1990; Liang et al. 2015). We iteratively calibrated the growth rates and NPGS for each species using forest inventory data and old-growth studies; for further details on model calibration and evaluation see Wang et al. (2014b). In addition, in order to test the sensitivity of the growth rates and NPGS parameters, we performed a sensitivity analysis for these two parameters (see Appendix A in Supplementary material).

Parameters specific to LANDIS-II included biomass for each species age cohort at each cell, ANPPmax by species, Bmax by species, foliar longevity and foliar lignin. We estimated ANPPmax from PnET-II as the combination of wood and foliar NPP and derived Bmax for each species from previous studies (Feng et al. 1999; Luo et al. 2013). Additional information about species vital attributes (e.g., foliar longevity, foliar lignin) was based on Flora of China (http://frps.eflora.cn/) or other literature (Li and Lei 2010). We calibrated the species' growth and mortality curve parameters using the approach described in Scheller and Mladenoff (2004). In addition, in order to test the sensitivity of the mortality and growth shape parameters, we performed a sensitivity analysis for these two parameters (see Appendix A in Supplementary material).

Calibration for these two models was carried out by comparing the shared output variables (such as species' biomass and total AGB). We initialized these two models using forest inventory data from year 2000, ran each model to 2010, and compared the simulated biomass at year 2010 with the 2010 forest inventory data. We iteratively adjusted the species' growth rates (age-DBH relationship) in LANDIS PRO

Table 1 Species parameters for vital attributes in the LANDIS forest landscape model

Genus	Species	LONG[a]	SMA[a]	ST[a]	ED[a]	MD[a]	VP[a]	MINS[a]	MAXS[a]	MaxDBH[b]	MaxSDI[b]	NPGS[b]	FL[c]	FLI[c]
Pinus	Korean pine	300	40	4	50	150	0	0	0	110	550	20	3.0	0.25
Picea	Spruce	300	30	4	50	150	0	0	0	90	600	20	4.0	0.25
Quercus	Oak	300	20	2	50	200	1	50	110	95	600	20	1.0	0.25
Ulmus	Elm	250	20	3	300	800	0.5	60	100	90	600	25	1.0	0.20
Tilia	Basswood	300	30	3	50	200	0.8	30	110	85	650	20	1.0	0.20
Betula	White birch	150	15	1	200	2000	0.8	50	60	50	800	30	1.0	0.20

LONG species longevity (years), *SMA* age of sexual maturity (years), *ST* shade tolerance class (1–5, 1 = the least tolerant, 5 = the most tolerant), *ED* effective seedling distance (m), *MD* maximum seedling distance (m), *VP* vegetative reproduction probability (0–1), *MINS* minimum sprouting age (years), *MAXS* maximum sprouting age (years), *MaxDBH* maximum diameter at breast height (cm), *MaxSDI* maximum stand density index (number of 10-inch trees per ha), *NPGS* number of potential germination seeds per mature tree (number/cell area), *FL* foliar longevity (years), *FLI* foliar lignin (% of mass)

[a] These are the shared parameters of the LANDIS PRO 7.0 and LANDIS-II 6.0 with Biomass Succession extension

[b] These are the specific parameters of the LANDIS PRO 7.0 model

[c] These are the specific parameters of the Biomass Succession extension for LANDIS-II 6.0 model

and the species' growth and mortality curve parameters in LANDIS-II until biomass derived from each model matched the summarized forest inventory data from year 2000 at the landscape scale (pass Chi square test for no differences in biomass).

Experimental design and data analysis

We simulated forest changes under two scenarios: (a) succession only scenario, (b) succession and harvest scenario (with harvest regime reflecting the current harvest activities). We used both models to simulate 15 dominant tree species (Table 1) from year 2000 to 2300 using 10-year time step at 100 m resolution with five replicates to capture model stochasticity. For each scenario the same forest initialization was used.

We summarized the species' distribution (quantified by species' percent area), species' biomass, and total AGB by averaging simulation results from the five replicate simulations for each scenario. We first evaluated the differences in trajectories of species' distribution and biomass, and total AGB between the two models from year 2000 to 2300. We then assessed the differences of species' distribution and biomass from the two models at short- (2000–2050 year), medium- (2060–2100 year), and long- (2110–2300 year) term using the relative mean absolute error (MAE %) (Miehle et al. 2006; Wang et al. 2014b):

$$MAE\% = 100\sum_{i=1}^{n}|D_i - P_i|/n/\overline{D}$$

where D_i was the simulated result from LANDIS PRO at year i, P_i was the simulated result from LANDIS-II at year i, n (n = 5, 5, 20) is the number of simulation years for each of short-, medium-, and long-term, respectively. In order to avoid the same percent area with different spatial patterns derived from two models, we used cell-wise values to assess the differences of species' distribution. Furthermore, we compared spatial patterns of species' distribution between these two models. All statistical analyses were operated in the language and environment R Team (2011). We found that six species (Korean pine, spruce, oak, elm, basswood and white birch) could capture the response patterns of 15 species, thus we represented the simulations results of these six species.

