Improving the formulation of tree growth and succession in a spatially explicit landscape model

Sabine Schumacher⁎, Harald Bugmann, David J. Mladenoff

⁎ Department of Environmental Sciences, Swiss Federal Institute of Technology Zurich, Mountain Forest Ecology, ETH–Zentrum, CH-8092 Zurich, Switzerland

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Abstract

Long-term forest landscape dynamics are determined by a set of driving forces including large-scale natural disturbances, land-use, the physical environment, and stand-scale succession processes. Landscape models have an important role as tools for synthesizing existing information and making projections of possible future vegetation dynamics on large spatial scales. However, current landscape models cannot readily be used to study: (1) the change from weakly to strongly disturbed landscapes; (2) the impact of changing climatic parameters on landscape-scale dynamics; and (3) the effects of such changes on vegetation structure. Using European mountain forests as a case study, this paper focuses on improving the well-established LANDIS landscape model so that it can be applied to study these research questions.

We integrated a simple tree succession sub-model in LANDIS, which incorporates quantitative descriptions of forest structure, and included sub-models to capture the influences of competition as well as climatic and edaphic parameters on tree population dynamics.

The new model was subjected to a number of quantitative tests against measured data. It accurately predicted the altitudinal distribution of vegetation properties under managed as well as unmanaged conditions in the Dischma valley (Switzerland), and it provided realistic and accurate patterns of vegetation recovery following wind disturbance events, in spite of the very simple model formulations.

To demonstrate the utility of the added detail, we applied the model in scenario mode under a range of changes in climatic and disturbance parameters, assuming a continuation of the current management regime. The simulations showed that the various driving forces have quite different effects on different species, and that their combined effect differs from one scenario to the next. Notably, there are few models that integrate forest growth and succession with disturbance dynamics in a semi-mechanistic manner. Our version of LANDIS achieves this integration based on simple concepts and methods that do not require

⁎ Corresponding author. Tel.: +41 1 6320 759; fax: +41 1 6321 146.
E-mail address: sabine.schumacher@env.ethz.ch (S. Schumacher).
many parameter estimates. We conclude that the new model has the potential to provide an integrated picture of the impacts of both direct and indirect effects of climate change on forest landscape dynamics.

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1. Introduction

Mountain forests are characterized by complex spatial vegetation patterns. Steep environmental gradients and topographic differentiation generate micro-scale conditions that limit tree establishment and growth (Ott et al., 1997). In addition, periodic natural (e.g., windstorms, wildfires, avalanches) and anthropogenic (e.g., management) disturbances strongly influence vegetation patterns in mountain landscapes. Understanding the long-term dynamics of these systems is essential for planning forest management and for predicting the consequences of environmental changes, to name just a few research issues. Thus, we need to be able to predict the effects of the complex interaction of the various agents that drive forest dynamics at the landscape scale.

The limitations of empirical studies in addressing the questions that relate to landscape dynamics are evident. To study landscape changes, research on spatial and temporal scales larger than those amenable to experiments or stand-level observational studies is required. Often, models are the only way to consider the interactions and changes within forest landscape systems that cannot be tested under real-world conditions. Thus, landscape-level ecological models are essential to improve our understanding of the dynamics of large-scale processes and as a crucial basis for analyzing the consequences of changes in the ecological factors involved.

Typically, the landscape models developed in recent years were designed to predict changes in land cover patterns across large geographic areas (the scale of $10^3$–$10^6$ ha) and over long time spans (e.g., hundreds of years) (e.g., Baker, 1989; Mladenoff and Baker, 1999). Landscape models usually focus on processes such as seed dispersal, wind and fire disturbances, insect infestations and harvesting. For this reason, they typically include simplified representations (parameterizations) of stand-scale ecological processes such as tree growth and competition. Also, the description of stand structure in these models is often greatly simplified (Roberts, 1996; He and Mladenoff, 1999b). Such simplified formulations of vegetation dynamics may be sufficient to represent landscapes where fine-scale patterns and processes are frequently overridden by large-scale disturbances. In landscapes that are disturbed only infrequently today, it is difficult to apply these models. To study weakly disturbed systems and particularly those where a change of disturbance regime is anticipated in coming decades as an impact of Global Changes, landscape models that contain a more detailed representation of stand-scale processes and of their interactions with the large-scale disturbance regime may be required.

European mountain forests, on which our study focuses, are influenced today to a certain extent by large-scale processes such as windthrow, and may be increasingly subject to a changing wildfire regime. At the same time, landscape-scale dynamics in these systems are also strongly determined by a range of factors and processes that operate at the stand and patch scales (Ott et al., 1997). To investigate the landscape-scale dynamics of European mountain forests, we based our study on the well-established LANDIS landscape model (He and Mladenoff, 1999b; He and Mladenoff, 1999a; He et al., 1999a; He et al., 1999b; Mladenoff and He, 1999) as a starting point. LANDIS integrates the range of large-scale processes relevant for our project. However, we were not able to realistically reproduce landscape patterns in the European Alps with the unmodified version 3.40 (He and Mladenoff, 1999b) of this model, for the reasons outlined below.

LANDIS does not explicitly simulate tree growth, and does not account for inter-specific competition effects during stand development. Instead, it is based on the assumption that establishment probabilities reflect the factors affecting the species’ performance during succession. Once established, trees die only because of large-scale disturbances, or when they approach their maximum lifespan. Thus, applying the model to weakly disturbed landscapes resulted—in the long run—in the domination of shade-tolerant species with long
lifespans, even if they were assigned very low establishment probabilities. Under the current weak disturbance regime of the central European Alps, LANDIS produced a strong dominance of subalpine (1600–2300 m a.s.l.) landscapes by *Pinus cembra* instead of the widespread *Picea abies* (cf. Ellenberg, 1996). In reality, *P. cembra* may reach old age, but is not normally competitive against *P. abies* except at the highest elevations and in dry continental climates. We had to conclude that the forest stand description and stand-scale ecological processes included in the model were too simplistic to realistically simulate forest dynamics in weakly disturbed landscapes, thus making it impossible to study their fate under a changing disturbance regime.

In addition, the establishment probabilities in LANDIS have to be defined by the user, i.e. they do not emerge from the interactions of the modeled processes. This does not allow the user to simulate the effects of a changing environment (e.g. climate change) on landscape properties, or to simulate transitions of species composition over a climatic gradient without basically prescribing the outcome of such changes via modified parameter values. Thus, establishment probabilities have a decisive effect with regard to determining species composition across the landscape.

