Assessing the effect of cell-level uncertainty on a forest landscape model simulation in northeastern China

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Abstract

LANDIS is a cell-based spatially explicit forest landscape model designed to explore successional dynamics under natural and anthropogenic disturbances. Species age cohort (10-year cohort of a given tree species) information is required for each cell in LANDIS. However, providing such information for a landscape comprising millions of cells is challenging. In this study, a stand-based assignation (SBA) approach was developed to stochastically assign species age cohorts to each cell based on forest inventory data. As a probability-based approach, SBA will introduce errors in LANDIS input. In order to assess the effect of errors produced by SBA on LANDIS results, 20 Monte Carlo simulations were produced. For each species simulated in LANDIS, the recurrence frequency (RF) of the majority species age cohort (MSAC, the most frequently occurring species age cohort) from 20 Monte Carlo simulations was used to quantify the uncertainty in species age cohorts for individual cell. Average recurrence frequency (ARF) of the MSAC was used to quantify the overall uncertainty in species age cohorts at the cell level. For each species, the coefficient of variation (CV) for the percent area and an aggregation index for the 20 Monte Carlo simulations was used to quantify the uncertainty at the landscape level. Results showed that at the cell level, uncertainty was relatively low at the beginning of the simulation (ARF was larger than 10). Seed dispersal, seedling establishment, mortality, and fire disturbance caused uncertainty to increase with simulation year. The uncertainty finally reached an equilibrium state, where input errors in original species age cohorts had little effect on the simulation outcomes. At the landscape level, species percent area and their spatial patterns were not substantially affected by the uncertainties in species age structure at the cell level. Since the typical use of LANDIS is to predict the long-term landscape pattern change, SBA can be used to parameterize species age cohorts for individual cells.

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1. Introduction

In the last decade, many spatially explicit forest models have been developed to simulate forest succession dynamics (e.g. Baker et al., 1991; Gardner et al., 1996; Mladenoff et al., 1996; Mladenoff and He, 1999; Urban et al., 1999; Wallin et al., 1994). Most of these models employ a raster data format, and the forest landscape is conceptualized as a grid of equal-sized cells or sites. Each cell requires the input of dominant canopy tree species, secondary tree species, and/or other stand-related parameters (e.g. age). Since the study landscape generally comprises millions of cells, it is often unfeasible to obtain cell-level information through ground survey. Thus, methods have been developed to derive such information from satellite imagery, forest inventories, or some combination (e.g. He et al., 1998). However, these methods cannot guarantee the accuracy at each cell and this raises a question: can the spatial information generated by such methods produce robust model results? To address this question, uncertainty analysis is necessary.

Uncertainty analysis assesses the uncertainty in the model output as the result of error propagation through the model from the input data and uncertainties in the model itself (Crosetto and Tarantola, 2001). Several approaches including simple sensitivity analysis (Tomovic, 1963; Elston, 1992), the analytical solution of stochastic differential equations (Soong, 1973), generic expectation function (Tyagi and Hann, 2001), and the Monte Carlo method have been developed to assess the uncertainty in model predictions. The Monte Carlo method assesses uncertainties through repeated model runs, with parameters drawn from specified probability distributions. It has been widely used in uncertainty analysis for non-spatial models (e.g. Kremer, 1983; Hettwich et al., 2000; Annan, 2001; Hofer et al., 2002). Attention has recently been directed to the spatial uncertainty in model prediction (Goovaerts, 1997). Phillips and Marks (1996) used 100 Monte Carlo simulations of a model of potential evapotranspiration (PET) to incorporate uncertainties produced by kriging interpolation of temperature, humidity, and wind data, and mapped the uncertainty of PET prediction using the coefficient of variation of PET in the Monte Carlo ensemble. Canters et al. (2002) used 20 Monte Carlo simulations of a landscape classification model to incorporate uncertainty in land-cover type produced by a field-based classification method, and mapped the uncertainty of landscape classification by displaying the frequency of the majority landscape class (landscape class that appears most frequently in the Monte Carlo ensemble). Aronica et al. (2002) used 500 Monte Carlo simulations of a spatially distributed hydraulic model (LISFLOOD-FP) to incorporate uncertainty in a flood inundation prediction and mapped the uncertainty of inundation using a weighted measure of fit of the Monte Carlo ensemble with observed data.