Results

Species' distribution

The trajectories of distribution varied among species and time and differed significantly between the two models. The simulated percent area for white birch, Korean pine and spruce from the models showed similar trends across the 300 years' simulation period under the succession only scenario (Fig. 3). MAE % averaged 2–10 % for these three species at the three temporal terms (Fig. 4). The differences in trajectories of percent area for oak, elm, and basswood between the two models increased over time and were significant in the long-term (Fig. 3). For example, the MAE % for oak, elm and basswood in the long-term (14, 29, and 27 %) were larger than those in the short-term (8, 15, and 7 %), respectively (Fig. 4). The results of spatial pattern of species' distribution were consistent with results of species percent area. For example, spatial pattern of distribution of oak simulated by LANDIS PRO at year 2100 was larger than that simulated by LANDIS-II, whereas for early successional species (e.g., white birch), spatial pattern of distribution was similar between these two models at year 2100 (see Appendix B in Supplementary material).

Total aboveground biomass (AGB)

The predictions of total AGB varied considerably between the two models (Fig. 5). Total AGB simulated by LANDIS PRO gradually increased and peaked around simulation year 2200 (176 t/ha), and then gradually decreased hereafter. Total AGB simulated by LANDIS-II increased more quickly to the peak around the simulation year 2070 (178 t/ha) followed by a 100-years' stable fluctuations and decreased dramatically to its lowest point (80 t/ha) at the simulation year 2260. The results of MAE % for total AGB were less than 10 % in the short- and medium-term, whereas large in the long-term (22 %) (Fig. 7).

The trajectories of total AGB under the harvest scenario coincided basically with those under the succession only scenario (Fig. 5). MAE % for total AGB in the short-, medium-, and long-term (8, 8, and 13 %) under the harvest scenario were smaller than those under the succession only scenario (9, 10, and 22 %) (Fig. 7).

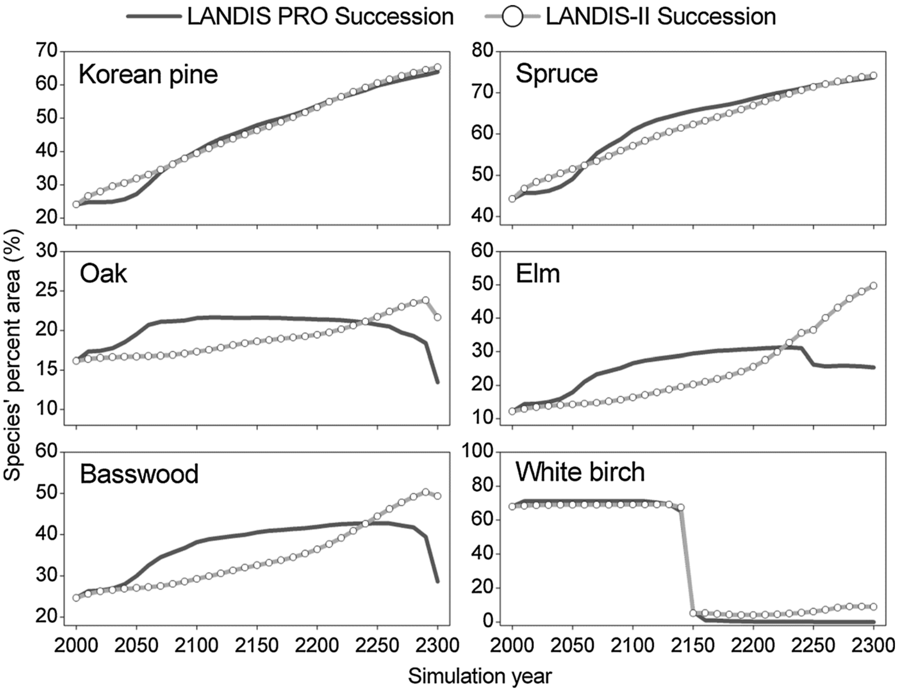


Fig. 3 The trajectory of species' distribution (quantified by species percent area) simulated by LANDIS PRO and LANDIS-II across the simulation period under succession only scenario

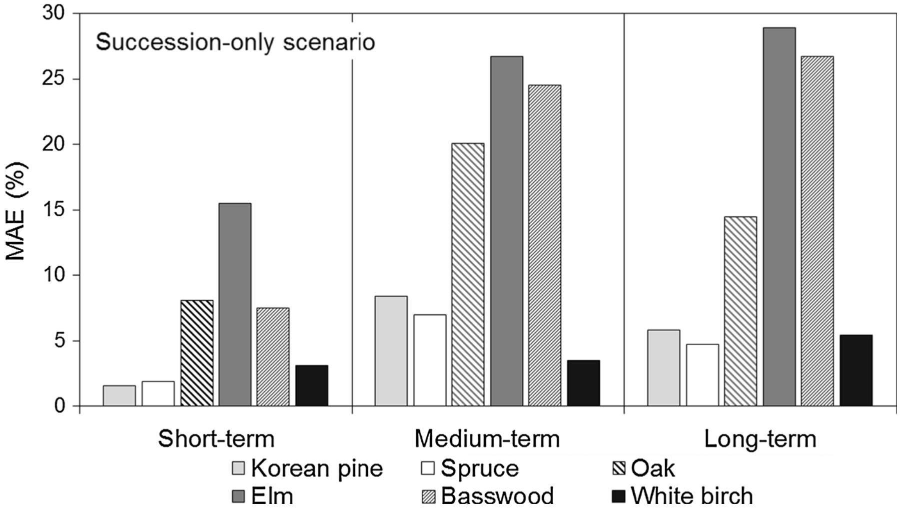


Fig. 4 Differences (quantified by the relative mean absolute error, MAE %) in species' percent area between two models in the short-, medium- and long-term under succession only scenario. The greater MAE % were, the greater the differences between two models