Finally, LANDIS incorporates only presence/absence data of tree age-classes, and thus does not provide any quantitative detail about stand composition or stand structure at the level of the individual grid cell. Therefore, based on these simple variables it is difficult to model succession (i.e., processes such as competition between trees) more accurately, or to use LANDIS to assess the effects of landscape properties on, for example, ecologically relevant variables such as habitat suitability for wildlife.

To overcome these shortcomings, we replaced the stand-level model parts of LANDIS with an improved tree growth and succession sub-model. This sub-model contains (1) a more detailed quantitative description of forest structure in each simulated grid cell, and (2) more mechanistic formulations of growth and competition than currently incorporated in landscape models. Tree- and stand-scale ecological processes in the new model are mostly derived from approaches in the widely used gap models (e.g. Shugart, 1984; Urban and Shugart, 1992; Liu and Ashton, 1995; Bugmann et al., 1996), but they were simplified considerably compared to their original implementation.

We introduced these model modifications with the following three objectives: (1) to be able to investigate the influence of a changing disturbance regime on landscape properties, i.e. to study the transition from currently weakly disturbed to more strongly disturbed landscapes in the future; (2) to be able to study the impacts of changing climatic parameters on landscape dynamics without having to make a priori assumptions about these effects, i.e. to obtain a landscape-level model that is sensitive to climate and soil properties, and (3) to investigate landscape properties that are relevant for ecosystem management, based on variables relating to stand biomass, species composition, and stand structure.

2. Model description

We first give a brief overview of the original LANDIS model, followed by a description of the expanded model that introduces the overall model structure and describes major model modifications.

2.1. Overview of the original LANDIS model

The LANDIS model has been described in detail elsewhere (He and Mladenoff, 1999b; He and Mladenoff, 1999a; He et al., 1999a; He et al., 1999b; Mladenoff and He, 1999). It is a spatially explicit, raster-based, and stochastic model designed to simulate forest change in combination with disturbance regimes, such as fire, windthrow, and forest management. The model simulates vegetation dynamics on large landscapes (on a scale of $10^4$–$10^6$ ha) and over long time spans (e.g. hundreds of years) in 10-year time steps. It simulates forest stands on a rectangular grid with a user-defined size (usually 30 m × 30 m). Each grid cell contains coarse vegetation information at the species level. Vegetation status is defined by the presence/absence data of 10-year age cohorts of each species. Actual size and number of trees are not modeled. For each species, a set of attributes such as longevity, age of first reproduction, shade and fire tolerance, and seeding distance are driving vegetation dynamics. Furthermore, each grid cell belongs to a so-called “land type”. These user-defined land types are the basis for distinguishing between different site characteristics, environmental
conditions, and species-specific establishment probabilities.

The establishment of new tree cohorts is modeled based on seed availability and a simple parameterization of light and site conditions (Mladenoff and He, 1999). Seed availability is determined by seed travel distances and the age of maturity of each tree species. Seed travel distance is defined by species-specific effective and maximum parameters (He and Mladenoff, 1999a). Species’ differences in their ability to reproduce vegetatively after disturbances are also taken into account in the model. For successful establishment, propagules have to be available in the grid cell, and light conditions have to be favorable. Species can establish only if they are more shade-tolerant than any other species that is already occurring in the grid cell. Whether a new cohort will actually establish is further dependent on species-specific establishment coefficients, as discussed above. They reflect the relative potential of the various species to successfully establish under different environmental conditions.

In LANDIS, tree growth is not modeled explicitly. Only the age of the surviving tree cohorts (see below) is incremented in each time step. Thus, the model is based on the implicit assumption that establishment probabilities also reflect the factors affecting the species’ growth success (cf. Roberts, 1996).

Mortality is implemented in LANDIS as an age-dependent function. Age-dependent background mortality occurs in the last fifth of a species’ potential lifespan, during which the mortality probability increases gradually with age. In addition (and very importantly), mortality is also caused by the various disturbance regimes, as outlined below.

Wildfires are simulated stochastically using mean fire return intervals and fire sizes, which are parameters by land type. Fire severity is simulated based on fire intensity (determined by time since last disturbance), the age of a cohort, and fire tolerance (He and Mladenoff, 1999b). Windthrow is simulated stochastically, in a manner similar to fire. Susceptibility to windthrow is approximated based on the maximum lifespan and the current age of the trees. The interaction of wind and fire regimes is implemented by increased fire intensity after windthrows, to represent the effects of fuel accumulation (He and Mladenoff, 1999b). The harvest module is based on management areas with specific management objectives. Each management area is divided into stands. Timber harvesting can be restricted to stand boundaries or may be allowed to ‘spread’ until a defined harvest size is covered. The order in which stands are treated is determined by ranking algorithms that prioritize stands by criteria such as stand age or economic value. Harvest events remove selected age cohorts of selected tree species from each cell (Gustafson et al., 2000).

2.2. Design of the modified model

We extended the patch-scale formulations of LANDIS by (1) introducing a more detailed description of the properties of tree cohorts; (2) incorporating new formulations for tree growth and succession; and (3) adding routines describing the physical environment, i.e. light availability, temperature, and soil moisture. This resulted in a model that consists of two main parts: a ‘local’ succession model that operates on each grid cell with a time step of 1 year, and a landscape model that contains processes operating over several cells in 10-year time steps (Fig. 1).

2.2.1. Stand-scale processes

Forest stand structure is modeled based on quantitative information of tree age cohorts, i.e. groups of trees of the same species and age. These cohorts are characterized by the average biomass of an individual tree ($B_i$) and the number of trees in the cohort ($N_c$), not just presence/absence data as in the original LANDIS model. Thus, the biomass of a cohort ($B_c$) is calculated...
according to Eq. (1).

\[ B_c = B_i N_c \]

(1)

The change of cohort biomass is tracked using a yearly time step in the model (cf. Fig. 1). Differentiation of Eq. (1) yields

\[ \frac{dB_c}{dt} = \frac{dB_i}{dt} N_c + \frac{dN_c}{dt} B_i \]

(2)

The first term represents changes in biomass of individual plants (growth), whereas the second term tracks changes in the number of individuals that form an age cohort (mortality).