The Monte Carlo method has also been employed to address uncertainty in spatially explicit forest model simulation studies. Pacala et al. (1996) used 100 Monte Carlo simulations of a spatially explicit forest model (SORTIE) to identify predictions that were robust, given the level of sampling uncertainty. In this study, we use the Monte Carlo method to investigate the effect of cell-level uncertainty on the simulation results of a spatially explicit forest model (LANDIS) for a boreal forest landscape in northeastern China. We developed a stand-based assignation (SBA) approach to derive species and species age information for each cell from existing forest inventory data. As a probability-based approach, SBA will introduce cell-level uncertainty in LANDIS input. The objectives of this study were to assess: (1) how the uncertainty at the cell level propagates through model simulations, and (2) what are the effects of uncertainty at the cell level on the simulation results at the landscape level (entire study area).

2. Material and method

2.1. Description of study area

The 937,244-hectare study landscape, called Huzhong area, is located in northwestern Heilongjiang Province in northeastern China (52°25′00″N 122°39′30″E to 51°14′40″N 124°21′00″E). The Huma River originates from Dabai Mountain located in the southwestern region of the study area and runs across the study area. The vegetation of this area is a cool temperate coniferous forest at the southern extension of the eastern Siberian bright coniferous forest (Zhou, 1991). The forest area accounts for 86.98% of the study area.
and the timber volume is estimated at 63,613,536 m$^3$.

The canopy species composition is relatively simple, including larch (Larix gmelinii), pine (Pinus sylvestris var. mongolica), spruce (Picea koraiensis), birch (Betula platyphylla), two aspens (Populus davidiana and P. suaveolens); for notational convenience, we refer to P. davidiana as aspen-D and P. suaveolens as aspen-S), and willow (Chosenia arbutifolia). We also modeled a very important understory pine species (Pinus pumila; for notational convenience, we refer to P. sylvestris var. mongolica as pine-S and P. pumila as pine-P) (Zhao et al., 1997). Larch is widely distributed, except in some riparian wetlands, comprising about 78.4% of the forest area. Birch is an early successional species with strong colonization ability. It is always mixed with larch in most areas, which is due to fire disturbances and forest harvesting, and accounts for 15–20% of the study area. Pine-S, which has a small distribution, always coexists with larch. Aspen-S and willow are confined to the terrace of the river, where water is plentiful. Spruce is a highly shade-tolerant species and its distribution is limited to valley bottoms. Pine-P is found mainly on ridge tops and the upper part of the mountain, where the altitude is above 1000 m (Zhou, 1991; Zhao et al., 1997; Xu, 1998). Because larch and birch are the two most widely distributed species in our study area, for notational convenience, we refer to these two species as major species and other species as minor species.

2.2. Description of LANDIS

LANDIS is a cell-based spatially explicit forest landscape model of disturbance, succession, and management (Mladenoff et al., 1996; Mladenoff and He, 1999). It simulates species-level forest dynamics by tracking the presence/absence of species age cohorts (10-year cohort of a given tree species) at 10-year time steps under natural and anthropogenic disturbances, including fire, windthrow, insects and disease, harvesting, and fuel management. Detailed descriptions of LANDIS structure, seed dispersal, fire disturbance, and harvesting can be found in He et al. (1999), He and Mladenoff (1999a,b), and Gustafson et al. (2000), respectively. For the ease of understanding, we briefly described the seed dispersal and seedling establishment process and the fire disturbance process in LANDIS.

2.2.1. Seed dispersal and seedling establishment process

Seed dispersal and seedling establishment process in LANDIS are simulated as three steps: dispersal, light condition checking, and site condition checking (Mladenoff and He, 1999; He and Mladenoff, 1999a). First, the seed sources are identified by locating cells; where there exists species whose age is older than the maturity age. Then, seeds from the source stochastically disperse. The seed dispersal probability is modeled as a function of its effective and maximum seeding distance. Effective seed distance (ED) is the distance within which seed has the highest probability of reaching a site (e.g. $P > 0.95$). Maximum seed (MD) dispersal distance is the distance beyond which there is little possibility of reaching (e.g. $P < 0.01$). Seed dispersal probability ($P$) between ED and MD follows a negative exponential distribution

\[
P = e^{-b(x/\text{MD})} \quad \text{ED} < x < \text{MD} \quad (1)
\]