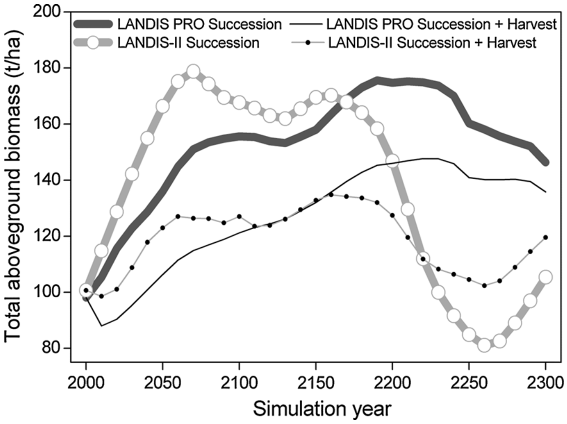


Fig. 5 The trajectory of total aboveground biomass simulated by LANDIS PRO and LANDIS-II across the simulation period under succession only scenario and harvest scenario

Species biomass

The trajectories of biomass between the two models varied among species and time with generally increasing differences over time. The trajectories of biomass from the two models for white birch were similar under the succession only scenario. MAE % averaged 5 % for white birch over time. Biomass for white birch from both models increased in the short-term followed by dramatic decreases in the medium-term, and approximated zero in the long-term. The trajectories of biomass for spruce, elm, and oak were similar in the short- and medium-term but varied substantially in the long-term under the succession only scenario. MAE for spruce, elm, and oak were 28, 32, and 28 %, respectively, in the long-term. The simulated biomass for oak from LANDIS PRO gradually increased and peaked around the simulated year 2230, and then slowly decreased to year 2300. However, in LANDIS-II, it increased much more quickly and peaked around the simulated year 2180 followed by drastic decreases under the succession only scenario (Fig. 6). The trajectories of biomass for Korean pine and basswood between both models had relatively stable differences over time. MAE % averaged 20 % for Korean pine and 21 % for basswood, which fell between white birch and spruce, elm, and oak.

The trajectories of species' biomass under the harvest scenario coincided with those under the succession only scenario (Fig. 6). Differences in biomass for white birch were also smaller than those for other species under the harvest scenario. Larger differences of species' biomass in the medium- and long-term were observed under the harvest scenario (Fig. 7). Harvest mediated the differences between the two models (Figs. 6, 7). The differences in biomass for most species from the two models under the harvest scenario were smaller than those under the succession only scenario (Fig. 7). For example, MAE % for Korean pine, oak, and elm (16, 22, and 13 %) under the harvest scenario were smaller than those under the succession scenario in the long-term (20, 32, and 28 %). By contrast, spruce had an opposite situation. MAE % for spruce in the short-, medium-, and long-term (6, 21, and 35 %) under harvest scenario were larger than those (1, 5, and 28 %) under the succession only scenario (Fig. 7).

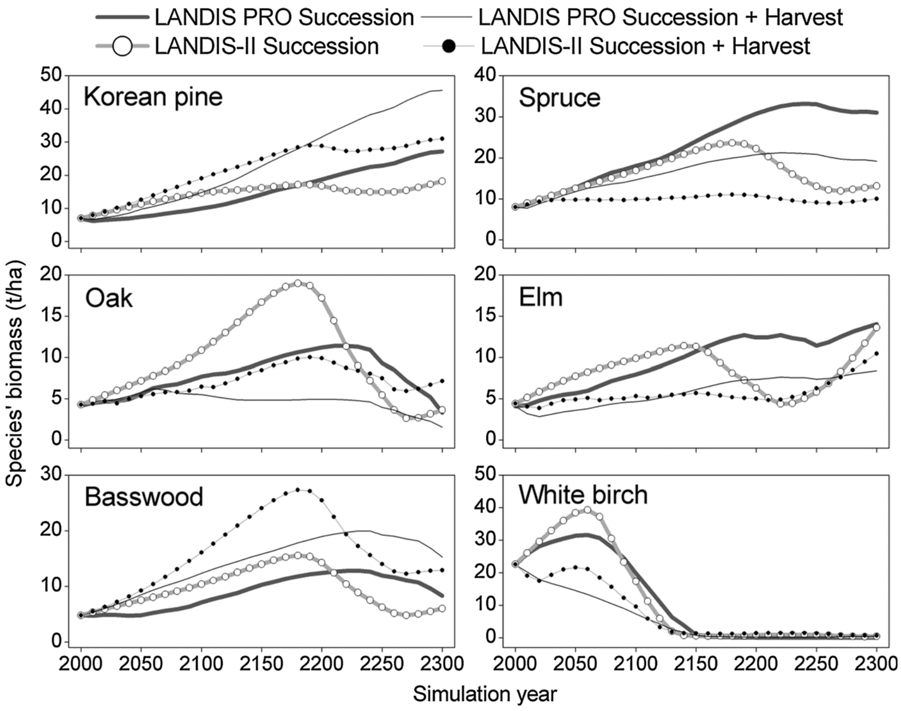


Fig. 6 The trajectory of species' biomass simulated by LANDIS PRO and LANDIS-II across the simulation period. Korean pine and basswood had higher biomass under the harvest scenario in both models than that under the succession only scenario because harvest of Korean pine and basswood were prohibited in China and harvest of other species promoted Korean pine and basswood

Discussion

Our simulation results indicated that site-scale processes such as tree growth, establishment, inter- and intra-species competition, and mortality influenced tree species' distribution and biomass modeled with FLMs. This is consistent with results from previous studies on the effects of site-scale processes on landscape-scale predictions using other forest landscape models (Elkin et al. 2012; Liang et al. 2015). Moreover, the effects of site-scale processes on landscape-scale predictions likely depend on species' ecological traits.