2.2.1.1. Tree growth. The growth model is based on the a priori assumption of a logistic growth relation (Eq. (3)) for the isolated plant (Eq. (3)). Note that in the present context, this equation simply represents a phenomenological description of individual tree growth, not a model of population-level dynamics.

\[ \frac{dB_i}{dt} = r_i(t) \left( 1 - \frac{B_i(t)}{K_i(t)} \right) B_i(t) \]

(3)

The individual growth rate, \( r_i(t) \), is derived from a species-specific maximum growth rate (\( r_s \)), which represents growth under optimum environmental conditions. The growth rate \( r_i(t) \) is calculated as a function of three growth-limiting factors, light availability (light\( rf \)), the sum of degree-days (DD\( rf \)) and a drought index (DrStr\( rf \)), as described below. We applied Liebig’s “Law of the Minimum” to combine these growth response factors.

\[ r_i(t) = r_s \min(light rf(t), DD rf(t), DrStr rf(t)) \]

(4)

Also, maximum plant size, \( K_i(t) \), is implemented as a function of environmental conditions (Eq. (5)). It is reduced by degree-days (DD\( rf \)) and drought (DrStr\( rf \)), starting from a species-specific maximum plant size under optimal environmental conditions (\( K_s \)).

\[ K_i(t) = K_s \min(DD rf(t), DrStr rf(t)) \]

(5)

The light response function (light\( rf \)) is implemented as it is in a range of gap models similar to the formulation suggested by Urban and Shugart (1992) (cf. Fig. 2a). We assumed that this growth reduction is effective only within a closed canopy; canopy openness is defined by available light at the forest floor (\( \text{avL}_{ff} \geq \text{avL}_{open} \); cf. Table 1). A proxy for light availability is calculated for each cohort using the Beer–Lambert law (Monsi and Saeki, 1953); the corresponding light extinction coefficient is given in Table 1. Total leaf area for each tree cohort is estimated from tree diameter at breast height using the allometric equations by Bugmann (1994). Tree diameter is calculated from aboveground biomass based on the equation by Schroeder et al. (1997). In the model, a cohort is
assumed to be shaded by the leaf area of all cohorts in the same cell that have trees of larger individual biomass, and thus can assumed to be taller than the target cohort. In addition, based on empirical evidence from Schulze et al. (1977), we assume that one third of the leaf area of a cohort is responsible for self-shading.

To express temperature limitations on tree growth, we used the degree-day response function (DD$_{fj}$) introduced by Bugmann and Solomon (2000, p. 99, Eq. (3); cf. Fig. 2a). For this, the annual sum of growing degree-days (DD) is derived based on the method described by Bugmann (1996). Finally, the drought response function (DrStr$_{fj}$) is based on the relationship proposed by Bassett (1964), which was also used in the model by Bugmann (1994, p. 66, Eq. (3.26); cf. Fig. 2c). This relationship is based on a drought index (Bugmann and Solomon, 2000, p. 98, their Eq. (1)), calculated using the water balance model by Bugmann and Cramer (1998).

The latter two growth-limiting factors require climatic input data, i.e. the mean monthly temperatures and the monthly sums of precipitation. The simulation model obtains this data for each simulation year by randomly selecting a year from a historical climate data set from a nearby weather station. The climatic parameters for every grid cell are adjusted for elevation using lapse rates, thus resulting in a landscape-wide input data set of weather conditions in any given simulation year. In addition, each grid cell in the model has a user-specified elevation, slope, aspect, and soil type, which are required by the soil water balance model.

2.2.1.2. Tree mortality. In analogy to the growth part of the model, a yearly mortality rate, $m_i(t)$, is implemented as follows:

$$\frac{dN_i}{dt} = -m_i(t)N_i$$  \hspace{1cm} (6)

The mortality rate is composed of a growth-dependent ($m_{\text{stress}}$), a density-dependent ($m_{\text{dense}}$) and an intrinsic ($m_{\text{age}}$) component. These three factors do not operate independently. The first two factors represent the effects of competition, and therefore cannot be effective simultaneously. In addition, it is well known that low growth rates often represent an adaptation to low resource availability (cf. Loehle, 1988), which leads to potentially high longevity. To represent this ecological tradeoff, we assume that trees exposed to competition-related mortality are not at the same time subject to intrinsic mortality. Consequently, a maximum function was chosen to combine these three mortality factors.

$$m_i(t) = \max(m_{\text{stress}}(t), m_{\text{dense}}(t), m_{\text{age}}(t)) \hspace{1cm} (7)$$

The stress-dependent mortality factor ($m_{\text{stress}}$) is based on the assumption that only 1% of species would survive 10 years of consecutive stress. Stress is defined here as the condition when one of the three growth response factors described above drops below a threshold value, $m_{\text{fj}}$. Stress-related mortality occurs only when a minimum number of consecutive stress years ($\text{minYrs}$) has accumulated (Eq. (8)). The counter for the number of stress years ($\text{sYrs}$) is increased by one each time ‘stress’ occurs, and is set back to zero otherwise.

$$m_{\text{stress}} = \begin{cases} 1 - e^{0.01/10} & \text{sYrs} \geq \text{minYrs} \\ 0 & \text{else} \end{cases} \hspace{1cm} (8)$$

Density-dependent mortality ($m_{\text{dense}}$) occurs if total stand biomass exceeds maximum stand biomass ($\text{maxB}_f$). This value approximates the carrying capacity of a forest stand and is user-defined. The mortality rate is calculated based on the difference between maximum stand biomass, $\text{maxB}_f$, and simulated stand biomass $B_i$. This excess cover is divided by the number of cohorts that occur on the cell ($\text{numCoho}_i$) to determine the excess biomass of each cohort. This biomass is then used to reduce the cohort’s biomass:

$$m_{\text{dense}} = \max(\text{maxB}_f - B_i, 0) \frac{1}{\text{numCoho}_i} \hspace{1cm} (9)$$

Intrinsic mortality is accounted for by a constant probability of death throughout the lifetime of the tree, assuming that 1% of trees belonging to particular species reach their maximum longevity ($\text{maxAge}_f$). We used the equation as commonly implemented in forest gap models (e.g., Botkin, 1993; Bugmann, 1996):

$$m_{\text{age}} = 1 - e^{0.01/\text{maxAge}_f} \hspace{1cm} (10)$$

In addition to these annual mortality rates, large-scale disturbances can cause mortality. These exogenous mortality causes are simulated only once each decade (see below).