where $x$ is a given distance from the seed source and $b$ is a coefficient, which is set to 1 in LANDIS 3.6. A random number ($P_r$) from a uniform random number pool ranging from 0 to 1 is generated to compare with $P$ to decide if the seed can successfully disperse to a specified site. The seed successfully disperses to a site if $P_r < P$. Once the seed successfully reaches the site, the light condition checking procedure is implemented. The shade tolerance rank of the arrived species is compared to that of the species already established on the site to check if the site favors the species arrived. In LANDIS, the shade tolerance of species is divided into five classes with class 5 corresponding to the most tolerant and class 1 the least tolerant. For arrived species whose shade tolerance rank is lower than class 5, the site favors the species if its shade tolerance rank is higher than or equal to the highest shade tolerance rank of the already established species. For arrived species whose shade tolerance rank equals to class 5, the site favors the species only if the oldest cohort in the arrived site has an age older than the minimum age of cohort growth required before enough shade is created so that a shade tolerance 5 species can seed into the site, which is an input of LANDIS. If the light condition on the site favors the species, the site condition checking procedure is implemented. A random number ($P_r$) is generated to compare with the
arriving species’ establish coefficient \( C \). The seedling successfully establishes if \( P_r < C \). Establish coefficient is a floating number from 0 to 1 used to represent the relative scaling of how environmental conditions (e.g. moisture, climate, and nutrient) favor various species (Mladenoff et al., 1996; Mladenoff and He, 1999).

2.2.2. Fire disturbance

LANDIS uses a stochastic simulation approaches to simulate the fire disturbance (He and Mladenoff, 1999b). The fire probability \( P \) of each cell is determined by the following formula

\[
P = B \times IF \times MI^{-(e+2)}
\]

where \( MI \) is the mean fire-return interval of a given land type, \( B \) is the fire probability coefficient designed for model calibration, and \( IF \) is the time since last fire. In order to simulate the fire disturbance, LANDIS firstly locates the ignition point on each land type randomly. The number of the ignition points \( N_{ip} \) is determined from the ignition coefficient, which is user-defined \( N_{ip} = \text{ignition coefficient} \times \text{total cell number of each land type} \). Secondly, LANDIS calculates the fire probability \( P \) of the cell where the ignition point locates by Eq. (2). A random number \( P_r \) is then generated to check if this cell will be ignited. The fire is successfully ignited given \( P_r < P \). Thirdly, if the cell were ignited, LANDIS simulates the fire spread. The coordinates of the four adjacent cells are entered in a priority queue in a random order. The fire probabilities of all the four adjacent cells are calculated using Eq. (2), and a random number is generated to check if the fire will be spread to the adjacent cell. Fire spreads until either the desired fire size is reached, or the surrounding cells cannot burn, or non-forest surrounds the cell.

Important LANDIS outputs include an age cohort map for each species and the species distribution map at each 10-year time interval. If there are multiple age cohorts for a species, only the oldest age cohort is output. The species distribution map records presence/absence of species at each cell.

2.3. LANDIS parameterization

The available materials for LANDIS parameterization include a forest stand map and the stand attribute database compiled from a forest inventory in the Huizhong area in 1990, two scenes of Landsat TM imagery collected in 1990, the fire records from 1990 to 2000, and a DEM derived from the contour lines delineated by the general staff of the Chinese People’s Liberation Army from aerophotographs taken in 1971. The forest stand map records boundaries of stands and compartments. Compartment is a unit of forest inventory and generally contains 10–100 stands. The stand attribute database provides the relative percentage occurrence of each canopy species, the average age of dominant canopy species, timber volume, and crown density.

Required life history attributes for each species modeled in our study were interpreted from the literature (Ai et al., 1985; Duan, 1991; Xu, 1998; Hu et al., 1991), and are listed in Table 1. The maximum fire size in the fire records database was 8,700 ha, and mean fire size 203.7 ha. The mean fire return interval for each land type is listed in Table 2. The spatial input data needed for LANDIS include land type map and initial species age cohort information at each cell.