For early successional species, the simulated distribution and biomass were more robust with respect to different formulations of site-scale processes. For example, trajectories of distribution for white birch modelled with LANDIS PRO and LANDIS-II were very similar. This is because early successional species are usually fast growing, can better use resources, and have high seed dispersal capacity. These traits may potentially overcome low establishment probabilities in less suitable areas (He and Mladenoff 1999; Liang et al. 2015). Thus, distribution predictions for these early successional species were not sensitive to the formulation of site-scale processes. In addition, early successional species tend to occur as even aged stands in response to clear cutting 30–40 years ago in our study area (Feng et al. 1999; Bu et al. 2008). Thus, biomass can be similarly allocated to one age cohort in both models, which eliminates the potential differences in allocating biomass to multiple age cohorts. Moreover, the even aged stands decreased simultaneously in simulated distribution at the same time when they approach their maximum lifespan. Since age-related mortality was simulated similarly in both models, simulated biomass for these species tends to be similar. Other observational studies also found no apparent effects of site-scale processes such as seed mass on the growth and distribution of early successional species (Dalling and Hubbell 2002).

For mid- and late-successional species, simulated distribution and biomass were sensitive to the formulation of site-scale processes. Distribution was mostly influenced by seed dispersal, which was simulated differently in the two models. Both LANDIS PRO and LANDIS-II used probability decay function in simulating seed dispersal, i.e., the probability for an arriving seed decreased with increasing seeding distance (He and Mladenoff 1999). However, since LANDIS PRO tracked the number of arriving seeds,

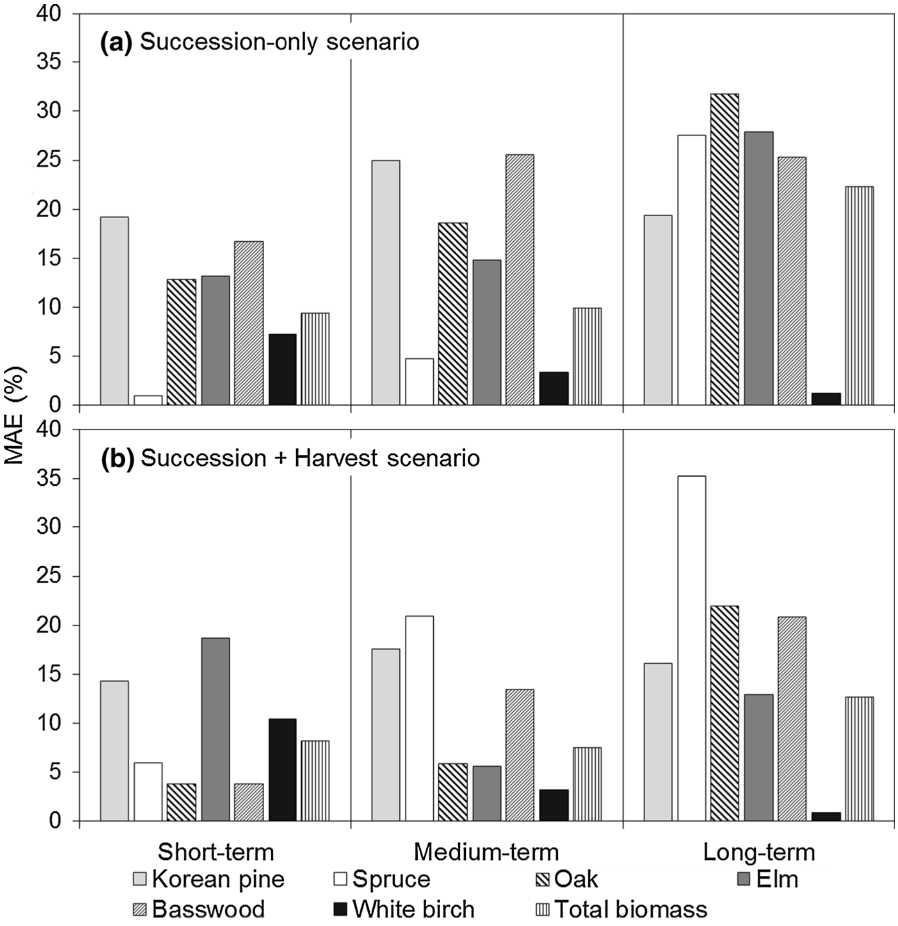


Fig. 7 Differences (quantified by the relative mean absolute error, MAE %) in species' biomass between two models in the short-, medium- and long-term. The greater MAE % is, the greater was differences between two models

it checked each seedling for establishment as opposed to LANDIS-II, which checked the youngest cohort (seed) for establishment. Hence LANDIS PRO potentially had higher chance of establishment and larger distribution than those simulated by LANDIS-II. In order to demonstrate this point, we simulated a hypothetical landscape (99 × 99 cells, 9801 ha) at 100 m resolution, which contained only one landtype and two species in order to eliminate the effect of interspecies competition. The central cell was initialized to Korean pine, whereas the surrounding cells were initialized to oak. We recorded the numbers of cells that Korean pine spread to the surrounding cells during the entire simulation period. The result showed that the number of cells in LANDIS PRO model was generally larger than that in LANDIS-II model (Fig. 8). This difference in distribution predictions between these two models was evident especially when seed sources were not abundant or concentrated such as those shade-tolerant species (e.g., Korean pine, spruce) (Gross 1984; Howe et al. 1985; Tripathi and Khan 1990; Paz et al. 1999; Turnbull et al. 1999), unlike those early successional species.