2.2.1.3. Tree regeneration. Tree regeneration is simulated based on seed availability and environmental
In the first step, the biomass of newly established cohorts \( B_i(t=10) \) at the end of a given decade is calculated from an initial tree biomass, which is the same for all species \( B_i(t=0) \). Biomass increment over 10 years is tracked by an exponential growth function (Eq. (11)). Growth rates \( \beta_i \) are reduced every year by environmental conditions in an analogous manner to those described in the ‘tree growth’ sub-model (Eq. (4)). This results in larger establishment biomass for species with higher growth rates and for those with a higher tolerance of unfavorable environmental conditions.

\[
B_i(t = 10) = B_i(t + 1) = B_i(t)(1 + \beta_i(t)) \tag{11}
\]

In the second step, the model tracks the number of years (out of 10) in which environmental conditions have been favorable for the establishment of a given species \( estYrs_s \). The routine that checks site conditions every year was implemented similarly to those found in gap models (e.g., Bugmann, 1994, 1996; Shugart, 1984): a particular year is favorable for establishment only if the following four criteria are met: (1) available light at forest floor has to be higher than a species-specific threshold value \( minL_s \); (2) winter temperature (mean temperature of the coldest month) has to be higher than a threshold minimum temperature \( minT_c \); (3) the sum of growing degree-days has to exceed the minimum species-specific requirement \( minDD_s \); (4) browsing probability is calculated after Bugmann (1994, p. 60, Eq. (3.4)) based on browsing pressure \( brows \) and a species-specific browsing tolerance \( brTol_s \); it has to be smaller than a uniformly distributed random number. In addition, actual tree establishment occurs only in a fraction of the years when all four factors are favorable, to take into account that additional factors which are not explicitly modeled may prevent establishment. This is expressed by the user-defined establishment coefficient \( estCoeff_s \).

more, after each 10 year period, the establishment routine continues only if total stand biomass is at least ten percent smaller than maximum stand biomass \( (maxB_f) \). If stand biomass is higher, newly established cohorts would die in the next growth period due to density-related mortality (see section ‘Tree mortality’, above).

Finally, if stand biomass permits establishment, the density of newly established trees \( N_{est}(t = 10) \) is determined. \( N_{est}(t = 10) \) is calculated based on a user-defined maximum establishment density \( (potDem_s) \), which is reduced linearly by light availability at the forest floor \( (avL_f) \), resulting in smaller densities of tree regeneration under a dense canopy. The resulting tree density is distributed among all tree species with available seeds \( (sumSpec_s) \) proportionally to the species’ growth performance in the establishment layer, as an assessment of plant vigor. Growth performance \( (grPer_s) \) is defined here as the ratio of realized growth increment during the last 10 years to the maximum possible growth increment under optimal environmental conditions. We assumed that species with better growth performance are capable of establishing more trees than species whose saplings do not grow well. Furthermore, the potential regeneration density of each species is reduced proportionally to the species-specific number of years over the last 10-year period when establishment would have been possible \( (estYrs_s) \), to take into account that unfavorable establishment years cause a reduction of the establishment density of a species cf. (Eq. (12)).

\[
N_{est}(t = 10) = potDem_s \times avL_f \times \frac{grPer_s \times estYrs_s}{\sum_{s=1}^{sumSpec_s} grPer_s \times 10} \tag{12}
\]

2.2.2. Landscape-scale processes

Tree mortality is caused not only by the ‘endogenous’ mechanisms included in the succession sub-model described above. Exogenous sources of mortality included in LANDIS are windthrow, fire and forest management. These large-scale disturbance regimes are simulated with a 10-year time-step and are largely unchanged from the original LANDIS model. Minor modifications had to be made to adjust these processes to the altered model structure described above. First, we defined tree susceptibility towards disturbances, and tree selection for harvesting based on the tree diameter classes (derived from biomass) instead of life span and
Table 2  
Windthrow susceptibility classes defined by diameter class with associated mortality probability of single trees for each class as implemented in the model. The values were estimated based on literature data (e.g., Canham et al., 2001).

<table>
<thead>
<tr>
<th>Diameter (dbh) class (cm)</th>
<th>Mortality probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;10</td>
<td>0.25</td>
</tr>
<tr>
<td>10–20</td>
<td>0.50</td>
</tr>
<tr>
<td>20–30</td>
<td>0.70</td>
</tr>
<tr>
<td>30–40</td>
<td>0.90</td>
</tr>
<tr>
<td>&gt;40</td>
<td>1.00</td>
</tr>
</tbody>
</table>

The model requires parameter sets describing tree species, physical site conditions and disturbance regimes. General parameters used in the modified model are given in Table 1. Species parameters include life-history traits, environmental responses, and demographic rates. These were estimated based on data from literature and are summarized in Table 3. Site parameters can be defined by ecoregions (land types), but in this study, we defined only one ecoregion (cf. Table 4).

3.2. Model parameters

We studied landscape dynamics in the Dischma valley, which is located near Davos at 46.8°N, 9.8°E in the eastern part of the Swiss Alps. It is a typical Alpine valley extending from 1500 to 3200 m a.s.l. Mean annual rainfall at 1560 m a.s.l. (climate station Davos–Platz) is 1043 mm, while nearby at 2560 m a.s.l. (Weissfluhjoch), it amounts to 1276 mm (SMA, 1960–2000). The mean annual temperature in Davos is 3.2°C and at Weissfluhjoch –2.4°C (SMA, 1960–2000). The main soil types are brown soil, brown podzols, and podzols. In this study, we focused only on the northern part of the valley. This part of the valley consists of about 1700 ha of which 450 ha are forested today. Forests up to 2000 m a.s.l. are typically dominated by Picea abies, while forest composition at higher elevations is dominated increasingly by Larix decidua and Pinus cembra. The current tree line is located at ca. 2100 m a.s.l., well below the natural tree line because of century-long human influences (alpine pastures).