2.3.1. Land types

Land type in LANDIS stratifies the heterogeneous landscape into relatively homogeneous units. Within each land type, similar environments for species establishment are assumed (Mladenoff and He, 1999). In this study, we derived six land types based primarily on terrain attributes: southern slope, northern slope, ridge top, terrace, residential land, water body. All land types were interpreted from the TM images and the DEM. Non-active land types (not simulated in LANDIS) (water and residential areas) account for 0.76% of the total area, whereas terrace, southern slope, northern slope, and ridge top account for 4.78, 37.25, 42.53, and 14.68% of the study area, respectively. Terrace is a linear feature and in most cases has a width of 2500 m along the Huma River. The attributes for each type are listed in Table 2.

A critical feature of each land type is how readily species can become established on that land type. The establishment coefficient is the probability that a seed can become established given the favorable light condition for species. The establishment coefficients for all species are listed in Table 2, derived from available literature (Li et al., 1987; Zhao et al., 1997; Xu, 1998; Liu et al., 1999).
2.5.2. Initial species age cohort information

For each cell in a stand, we used the SBA approach to generate the species age cohort information based on the forest inventory data. The algorithm assumes that each cell in a stand has a probability of being assigned with a species, which is determined by the relative occurrence of the species within the stand (\(0 \sim 1\)). For example, if a stand has a relative occurrence \(P_1)\) for species 1 and a relative occurrence \(P_2)\) for species 2, for each cell in that stand, a random number \(r\) is drawn from a uniform random number pool, ranging from 0 to 1, to determine which species will be assigned. If \(P_1 < P_2\), then the cell will be assigned with species 1, whereas if \(P_2 < P_1\), then the cell will be assigned with species 2. If \(P_1 = P_2\), then the cell will be blank (no species assigned). If there are no species present in the stand, then all the cells in the stand will be blank. If there is only one species present in the stand (e.g. species 1), a similar algorithm with two probability bins will be implemented. If \(P_1 < P_1\), then the cell will be assigned with species 1, whereas if \(P_1 > P_2\), then the cell will be blank. If there are more than two species in the stand, then similar algorithms with more probability bins will be implemented.

The species assigned to each cell is also assigned to an age cohort. If it is a dominant species in the stand, it will be directly assigned with the age cohort of the dominant species recorded in the stand attribute table. Because there was no age information available for non-dominant species in the stand, we assigned non-dominant species to age cohorts determined by the area weighted average age of this species in the corresponding compartment (calculated from the stands where the species of interest is the dominant species). If there are no stands in the corresponding compartment where the species of interest is the dominant species, the non-dominant species is assigned to age cohort determined by the area weighted average age of this species in the whole study area. This was based on

### Table 2

<table>
<thead>
<tr>
<th>Attributes for each land type of Huzhong area in northeastern China</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Land type</strong></td>
</tr>
<tr>
<td>Southern slope</td>
</tr>
<tr>
<td>Northern slope</td>
</tr>
<tr>
<td>Ridge top</td>
</tr>
<tr>
<td>Terrace</td>
</tr>
<tr>
<td>Residential land</td>
</tr>
<tr>
<td>Water body</td>
</tr>
</tbody>
</table>

**Notes:**
- **MAS** = minimum age of cohort growth required before enough shade is created so that a shade tolerance 5 species can seed into the site;
- **MFRI** = mean fire return interval in years;
- **FI** = fire ignition coefficient;
- **FP** = fire probability coefficient;
- **TLW** = time since last wind throw disturbance;
- **TLF** = time since last fire disturbance;
- **EC1** to **EC8** are the establishment coefficients for larch (Larix gmelini), pine-S (Pinus sylvestris var. mongolica), spruce (Picea koraiensis), pine-P (Pinus pumila), birch (Betula platyphylla), aspen-D (Populus davidiana), aspen-S (Populus maximowiczii), and willow (Chosenia arbustifolia), respectively.
the assumption that the area weighted average age of species at the compartment level or the landscape level (whole study area) reflects the age of this species at the stand level. Age information for pine-P was missing in the forest inventory. In this study, we arbitrarily assigned all cohorts of pine-P to the 90–100-year cohort. Because the purpose of our study is not to predict the succession dynamics of pine-P, but to explore the uncertainty propagation, this arbitrary assignment is acceptable.

Because of the probabilistic nature of the SBA approach, the input map does not reflect the exact species age cohort information for each cell on the ground. But the algorithm does accurately reflect species composition at the stand level. The SBA approach we used is based on the assumption that there is only one species present on each cell. Even though this is not realistic on the ground especially when the cell is large, it does provide a reasonable data set to conduct uncertainty analysis.