For the simulated biomass, mid- and late-successional species tended to occur in stands with relatively complex structures. Allocation of total biomass by species to each age cohort in LANDIS-II may lead to differences which propagate through simulation years. For example, oak, the moderate shade tolerant species in this study showed obviously different biomass predictions between the two models. Although oak species showed a decrease in both models when approaching its maximum lifespan, biomass trajectories during the entire simulation period in LANDIS-II showed a larger amplitude oscillation than those in LANDIS PRO. This was because the LANDIS-II "spin-up" method led to a larger allocation of biomass to the oldest age cohort than that in LANDIS PRO.

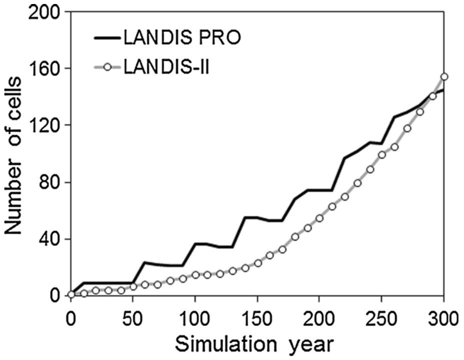


Fig. 8 We simulated a 9801 ha square landscape (99 × 99 cells) at a resolution of 1 ha containing only one landtype. The central cell was initialized to Korean pine, the surrounding cells were initialized to oak. The *Y-axis* represented how many cells have Korean pine with seed dispersal across the simulation period

LANDIS-II does not use ecophysiology while simulating biomass dynamics. It uses an empirical equation to allocate biomass to cohorts. We randomly chose approximately 4500 cells of oak stands with multiple age cohorts from our study area to examine allocation of biomass for the oldest age cohort at the simulated year 2000, 2050, 2100, and 2200, respectively. The result showed that the biomass of the oldest age cohort in LANDIS-II was eight-fold larger than that in LANDIS PRO at the simulated year 2000 (initial year), whereas six-fold was found at the simulated year 2100 (Fig. 9a). When a large portion of biomass reached longevity and was removed, the rate of mortality outpaced the rate of forest regrowth, making LANDIS-II more sensitive to cohort senescence than LANDIS PRO. This finding was magnified in our simulations due to the lack of gap scale disturbance, which may mediate the succession only effects (also see discussion below).

As expected, prediction of total AGB was also highly sensitive to the formulation of site-scale processes, which stemmed from different mechanisms determining biomass at the site scale. The maximum in total AGB simulated by the two models was similar (nearly 180 t/ha), which was supported by field-based studies in this region (Hu et al. 2015). Total AGB simulated by LANDIS-II increased much more quickly to the maximum in the simulated short-term and decreased dramatically to the minimum as cohort senescence in the simulated long-term. By contrast, predictions of total AGB showed less variation in LANDIS PRO. In order to explain this phenomenon, we analyzed species biomass increment (e.g., oak) by time step (10 years) at various age cohorts (regeneration, early-stage, mid-stage, late-stage and old-growth) simulated by these two models. The results showed that biomass increments at late-stage and old-growth in LANDIS-II were larger than those in LANDIS PRO, whereas the increments at regeneration, early-stage, mid-stage in LANDIS-II were smaller (Fig. 9b). The more rapid increase of total AGB in LANDIS-II than LANDIS PRO in the simulated short-term resulted from a larger biomass increment of age cohorts at late-stage in LANDIS-II (the initial age of dominant mid- and late- successional species typically range from 60 to 80 years). When a large portion of biomass reached longevity and was removed, the increase in regenerated biomass was much less than the decrease in biomass caused by mortality in LANDIS-II, making biomass decrease dramatically. In contrast, the total AGB simulated in LANDIS PRO decreased gradually after approaching longevity due to the supplement in regenerated biomass. This illustrates that LANDIS PRO, including tree density, size, and seed number, and stand development processes, can capture ecosystem inertia.

The differences in species' biomass between the two models were generally larger than those in species' distribution (Figs. 4, 7). This is probably because biomass dynamics were mainly driven by establishment, competition, and mortality, whereas distribution change was mostly affected by establishment and dispersal (Scheller et al. 2007; Xu et al. 2009; Wang et al. 2013, 2014a, b). Thus, site-scale processes played greater roles in biomass dynamics than in distribution, resulting in greater difference in biomass between the two models. In addition, the differences in predictions from the two models varied over time. They were minimal in the short-term, but increased from medium- to long-term.