3.3. Simulation experiments

We ran various sets of simulation experiments to test and apply the model in the Dischma Valley. We started...
Table 3
Species life-history parameters

<table>
<thead>
<tr>
<th>Species</th>
<th>r (year⁻¹)</th>
<th>Ks (m)</th>
<th>maxAge (year)</th>
<th>matu (year)</th>
<th>EDs (m)</th>
<th>MDs (m)</th>
<th>spAge (year)</th>
<th>folType</th>
<th>shdTol</th>
<th>minDD (d)</th>
<th>minT (°C)</th>
<th>drTol</th>
<th>brTol</th>
</tr>
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<tbody>
<tr>
<td>Abies alba</td>
<td>0.04</td>
<td>17.6</td>
<td>700</td>
<td>70</td>
<td>50</td>
<td>160</td>
<td>0</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>641</td>
<td>6</td>
<td>3</td>
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<tr>
<td>Larix decidua</td>
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<td>13.5</td>
<td>850</td>
<td>30</td>
<td>60</td>
<td>200</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>523</td>
<td>11</td>
<td>3</td>
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<tr>
<td>Pinus alba</td>
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<td>1</td>
<td>5</td>
<td>3</td>
<td>385</td>
<td>11</td>
<td>2</td>
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<td>90</td>
<td>300</td>
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<td>1</td>
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<td>0</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>610</td>
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<td>5</td>
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<td>20</td>
<td>30</td>
<td>100</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>610</td>
<td>99</td>
<td>1</td>
</tr>
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<td>20</td>
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<td>1</td>
<td>30</td>
<td>2</td>
<td>2</td>
<td>272</td>
<td>99</td>
<td>2</td>
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<td>1.7</td>
<td>170</td>
<td>20</td>
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<td>700</td>
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<td>30</td>
<td>2</td>
<td>1</td>
<td>498</td>
<td>99</td>
<td>3</td>
</tr>
<tr>
<td>Populus nigra</td>
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<td>10.6</td>
<td>280</td>
<td>20</td>
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<td>800</td>
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<td>2</td>
<td>662</td>
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<td>1</td>
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<td>Populus tremula</td>
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<td>3.8</td>
<td>140</td>
<td>20</td>
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<td>800</td>
<td>1</td>
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<td>2</td>
<td>2</td>
<td>810</td>
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<tr>
<td>Salix caprea</td>
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<td>430</td>
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<tr>
<td>Sorbus aucuparia</td>
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<td>1.8</td>
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<td>300</td>
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<td>1</td>
<td>5</td>
<td>5</td>
<td>498</td>
<td>99</td>
<td>4</td>
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</tbody>
</table>

r: maximum above-ground biomass growth rate (Flury, 1895; Burger, 1943, 1947, 1948, 1950a, 1951, 1952, 1953; Assmann, 1961; Grosset, 1977; Burger, 1945, 1947, 1948, 1950a, 1951, 1952, 1953; Bugmann, 1994); maxAge: expected longevity (Bugmann, 1994); matu: maturity age for seed production (Rohmeder, 1972, p. 35); ED: effective seeding distance (m); MD: maximum seeding distance (m) (Rohmeder, 1972); spAge: maximum age for vegetative reproduction (Burschel and Huss, 1997); folType: Foliage type (Bugmann, 1994); shdTol: species shading tolerance (ordinal number between 1 and 5, 1 denotes least shade-tolerant) (Ellenberg, 1998 p. 119); minDD: minimum annual degree-day sum (Bugmann, 1994); minT: minimum temperature for establishment (Bugmann, 1994); drTol: drought tolerance of species (1, very intolerant; 5, very tolerant) (Bugmann, 1994; Bugmann and Cramer, 1998); brTol: browsing tolerance (Bugmann, 1994).
all the simulations on an empty landscape. At the beginning of the simulations, all species had a probability of 10% to contribute seeds to a cell. The first 1000 years of each simulation were used to allow for the establishment of trees and to reach equilibrium between climatic conditions, the disturbance regime, and vegetation structure and composition. Model evaluation started following this “spin-up” period of the simulation. We ran the simulations on a Dell OptiPlex GX260 computer with a Pentium 4 processor at 2 GHz. The current code, which has not yet been optimized for performance, required approximately 3 min for a simulation of 100 years.

The first test consisted of running the model using a harvest regime similar to the harvest regime of the last 300 years in the study area, so as to evaluate current landscape composition. This simulated landscape composition was compared with forest inventory data collected in the context of the MAB project (Hefti et al., 1986). The comparisons were based on biomass and species composition, aggregated over an elevational gradient for the entire currently forested area (excluding avalanche tracks). The ‘historic’ harvesting regime was started after the first 1000 simulation years (see above) and continued for 200 years, to mimic the period from 1700 to 1900 A.D. (before 1700 A.D., harvesting activities had presumably been minimal). In this period, the harvesting regime was quite intensive, as the forests were used by the local community for multiple purposes: mowing, cattle and goat grazing, firewood collection, wood extraction for fence posts, single stem extraction for housing construction (local use), and clear-cutting for timber trading (Günther, 1981). After 1900 A.D., the ‘historic’ harvest regime was replaced in the simulation by a ‘current’ harvesting regime, which consists of single tree selection in only a small fraction of the area (Hefti et al., 1986). These simulations were conducted under current climatic conditions and the current wind regime. To account for random effects, the mean values of fifty simulation runs were evaluated.

In a second set of simulations, model behavior under potential natural conditions (i.e., current climatic conditions and no forest management) was tested at the landscape scale by evaluating the distribution of forest properties over an elevational transect from the valley bottom to the tree line. The potential forest area for these simulations was defined as the total area of the valley except for current settlement and productive agricultural areas; that is, alpine pastures above the current tree line were treated as potential forest area. This allowed us to investigate whether the model is able to realistically simulate the change of species composition with altitude and the location of the potential natural tree line. To account for wind disturbance and other random effects, we averaged the years 1000–1500 of single simulations and then took the average result of 25 such simulation experiments.

In this second set of simulations, model behavior was also evaluated on a stand-scale. We examined natural (i.e., no forest management) stand development patterns after disturbance events. To explore model behavior on scales smaller than the entire landscape, we divided the landscape into elevation bands with a width of 100 m, assuming that vegetation behavior within these bands would be comparable, as the climate is similar. We sorted all cells within each band by age since the last disturbance, and then averaged the simulated stand structures according to age since the last disturbance. The basis for these analyses was a 3000-year simulation, of which the last 2000 years were examined.