2.4. Uncertainty analysis
2.4.1. Monte Carlo simulation

We repeated the SBA approach 20 times and generated 20 species composition maps (Fig. 1a). Each map was then used as a LANDIS input to simulate forest landscape change for 500 years. For each species and each species composition map, LANDIS generated a species age cohort map at each 10-year time interval (Fig. 1b). Then, all the 20 replicate maps for a single species were overlaid to generate a majority species age cohort (MSAC) map with each cell assigned with the species age cohort that appears most frequently in the overlaid stack (a set of 20 realizations of the same cell) (Fig. 1c). For example, if there are ten 10–20-year cohorts, three 50–60-year cohorts, and seven 80–90-year cohorts in the overlaid stack for larch, then the corresponding cell in the MSAC map for larch will be the 10–20-year cohort. The recurrence frequency (RF) is the number of replicates of the MSAC in the overlaid stack. In the example just given, RF = 10. If two species age cohorts tie for the highest RF in the stack, one of the two species age cohorts was randomly assigned to the corresponding cell in the MSAC map. If the most frequently occurring cohort in the stack is the "blank" species age cohort, then the corresponding cell in the MSAC map will be "blank". This means there are no cohorts of this species present on this cell, but there may be cohorts of other species present. After the overlaying process, a MSAC map was derived for each species at each 10-year time step. Because only the oldest species age cohort is represented on each cell in the species age cohort map from LANDIS simulation,

![Fig. 1. Uncertainty quantification for a single species. (a) Twenty species composition maps generated from repeated running of stand based assignation approach; (b) 20 species age cohort maps for a single species at time t generated from repeated running of LANDIS on each composition map; (c) the majority species age cohort (MSAC) map derived from overlaying cells at time t (MSAC is the species age cohort appears most frequently in the stack); (d) the map of the recurrence frequency (RF) of MSAC in the stack. The average recurrence frequency (ARF) of the species age cohorts on MSAC map is also calculated from the RF map to capture the overall uncertainty in species age cohort information at the cell level.](image)
there is only one species age cohort on each cell in the MSAC map.

2.4.2. Uncertainty quantification and analysis
For each species, the RF of the MSAC in the overlaid stack was used to quantify the uncertainty in species age cohort information on each cell. Low uncertainty is seen when the RF is high (in this study, 20 was the highest because we conducted 20 replicates), whereas high uncertainty is seen when RF is low (1 was the lowest). The calculation of RF for each species age cohort in the MSAC map resulted in a quantified uncertainty map (the RF map) for each species at each time step (Fig. 1d). The RF map shows the uncertainty in species age cohort information for individual cell, but it cannot explicitly provide the overall uncertainty on the entire MSAC map. Thus, we also calculated the average recurrence frequency (ARF) of the species age cohorts on the MSAC map to capture the overall uncertainty in species age cohort information at the cell level. For each species, ARF$_i$ (ARF for species $i$) was derived by

$$\text{ARF}_i = \frac{\sum_j N_i \cdot \text{RF}_{ij}}{N_i}$$

where $N_i$ is the total number of species age cohorts on the MSAC map for species $i$ and RF$_{ij}$ is the RF of the $j$th species age cohort on the MSAC map. Because there is only one species age cohort on each cell in the MSAC map, $N_i$ equals the number of cells where there is a species age cohort present in the MSAC map. If there are no species age cohorts present on the MSAC map, ARF is set to 0.

For each species, we derived a RF map and an ARF from the MSAC map. ARF allowed us to gain insights into the change in overall uncertainty in species age cohort information at the cell level, while the RF map allowed us to analyze the temporal propagation of uncertainty in species age cohort information for individual cells. The examination of whole map uncertainty (ARF) over simulation years provided a general assessment on how uncertainty in species age cohort information changes, while the examination of uncertainty for individual cell (RF) casts light on how the uncertainty in species age cohort information propagates from cell to cell.