We found that harvest mediated the effects of site-scale processes on landscape-scale predictions, suggesting that strong landscape-scale disturbance may override site-scale processes. This may result from the removal of mature trees. If a harvest removes the mature trees, it will reduce the seed sources and make the effects of seed dispersal less important. Thus, differences in tracking seeds in LANDIS PRO and LANDIS-II may lead to different results (Scheller and Mladenof 2005). Harvest can also reduce competition

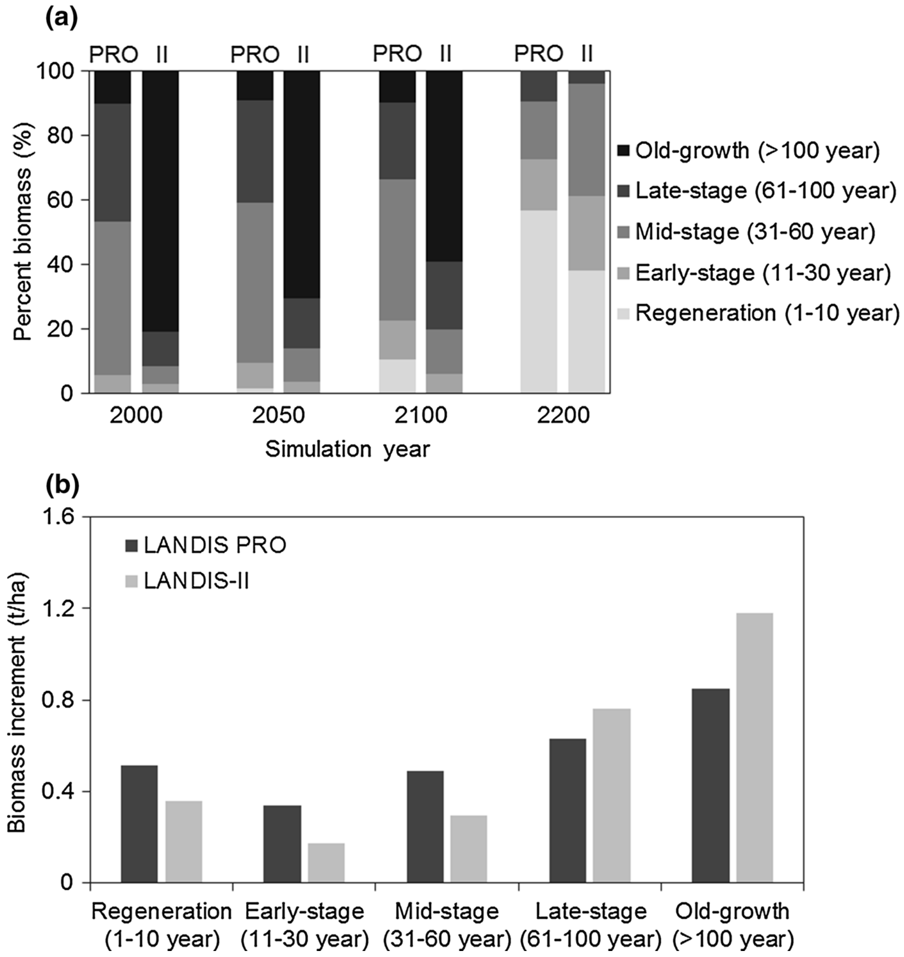


Fig. 9 Biomass allocation and annual biomass increment of oak at various age cohorts simulated by LANDIS PRO and LANDIS-II. About 15,000 cells in our study area had oak stand age over 100 year old age cohort, and 30 % of which (approximately 4500 cells) were randomly chosen to examine **a** allocation of biomass at regeneration, early-stage, mid-stage, late-stage and old-growth, simulated by LANDIS PRO and LANDIS-II at the simulation year 2000, 2050, 2100, and 2200 (PRO: LANDIS PRO; II: LANDIS-II); **b** the average biomass increment of oak by time step (10 years) at regeneration, early-stage, mid-stage, late-stage and old-growth simulated by these two models

and enable new species establishment especially for less shade tolerant species; which further mediated the effects of model results on site-scale processes. In deciduous or mixed deciduous and coniferous forests where large-scale disturbances (e.g., stand-replacing fire and clear-cut) are infrequent, site-scale processes are relatively more important than disturbances in driving in forests dynamics (Wang et al. 2013). Therefore, more detailed formations of site-scale processes may be needed to improve the predictions of forest changes in these regions.

The focus in this study was the effect of site-scale processes on forest succession, gap scale disturbances, such as windthrow, was not considered. This was because methods used to simulate gap-scale disturbances differed in these two models, which made it difficult to identify and separate the effects of site-scale processes from wind disturbances. Under scenarios with no windthrow disturbances, canopy gaps were not frequent or sizable enough to allow early successional species to establish. Thus, as expected, these species almost disappear in the long term. By contrast, stand heterogeneity would increase if windthrow were simulated, which may result in smaller differences between these two models. Another limitation in this study was the impossibility to parameterize the two models perfectly in parallel despite our best efforts. This was because of the differences in philosophy and methodology in the modeling approaches. Consequently, different biomass calculation metrics, allometric equations for LANDIS PRO (Jenkins et al. 2004) and biomass allocation in LANDIS-II (Scheller et al. 2007), resulted in differences in simulated biomass.