Finally, the model was applied to a range of possible future climate and disturbance scenarios to assess the sensitivity of the forest cover to Global Change. Based on the Third IPPC Report (IPCC, 2001), we developed simple scenarios that comprised an increase in temperature, a decrease of precipitation and an increase in wind disturbance frequency. We performed three sets of scenario runs: (a) ‘current’: current climate, current wind regime (400 years mean return interval); (b) ‘moderate’: mean temperature +2°C, precipitation −10%, mean return interval wind 400 years; and (c) ‘extreme’: temperature +4°C, precipitation −20%, return interval wind 200 years. The ‘current’ harvesting regime—single tree selection in a small fraction of the area—was applied in all three scenarios. The simulation results from the three scenarios were
compared in terms of biomass distribution (total biomass and species composition) and vertical stand structure classes (cf. Fig. 3), aggregating the results over the entire forested area (excluding avalanche tracks). To account for random effects, we again averaged the years 1000–1500 of single simulations and then took the average result of 25 such simulation experiments for each of the three scenarios.

4. Results

4.1. Model tests

4.1.1. Landscape-scale behavior

Applying the management regime to the years 1700–2000 a.d. resulted in a simulated landscape in the year 2000 a.d. which was dominated mostly by *Picea abies*, with scattered *Larix decidua* dominated cells and some *Pinus cembra* dominated areas at higher elevations, but rarely at low elevations (Fig. 4b). It should be noted that the simulation shown in Fig. 4b is just one realization of the stochastic process underlying the model, that is, depending on the particular simulation run, variation of the simulated patterns may occur. However, we found that the variation from one run to the other was not overwhelmingly large in this weakly disturbed landscape. The aboveground biomass and species composition in the simulated year 2000 a.d. (mean of fifty simulation runs) exhibited gradual changes with altitude (Fig. 5b). Biomass at lower elevations is slightly above 200 t/ha; above 1750 m a.s.l., it decreases gradually to about 50 t/ha at the upper

![Fig. 3. Definition of vertical structure classes as used in this paper.](image1)

![Fig. 4. Dominant tree species (i.e., species with biggest biomass on cell): (a) current forest map (Hefti et al., 1986); (b) simulated landscape with forest management and current alpine land use; and (c) simulated landscape under potential natural conditions (i.e. the forest cover was able to expand upwards until natural tree line).](image2)
Fig. 5. Biomass distribution aggregated over the entire landscape (excluding avalanche tracks): (a) current forest properties (Hefti et al., 1986); (b) simulated landscape with forest management and current alpine land use; and (c) simulated landscape under potential natural conditions.

forest border. Species composition changes from *P. abies* domination to *P. cembra* dominated forests in the uppermost forested areas.

The simulations under natural conditions allowed forests to expand beyond the current upper forest border (Fig. 4c). According to the model, these areas are dominated by *Pinus cembra* with a narrow *Alnus viridis* belt at the tree line. At lower elevations, stands are dominated by *Picea abies*, but there are also scattered areas dominated by *Larix decidua* (Fig. 4c). The simulated natural vegetation dynamics resulted in biomass values and species composition that also changed with altitude (Fig. 5c). Total aboveground biomass (excluding avalanche tracks) was highest at lower altitudes, declined slightly with altitude between 1550 and 1850 m a.s.l., and started to decrease more strongly at altitudes between 1850 m and 2250 m a.s.l. (Fig. 5c). Over the elevational gradient, there was a transition from *Picea abies* dominated forests at lower elevations to a *Pinus cembra* dominated forests in upper parts. *Larix decidua* biomass increased with altitude, and after reaching a maximum biomass at about 1800–1900 m a.s.l., it started to decline again (Fig. 5c).

4.1.2. Stand-scale behavior

The biomass development of stands during the 1000 years after a wind disturbance showed similar patterns at all elevations, therefore, only the results from one elevational band are shown (Fig. 6). However, successional processes were slower with increasing altitude. For example, the time until maximal stand biomass was attained was 200 years at the lowest elevations, 300 years at 1850–1950 m a.s.l., and exceeded 400 years above 1950 m a.s.l. Also, the relative abundance of different species changed with altitude (cf. Fig. 5c).

Examining tree diameter distributions over time (Fig. 6), we found that some trees, mostly small specimens, had typically survived the wind disturbance event (Fig. 6a); that is, complete blowdown events with 100% mortality were rare (cf. Table 2). New trees established mainly during the first 20 years after the windthrow, followed by a period of stem exclusion and self-thinning (Fig. 7). During the stem exclusion period, the number of trees in the smallest diameter class started to decline due to density-dependent mortality, and because some of them were growing into the larger diameter classes (Fig. 6b). As soon as some trees attained large dimensions (Fig. 6c), ongoing stem exclusion created space for stand re-initiation. Only shade-tolerant species (*Pinus cembra, Picea abies*) were able to establish under the existing canopy (Fig. 6c). Stand re-establishment, stem exclusion and growth into larger diameter classes of the new cohorts took place continuously while old cohorts were still present (Fig. 6d). Some single, large stems from the old cohorts remained in the stand for several hundred years (Fig. 6e). Because of this overlap of development phases in the old and new tree cohorts and the asynchronous succession of growth phases in the different grid cells, stands subsequently grew into an equilibrium with a broad range of
The pattern of stem numbers over time was similar for all stands up to 2050 m a.s.l. Above this altitude, stem number fluctuations ceased, and stem numbers were generally higher than those at the equilibrium phase in stands at lower elevations.

4.2. Model application

The sensitivity of the model to future climate scenarios was investigated by comparing total aboveground biomass, tree species composition and the fraction of stand structure types aggregated over the entire forested area (excluding avalanche tracks) (Fig. 8).

Under the ‘current’ scenario, total biomass yielded an average of 185 t/ha; under the ‘moderate’ future scenario, somewhat higher values were achieved, while the ‘extreme’ scenario resulted in less biomass (ca. −10%) than the ‘current’ scenario (Fig. 8a).

Also, the three scenarios resulted in different average species compositions (Fig. 8a). While the
Fig. 7. Simulated average mean tree biomass and stem number during stand development after windthrow (dots), displayed in 20 year time steps from right to left: the first dot (rightmost) is 20 year after the windthrow, and the last dot (leftmost) 200 years after the windthrow. The solid line has a slope of $-3/2$, as suggested by self-thinning models (e.g., Yoda et al., 1963).

'moderate' scenario was characterized by the continued dominance of *Picea abies* at the landscape scale, the biomass of *Abies alba* increased strongly, and a number of deciduous species (e.g. *Populus* spp.) were also able to grow in the landscape. In the 'extreme' scenario, strong changes of species composition occurred. *Abies alba* and *P. abies* became co-dominant, and deciduous species had a much larger share in the landscape.