Because one of the objectives of this study was to examine effects of uncertainty at the cell level on the simulation results at the landscape level, we also calculated percent area (PA) and aggregation index (AI) (He et al., 2000) for each species from the species distribution map in the LANDIS output. PA is the percent of the area occupied by a certain species in the study area and AI is a class specific landscape index used to quantify the spatial aggregation of classes. When AI equals 1, the landscape has the highest level of aggregation, and when AI equals 0, the landscape has the lowest level of aggregation. For each species, the coefficient of variation (CV) for PA and AI for the 20 Monte Carlo simulations was used to quantify the variability of species abundance and its spatial pattern at landscape level. Both PA and AI were calculated using APACK, software for calculating landscape metrics (Mladenoff and DeZonia, 2000). Higher CV values indicate higher uncertainty.

Because fire disturbances will certainly increase the complexity of uncertainty propagation, it would be difficult to analyze the uncertainty propagation based only on Monte Carlo simulations with fire disturbances. Thus, we also conducted 20 Monte Carlo simulations of LANDIS without fire disturbances. The results of uncertainty propagation derived from the Monte Carlo simulation without fire disturbance will help to analyze the uncertainty propagation with fire disturbances.

3. Results
3.1. Uncertainty at the cell level without fire disturbance

Results show that, for all species except for pine-S and aspen-S (species with a low probability of establishment), ARF decreases with simulation year and then tends to stabilize (Fig. 2). At simulation year 0, ARF for both larch and pine-P is larger than 16 and ARF for all other species is larger than 12 (Fig. 2). The high value of ARF at simulation year 0 suggests that the SBA approach does not create much uncertainty in the species age cohort input maps. Before simulation year 160, the ARF for larch is greater than 10, which indicates a reasonably low level of uncertainty. ARF is greater than 10 before simulation year 200 for spruce, 130 for pine-P, 110 for birch, 120 for aspen-
D, and 50 for willow. This suggests that uncertainty is relatively low at the beginning of the simulation. However, results show that ARF for most species decreases to a small value at a certain simulation year and then tends to stabilize. For larch and spruce, ARF stabilizes at simulation year 260 (Fig. 2a), at simulation year 150 for birch, at simulation year 170 for aspen-D, and at simulation year 190 for willow (Fig. 2b). These results suggest that the uncertainty in species age cohort information at the cell level increases through simulated time and finally approaches an equilibrium state.

A careful examination of a sample area in the RF map and MSAC map of larch (Figs. 3 and 4) shows that there are two reasons underlying the increase of overall uncertainty in species age cohort information at the cell level before the uncertainty approaches its equilibrium state: the relatively high variability of the species age cohorts in areas recently colonized by a species and the relatively low variability of the older species age cohorts, which are subsequently removed by species mortality. The patterns seen through time result primarily from the establishment and senescence of cohorts. At simulation year 0, larch age cohorts have relatively high RF (>10) and there is a large “open area” (area where there are no larch age cohorts, but there may be cohorts of other species) (Figs. 3a and 4a). At simulation year 50, most of the “open area” is now occupied by larch (Fig. 4b), but all the newly established larch age cohorts have relatively low RFs (<10) (Fig. 3b). This explains the sharp decrease of ARF between simulation year 0 and 50 (Fig. 2a). The low RF of larch age cohorts in these newly colonized cells is produced by the stochastic seed dispersal and seedling establishment process simulated in the model. In LANDIS, species disperse stochastically. But even if seed disperses into a cell, there are still uncertainties on whether the new seedling can establish, which is dependent on the species shade tolerance and establishment coefficient (He and Mladenoff, 1999a). Because of these uncertainties, the colonized areas are likely to have low RF of species age cohorts. At simulation year 150, a large “open area” occurs (Fig. 3d) due to the mortality of larch age cohorts as they reach their longevity (Fig. 4d). Because the larch age cohorts removed by mortality all have relatively high RFs (>10) (Fig. 3c), ARF for larch decreases drastically between the simulation year 100 and simulation year 150 (Fig. 2a). After simulation year 300, although there is mortality of old species age cohorts and establishment of young species
Fig. 3. RF map for larch at different simulation years. “Open area” is the area where there are no cohorts of larch, but there may be cohorts of other species.
Fig. 4. Majority species age cohort (MSAC) map for larch at different simulation years.
age cohorts (Fig. 4h–k). ARF for larch remains low and stable (Fig. 2a). This is because both the newly established species age cohorts and the older species age cohorts removed by mortality have low RFs (<6) (Fig. 3b–k).