The results about the effects of site-scale processes on landscape-scale predictions could be generalized and benefit other forest landscape modelling studies, whereas the differences in seed dispersal and biomass allocation, are relatively specific to these two models. Although model-to-model comparisons as in this study are meaningful and frequent in model evaluation, it is necessary to apply long-term, landscape-scale forest monitoring data to evaluate model predictions. The comparisons between model results and long-term monitoring data were not feasible in this study due to the insufficient long-term monitoring data in the study area. With continuing efforts of forest inventory, such data will eventually be available to aid model comparison and evaluation. In addition, temperate forests in the study area are influenced by global change such as climate change. Climate change may affect species establishment and mortality and alter species' distribution and biomass. Thus, model-to-model comparisons under climate change scenario are essential to evaluate model predictions, which is a next desirable step.

Conclusion

Site-scale processes affected the tree species' distribution and biomass modeled with FLMs. The effects of site-scale processes on landscape-scale predictions likely depend on species' ecological traits such as shade tolerance, seed dispersal, and growth rates, among other factors. For early successional species, the simulated distribution and biomass were insensitive to different formulations of site-scale processes. Conversely, the simulated distribution and biomass for mid- and late-successional species were sensitive to the formulations. Moreover, the differences in the simulated species biomass were generally larger than in the simulated species' distribution. In addition, harvest mediated the effects of site-scale processes on landscape-scale predictions, suggesting that strong landscape-scale disturbance may override site-scale processes. Results from this study revealed the agreements and differences between these two models with different site-scale process formulations. They may help narrow down prediction uncertainties and point to areas where representations of site-scale processes need to be enhanced in the future.

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References

Aber JD, Ollinger SV, Federer CA, Reich PB, Goulden ML, Kicklighter DW, Melillo JM, Lathrop RG (1995) Predicting the effects of climate change on water yield and forest production in the northeastern United States. Climate Res 5(3):207–222

Bu R, He HS, Hu Y, Chang Y, Larsen DR (2008) Using the LANDIS model to evaluate forest harvesting and planting strategies under possible warming climates in Northeastern China. For Ecol Manag 254(3):407–419

Burns RM, Honkala B (1990) Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654, USDA Forest Service, Washington, DC.

Condit R, Ashton P, Bunyavejchewin S, Dattaraja HS, Davies S, Esufali S, Ewango C, Foster R, Gunatilleke I, Gunatilleke C, Hall P, Harms K, Hart T, Hernandez C, Hubbell S, Itoh A, Kiratiprayoon S, LaFrankie J, de Lao S, Makana J, Noor M, Kassim AR, Russo S, Sukumar R, Samper C, Suresh HS, Tan S, Thomas S, Valencia R, Vallejo M, Villa G, Zillio T (2006) The importance of demographic niches to tree diversity. Science 313(5783):98–101

Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. J Ecol 90(3):557–568

Elkin C, Reineking B, Bigler C, Bugmann H (2012) Do small-grain processes matter for landscape scale questions? Sensitivity of a forest landscape model to the formulation of tree growth rate. Landscape Ecol 27(5):697–711

Feng Z, Wang X, Wu G (1999) Biomass and productivity of forest ecoystems in China. Science Press, Beijing

Fraser JS, He HS, Shifley SR, Wang WJ, Thompson FR (2013) Simulating stand-level harvest prescriptions across landscapes: LANDIS PRO harvest module design. Can J For Res 43(10):972–978

Gross KL (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. J Ecol 72(2):369–387

Gustafson EJ, Shifley SR, Mladenoff DJ, Nimerfro KK, He HS (2000) Spatial simulation of forest succession and timber harvesting using LANDIS. Can J For Res 30(1):32–43

Gustafson EJ, Shvidenko AZ, Sturtevant BR, Scheller RM (2010) Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol Appl 20(3):700–715

He HS (2008) Forest landscape models: Definitions, characterization, and classification. For Ecol Manag 254(3):484–498

He HS, Hao ZQ, Mladenoff DJ, Shao GF, Hu YM, Chang Y (2005) Simulating forest ecosystem response to climate warming incorporating spatial effects in north-eastern China. J Biogeogr 32(12):2043–2056

He HS, Mladenoff DJ (1999) The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems 2(4):308–319

Howe HF, Schupp EW, Westley LC (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). Ecology 66(3):781–791

Hu HQ, Luo BZ, Wei SJ, Wei SW, Sun L, Luo SS, Ma HB (2015) Biomass carbon density and carbon sequestration capacity in seven typical forest types of the Xiaoxing'an Mountains, China. Chin J Plant Ecol 39:140–158

Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2004) Comprehensive database of diameter-based biomass regressions for North American tree species. Gen. Tech. Rep. NE-319. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square

Keane RE, Cary GJ, Davies ID et al (2004) A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecol Model 179(1):3–27

Li H, Lei Y (2010) Estimation and evaluation of forest biomass carbon storage in China. China Forestry Press, Beijing

Liang Y, He HS, Wang WJ, Fraser JS, Wu Z, Xu J (2015) The site-scale processes affect species distribution predictions of forest landscape models. Ecol Model 300:89–101

Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecol Model 199(4):409–420

Loewenstein EF, Johnson PS, Garrett HE (2000) Age and diameter structure of a managed uneven-aged oak forest. Can J For Res 30(7):1060–1070

Löffler TJ, Lischke H (2001) Incorporation and influence of variability in an aggregated forest model. Nat Resour Model 14(1):103–137