The simulated effects on vertical stand structure were more gradual than those of total biomass and species composition (Fig. 8b). While the landscape properties under a perpetuated "current climate" scenario would be characterized by about 25% young stands, and about equal fractions (30%) of mature mono-layer and multi-layer forests, the share of young stands increases to 30% and nearly 40% in the two climate change scenarios, mostly at the expense of the fraction of mature mono-layer stands.

5. Discussion

5.1. Model tests

5.1.1. Landscape-scale behavior

The simulated distribution of dominant tree species in the landscape (Fig. 4b,c) is difficult to compare to the map of current species distribution, for two main reasons. First, the map of current stands (Fig. 4a) is derived from forest inventory data, which describe stand
structure well, but less so species composition (Hefti et al., 1986). Therefore, the estimated species distribution patterns may not be very accurate. Second, the simulated distributions (Fig. 4b,c) varied between simulation runs due to the stochastic processes embedded in the model. Still, it is evident that the model yields spatial vegetation patterns under the harvesting regime (Fig. 4b) that are similar to those of the current landscape (Fig. 4a). Below, we discuss model behavior as aggregated over the elevational gradient, and also at the stand-scale (cf. Section 5.1.2).

The simulated landscape for the year 2000 a.d. showed total biomass values of about 200 t/ha at lower elevations and gradually decreasing values with altitude (Fig. 5b). These values are similar to those derived from forest inventory data (Hefti et al., 1986; cf. Fig. 5a), and to values of 200–250 t/ha (300–400 m³/ha) for managed spruce forests reported by Leibundgut (1986). The simulation results match the measured values at lower elevations quite accurately, whereas at higher altitudes biomass seems to be somewhat underestimated by the model. Also, the model projects a rather linear decrease of total biomass between 1650 and 2100 m a.s.l., whereas the measured values at lower elevations (Fig. 5c) are considerably higher than under the management scenario (Fig. 5b), but still somewhat smaller than currently observed in the study area (Fig. 5a). Measurements of aboveground standing volume in a P. abies virgin forest that is similar to potential natural forests in the lower elevations of our study area resulted in biomass values of about 300 t/ha (550 m³/ha) (Hillgarter, 1971). Simulated values at lower elevations (Fig. 5c) are considerably higher than under the management scenario (Fig. 5b), but still somewhat smaller than this measured data. The presence of a belt of L. decidua/P. cembra forests above 2000 m a.s.l. agrees with literature data (e.g., Landolt et al., 1986, Ellenberg, 1996). Its biomass has been estimated to amount to 50–100 t/ha (100–200 m³/ha) (Leibundgut, 1986); again, simulated values are very similar, although somewhat lower above 2150 m a.s.l. Finally, the simulated presence of a strip of Pinus–Alnus ‘krummholz’ just below the tree line is quite realistic (Landolt et al., 1986). Similar experiments were conducted with a forest gap model (Bugmann, 1999; Bugmann and Pfister, 2000). They showed that the sequence of tree species and forest types simulated along altitudinal gradients is largely the result of competitive interactions, i.e. the realized niche of the species (Fig. 5c) is only partly dictated by the species’ autecological properties (their fundamental niche; cf. Table 3). Therefore, we can conclude that the simulated vegetation characteristics are an emergent property of the modeled processes.

The potential timberline (the upper elevation limit of closed forest; cf. Körner, 1998) in the study area is estimated to be located at about 2200 m a.s.l., i.e. about 100 m higher than the current timberline (Walder, 1983). This upper potential limit corresponds well to the simulated timberline elevation, where biomass of...
Pinus cembra drops below 50 t/ha and Alnus viridis starts to dominate (Fig. 5c). The tree line (i.e., the line connecting the highest patches of forest) in the study area is estimated to be around 100–200 m higher than the potential natural timberline (Walder, 1983; Körner, 1998). The highest A. viridis patches are simulated to occur roughly at this altitude. Hence, the simulated elevations of timberline and tree line agree quite well with empirical findings.

Overall, these results demonstrate the ability of the modified LANDIS model to simulate species composition in complex mountain landscapes from climatic and edaphic information alone, which is a distinct advantage over previous model versions.

5.1.2. Stand-scale behavior

Simulated stand-scale development is also an emergent property of the new model, i.e., these dynamics are not prescribed by model parameters, but result from the interactions between species and tree cohorts with different properties. Simulated stand development after wind disturbances showed the typical sequence that is well known from a host of empirical studies (cf. Oliver and Larson, 1996): stand initiation, stem exclusion, understory reinitiation, and multi-aged stage (Fig. 6). During the stand initiation phase, available growing space was partly occupied by advanced regeneration, and was filled with new trees that established shortly after the disturbance. The introduction of new trees caused an increase in stem numbers during the first 20 years. Recent investigations of recovery success in wind-disturbed areas at high altitudes suggest that the simulated establishment density of about 2700 trees per hectare 10 years after a disturbance may be high, but it is still within a realistic range: Schönenberger (2002) reported 1000–2500 saplings per hectare after wind disturbance events. Note that the Schönenberger (2002) data is from areas that are subject to considerable browsing by ungulates, which was not reflected entirely in our simulations. Competition between trees increased soon after stand initiation, thus causing stem exclusion and preventing the establishment of new trees. This self-thinning with an associated increase in stand biomass was estimated quite realistically by the model (Fig. 7) (cf. e.g., Yoda et al., 1963; Begon et al., 1996; Kikuzawa, 1999). During this stage, the forest develops to maturity: about 150 years after the wind disturbance, total biomass of trees bigger than 20 cm DBH was larger than total biomass of those smaller than 20 cm DBH. This corresponds well with the findings in a primeval forest similar to semi-natural Picea abies stands in the Dischma valley, where Hillgarter (1971) found that this ‘young forest’ phase lasts for 80–130 years. Also, stem numbers and diameter distributions were comparable between this field study and our simulation. For example, Hillgarter (1971) reported 500–800 stems per hectare in mature mono-layer stands. In years 150 and 200, when the majority of the simulated stand was composed of mature mono-layered forests, our simulation resulted in 652 and 411 stems per hectare, respectively. Furthermore, Hillgarter (1971) suggested that stands remain in the mature forest phase for about 200–260 years. This corresponds well with the simulation results, where the process of stand decay and understory re-initiation started after about 200 simulation years (Fig. 6c) and continued for the next 200 years (Fig. 6d,e) until the majority of the stand was composed of new tree cohorts (Fig. 6e). In the model, understory re-initiation started when the mortality of some larger trees created enough growing space for late-successional (here, moderately shade-tolerant) species to successfully establish under the canopy (Fig. 6d). Where the gaps created by the death of large trees are too big to be closed by other canopy species, the understory vegetation grows into the canopy, forming multi-aged stands (Fig. 6e,f). Thus, the early successional species Larix decidua, a very shade intolerant species, is replaced gradually (Fig. 6). This succession from forests with L. decidua (co-) domination to forests composed of late successional species has been observed in various studies (e.g., Mayer, 1966; Zöhre, 1969).