The stepwise decrease of ARF of pine-P with simulation year further illustrates the uncertainty propagation following species mortality. The ARF of pine-P decreases to 7 at simulation year 140 when all initial species age cohorts reach their longevity and die (Fig. 2a). The loss of areas where the RF is high caused the sudden decrease of ARF of pine-P. The stability of ARF of pine-P before year 100 and between year 140 and 220 is resulted from the fact that most young established species age cohorts are not represented in the MSAC map, because the most frequently occurred cell in the overlaid stack is “blank” cell. Therefore, uncertainty produced by the stochastic seed dispersal and seedling establishment process is mostly excluded in the RF map. That is why the ARF of pine-P tends to stabilize before simulation year 100. The decrease of ARF to 0 at simulation year 230 (Fig. 2d) is produced by the coincident death of species age cohorts in the MSAC map, which happens to be reproduced during a single simulation step.

3.2. Uncertainty at the landscape level without fire disturbance

For all species except for pine-S and pine-P, CV for both PA (Fig. 5) and AI (Fig. 6) do not increase with simulation year and are less than 5% throughout the simulation. This suggests that although the uncertainty of species age cohorts at the cell level for each species increases with simulation year, species percent area and their spatial pattern (measured by the aggregation index) are not substantially affected. Careful examination shows that the increase of CV of both PA (Fig. 5) and AI (Fig. 6) for pine-S and pine-P is not produced by uncertainties of species age structure at the cell level, but by the decrease of PA to extremely low values (PA < 1) (Fig. 7b). The decrease of PA produced more sparsely distributed species age cohorts and caused AI to decrease. Because CV is calculated as a percent of the mean, a given variability will produce higher CV values when centered on very low mean values.

![Figure 5](image-url)
3.3. Uncertainty at the cell level with fire disturbance

Although fire disturbance increases the complexity of uncertainty propagation, the effect of fire disturbance can be inferred by the results presented above. Similar to natural mortality, fire disturbance removes the old species age cohorts with high RF. Then the stochastic seed dispersal and establishment process will occur in the open area with young species age cohorts having low RF. Consequently, fire disturbance will increase the overall uncertainty in species age cohort information at the cell level (shown by a decrease of ARF). When the uncertainty in the species age cohort information in the recently colonized areas is equal to the uncertainty in the older species age cohort information, the overall
uncertainty will reach an equilibrium state. The ARF for larch of 20 Monte Carlo simulations with fire disturbance confirms this inference (Fig. 8). Results also show that, under fire disturbance, uncertainty increases more rapidly with simulation year. Without fire disturbance, ARF for larch approaches an equilibrium state at simulation year 260, whereas with fire disturbance, the equilibrium state is reached at simulation year 200.

3.4. Uncertainty at the landscape level with fire disturbance

CV of PA and AI for larch with fire disturbance maintain a relatively low value between simulation year 0 and simulation year 50 (Fig. 9). This is because no fires occurred between simulation year 0 and simulation year 50 because of the short time since last fire assigned at simulation year 0. This suggests that fire can slightly increase CV of PA and CV of AI. However, when fires occur after simulation year 50, although there are fluctuations in both CV of PA and AI (caused by the fluctuations of fire damaged area in different decades), they do not increase with simulation year and remain less than 1% throughout the simulation (Fig. 9). This shows that, under fire disturbance, species percent area and their spatial pattern measured by the aggregation index are also not substantively affected by uncertainties of species age structure at the cell level.

4. Discussion

4.1. Number of Monte Carlo simulation

In this study, the Monte Carlo method was successfully used to explore the temporal propagation of spatial uncertainty of a forest landscape model, LANDIS. Due to the large data volume produced by LANDIS (1.62 GB for the output of a single simulation) and complexity of output data analysis, it is unfeasible to conduct hundreds of replicates. Thus, it is important to...
use a relatively small number of simulations to capture the uncertainty propagation. As for Monte Carlo simulations without fire disturbance, ARFs, RF, and MSAC maps for larch showed that the dynamics of seed dispersal, seedling establishment, mortality, and succession continuously cause ARF to decrease or uncertainty to increase until the uncertainty in the species age cohort information of the recently colonized areas is equal to the uncertainty in the older species age cohort information. At this point, the overall uncertainty approaches an equilibrium state and the error in the original species composition map has little effect on model results. Because LANDIS simulates the succession dynamics for all species using the same algorithm, the mechanism of uncertainty propagation derived for larch is also applicable to all other species.