Long JN (1985) A practical approach to density management. For Chron 61(1):23–27

Luo X, He HS, Liang Y, Wang WJ, Wu Z, Fraser JS (2014) Spatial simulation of the effect of fire and harvest on aboveground tree biomass in boreal forests of Northeast China. Landscape Ecol 29(7):1187–1200

Luo Y, Wang X, Zhang X, Lu F (2013) Biomass and Its Allocation of Forest Ecosystems in China. China Forestry Press, Beijing

Miehle P, Livesley SJ, Li C, Feikema PM, Adams MA, Arndt SK (2006) Quantifying uncertainty from large-scale model predictions of forest carbon dynamics. Glob Chang Biol 12(8):1421–1434

Mladenoff DJ, He HS (1999) Design and behaviour of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff DJ, Baker WL (eds) Advances in spatial modeling of forest landscape change: approaches and applications. Cambridge University Press, Cambridge, UK, pp 125–162

Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model(ED). Ecol Mono 71(4):557–586

Murphy PA, Graney DL (1998) Individual-tree basal area growth, survival, and total height models for upland hardwoods in the Boston Mountains of Arkansas. S J Appl For 22(3):184–192

Oliver CD, Larson BC (1996) Forest Stand dynamics, Update edn. Wiley, New York

Paz H, Mazer SJ, Martínez-Ramos M (1999) Seed mass, seedling emergence, and environmental facts in seven rain forest psychotria(Rubiaceae). Ecology 80(5):1594–1606

Perry GLW, Enright NJ (2006) Spatial modelling of vegetation change in dynamic landscapes: a review of methods and applications. Prog Phys Geogr 30(1):47–72

R Development Core Team (2011) R: a language and environment for statistical computing. R Development Core Team, Vienna

Reineke LH (1933) Perfecting a stand-density index for even-aged forest. J Agric Res 46:627–638

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1(6):524–534

Scheller RM, Domingo JB, Sturtevant BR, Williams JS, Rudy A, Gustafson EJ, Mladenoff DJ (2007) Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol Model 201(3–4):409–419

Scheller RM, Miranda B (2015) LANDIS-II Biomass Succession v3.2 Extension User Guide, p 5

Scheller RM, Mladenoff DJ (2004) A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol Model 180(1):211–229

Scheller RM, Mladenoff DJ (2005) 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. Glob Chang Biol 11(2):307–321

Scheller RM, Mladenoff DJ (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. Landscape Ecol 22(4):491–505

Scheller RM, Van Tuyl S, Clark K, Hom J, La Puma I (2011) Carbon sequestration in the New Jersey pine barrens under different scenarios of Fire management. Ecosystems 14(6):987–1004

Schumacher S, Bugmann H, Mladenoff DJ (2004) Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol Model 180(1):175–194

Seidl R, Rammer W, Scheller RM, Spies TA (2012) An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol Model 231:87–100

Taylor AR, Chen HYH, VanDamme L (2009) A review of forest succession models and their suitability for forest management planning. For Sci 55(1):23–36

Thompson JR, Foster DR, Scheller RM, Kittredge D (2011) The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. Ecol Appl 21:2425–2444

Tripathi RS, Khan ML (1990) Effects of seed weight and microsite characteristics on germination and seedling fitness in two species of Quercus in a subtropical wet hill forest. Oikos 57(3):289–296

Turnbull LA, Rees M, Crawley MJ (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. J Ecol 87(5):899–912

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91(10):2833–2849

Wang WJ, He HS, Fraser JS, Thompson FR, Shifley SR, Spetich MA (2014a) LANDIS PRO: a landscape model that predicts forest composition and structure changes at regional scales. Ecography 37:225–229

Wang WJ, He HS, Spetich MA, Shifley SR, Thompson FR, Dijak WD, Wang Q (2014b) A framework for evaluating forest landscape model predictions using empirical data and knowledge. Environ Model Softw 62:230–239

Wang WJ, He HS, Spetich MA, Shifley SR, Thompson FR, Larsen DR, Fraser JS, Yang J (2013) A large-scale forest landscape model incorporating multi-scale processes and utilizing forest inventory data. Ecosphere 4(9):106–117

Wang WJ, He HS, Thompson FR, Fraser JS (2016) Changes in forest biomass and tree species distribution under climate change in the Northeastern United States. Landscape Ecol. doi:10.1007/s10980-016-0429-z

Wang WJ, He HS, Thompson FR, Fraser JS, Dijak WD (2015a) Landscape- and regional-scale shifts in forest composition under climate change in the Central Hardwood Region of the United States. Landscape Ecol 31(1):149–163

Wang WJ, He HS, Thompson FR, Fraser JS, Hanberry BB, Dijak WD (2015b) Importance of succession, harvest, and climate change in determining future forest composition changes in U.S. Central Hardwood Forests. Ecosphere 6(12):277

Ward BC, Mladenoff DJ, Scheller RM (2005) Landscape-level effects of the interaction between residential development and public forest management in northern Wisconsin, USA. For Sci 51:616–632

Xu C, Gertner GZ, Scheller RM (2009) Uncertainties in the response of a forest landscape to global climatic change. Glob Chang Biol 15(1):116–131

Yan X, Shugart HH (2005) FAREAST: a forest gap model to simulate dynamics and patterns of eastern Eurasian forests. J Biogeogr 32(9):1641–1658

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. J Biol 14:107–129