Thus, we can conclude that the modified LANDIS model is capable of accurately portraying stand-level processes after disturbance events, in spite of the simple assumptions that were used for formulating the modified succession sub-model.

5.2. Model application

Total aboveground biomass averaged across the entire landscape increased under the ‘moderate’ scenario of environmental change, compared to current conditions. The temperature increase led to increased productivity and thus increased biomass storage, whereas a moderate increase of drought occurrence (through
the increase of temperature coupled with the decrease of precipitation) and the increased incidence of windthrow events, reduced biomass. Taken together, the temperature effect by far outweighed the other two effects in this scenario. Under the ‘extreme’ scenario, however, aboveground biomass decreased considerably compared to current conditions, indicating that the effects of drought and windthrow are becoming more important than further temperature-induced increases of productivity.

No pronounced changes of species composition (Fig. 8a) are simulated under the ‘moderate’ scenario compared to current conditions, with *Picea abies* still keeping its dominant role at the scale of the entire valley. The increased abundance of *Abies alba* in this scenario is due to the increased temperature, whereas deciduous species such as *Populus* and *Salix* are favored due to the increased incidence of wind disturbances. Under the ‘extreme’ scenario, deciduous species are favored even more because of the strongly increased incidence of windthrow events, whereas drought limits the abundance of *Picea abies*, leading to a biomass decrease. Overall, both scenario results show that the various driving forces have quite different effects on the abundance of the different tree species.

The modified LANDIS model projects gradual changes in stand structure types (Fig. 8b) under this set of environmental scenarios. The simulated changes mostly reflect the changes in the disturbance regime, with more frequent wind disturbances leading to a higher fraction of young stands. The reduction of the fraction of mature mono-layer stands and old stands with rejuvenation may be counter-intuitive at first sight, but owing to more frequent wind disturbances, an increasing portion of the stands does not have enough time to develop into mature mono-layer forests, let alone into old-growth forests. The ‘mature multi-layer’ stands simulated by the model are often stands that are in the transition from young stands to mature mono-layer forests. Multi-layered forests also result when a wind disturbance does not blow down all of the large trees.

The tree growth model included in the present version of LANDIS is far less sophisticated compared to the carbon balance equations of global biogeochemistry models (e.g. Sitch et al., 2003; Churkina et al., 2003). However, there are few models at the landscape scale that integrate forest growth and succession with disturbance dynamics in a semi-mechanistic manner (e.g. Keane et al., 1996). Our version of LANDIS achieves this integration based on simple concepts and methods that do not require many parameter estimates. Thus, we suggest that the modified LANDIS model can be used as a basis for evaluating the relative importance of landscape-scale aboveground biomass storage of: (1) climate-induced changes in productivity; (2) tree population dynamics; and (3) changing disturbance regimes. This feature may be of utmost importance for determining the terrestrial carbon balance (cf. Körner, 2003).

6. Conclusions

Forest dynamics at the landscape scale are influenced by species-specific responses to environmental factors, by intra- and inter-specific competition as well as by exogenous disturbance regimes. We have integrated a new succession model within a landscape-scale model framework (LANDIS) to examine these complex interactions.

We tested the new model's ability to simulate forest dynamics in the European Alps on both the landscape and the stand-scale. We were able to show that the model simulates accurate biomass distribution and species composition for both managed and unmanaged stands, and it also simulates the characteristics and the elevation of the potential natural timberline well. Furthermore, the model produces patterns of stand recovery and the development of stand structure after windthrow events that are congruent with empirical findings. Thus, the modified LANDIS model is able to simulate vegetation processes in accordance with current ecological understanding, while the model structure is still simple and does not include the detail of stand-scale models.

The simulation results under several scenarios of environmental change show that the new model can be used to study the transition from weakly disturbed to strongly disturbed landscapes, a feature that was not present in earlier model versions. Particularly, by including a range of tree-tree interactions, the new model is able to simulate realistic vegetation development even in weakly disturbed landscapes, and is capable of simulating the influence of disturbances on vegetation properties as well as stand recovery.
after such events. Studying transitions from weakly to strongly disturbed landscapes is an important issue, as global environmental change is likely to bring about changes in the distribution of extreme climatic events, which may trigger changes in the large-scale disturbance regimes in many landscapes.

Because the modified model explicitly incorporates the effects of a range of climatic factors on tree regeneration and growth, it is more suitable for addressing the direct impacts of climatic changes on forested landscapes. Through a simple set of scenario calculations (which should not be mistaken as predictions), we were able to demonstrate that the model is sensitive to changing climatic parameters. Notably, the effects of climatic changes on forest landscape dynamics are emergent properties of the modified model, rather than being prescribed through site-specific or species-specific parameters, which was the case in earlier versions of LANDIS.

The modified model can also serve as a tool to help with decision-making in the context of long-term forest management. It provides variables—such as biomass, stand density, species dominance, or vertical structure—that can be used for assessing, for example, the habitat requirements of wildlife, and indices that are relevant to a range of other ecological questions. Also, variables, such as stand density and vertical stand structure are crucial for predicting the long-term consequences of forest management decisions, e.g. with respect to the ability of mountain forests to avert natural hazards, such as avalanches, rockfall or landslides.

Finally, the ability of the model to simulate landscape-scale aboveground biomass storage allows us to determine the effect of Global Change scenarios on aspects of the carbon balance of mountain ecosystems. Hence, the modified LANDIS model as described in this study has the potential to provide an integrated picture of the impact of both direct and indirect effects of climate change on forest landscape dynamics.

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References