However, results show that there are abnormal increments of ARF for pine-S and aspen-S (Fig. 2a–b). Careful examinations revealed that the extremely low establishment probability of aspen-S accounts for its abnormal increments of ARF. The low establishment probability is determined by its low establishment coefficient (0.07) in the terrace land type (Table 2) and low shade tolerance (class 1 in Table 1). If a species has a very low establishment probability, it is very likely that the most frequently occurring cell in the overlaid stack will be “blank”. Thus, few young established species age cohorts would be included in the MSAC map. After the removal of most old species age cohorts by mortality, only a small number of species age cohorts are present on the MSAC map. If occasionally there is a species age cohort in the MSAC map that has a high RF, then the ARF will increase abnormally. This suggests that if a species has a low probability of establishment and poor dispersal ability, a larger number of simulations should be conducted to capture the process of uncertainty propagation.

For pine-S, both its low shade tolerance (1, Table 1) and relatively poor dispersal ability (effective dispersal distance is 50) account for its abnormal increase of ARF. In most cases, pine-S is faced with unfavorable light conditions produced by high canopy cover, since early succession species will occupy the cell before the arrival of pine-S. Because light condition checking is one of the three steps for species establishment in LANDIS, the unfavorable light condition leads to a relatively low establishment probability. Thus, few new established species age cohorts would be included in the MSAC map. Combined with its relatively poor dispersal ability, only a small number of species age cohorts are present on the MSAC map after the removal of most old species age cohorts by mortality. If occasionally there is a species age cohort in the MSAC map that has a high RF, then the ARF will increase abnormally. This suggests that if a species has a low probability of establishment and poor dispersal ability, a larger number of simulations should be conducted to capture the process of uncertainty propagation.

4.2. Implication of results

A challenge in ecology is to understand broad scale patterns emerging from the complexity of interactions at lower scales (O’Neil, 1989; Wiens, 1989; Wiens and Milne, 1989; Levin, 1992; Levin et al., 1997). Spatially explicit forest models present a potential to meet the challenge. However, natural systems are always characterized by much uncertainty (Clark et al., 2001). In building or using these models, it is important to determine how much detail at the fine level is essential to predict more macroscopic regularities (Levin et al., 1997). Certain fine scale details and the uncertainty associated with them are not essential and will not have much effect on regularities at large spatial and time scales. Pacala et al. (1996) showed that the community level predictions (succession dynamics, intraspecifically clumped and interspecifically segregated spatial distributions) by a spatially explicit forest model (SORTIE) were robust given the level of sampling uncertainty in the study. Deutschman et al. (1999) showed that SORTIE was surprisingly insensitive to the amount of detail used in the calculation of the local resource, light.

The results of this study show that LANDIS simulation results at the landscape level (species percent area and their spatial pattern) are not sensitive to the uncertainty in species age cohort information at each cell level induced by SBA. This suggests that LANDIS can be used to predict the forest landscape change at broad spatial and temporal scales even if accurate species age cohort information at each cell is not available. However, results also show that uncertainty in species age cohort information at the cell level increases with simulation year before reaching its equilibrium state. Thus,
it would be inadvisable to predict the species age cohort distribution for specific cells using LANDIS. Just as Levin et al. (1997) have pointed out, “such models should not be expected to predict where every tree will be at each point in time; only aggregate statistical properties can be reliably predicted, typically over broad spatial and temporal scales”.

5. Conclusions

The Monte Carlo method was successfully used to access uncertainties in species age cohort information at the cell level. Twenty simulation runs were enough to capture species age cohort uncertainty for all but two species (pine-S and aspen-S). The results showed that overall uncertainty in species age cohort information was relatively low at the beginning of the simulation. The time period at which uncertainty substantially increased varied by species. Fire disturbance, seed dispersal, seedling establishment, mortality, and succession caused uncertainty to increase with simulation year. Finally, the uncertainty in species age cohort information reached an equilibrium state where the uncertainty in the original species composition map had little effect on later successional dynamics. Again, the time period at which this equilibrium was reached varied by species. Although the uncertainty in species age cohort information at the cell level increases with simulation year, species percent area and their spatial pattern measured by the aggregation index remain relatively unaffected (with or without fire disturbance). Since the purpose of research using LANDIS is to predict the overall landscape pattern change, cell-level uncertainty introduced by SBA method is acceptable.

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References