TreeMig: A forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale

Heike Lischke¹,* , Niklaus E. Zimmermann⁰, Janine Bolliger⁰, Sophie Rickebusch⁰, Thomas J. Löfflerᵇ

¹ Swiss Federal Research Institute WSL, Zürcherstr. 111, CH-8903 Birmensdorf, Switzerland
ᵇ Geological Institute, Swiss Federal Institute of Technology, Universitätsstr. 6, CH-8049 Zürich, Switzerland

Abstract
Landscape patterns result from complex endogenous dynamics and heterogeneity of environmental drivers. Landscape models are appropriate tools for analysing such patterns. We present the dynamic, spatially explicit, grid-based and spatially linked forest-landscape model TreeMig. In each grid cell, the forest dynamics is simulated with a multi-species, height structured forest model, based on growth, competition and death of the trees in each height class. Within-cell heterogeneity is accounted for by assuming that trees are randomly distributed resulting in Poisson distributions of tree densities and light. Reproduction is modelled explicitly by seed production, seed bank dynamics, germination and sapling development. The forests in the different cells interact spatially through seed dispersal. The model is flexible and can be applied on a range of spatial scales, from single stands to entire regions.

The model’s ability to generate patterns was tested in two case studies with different spatial resolutions. The first case study shows simulations of pattern formation by endogenous dynamics on a small spatial scale. The simulations are conducted under spatially and temporally homogenous environmental conditions, initialized with seeds of all species in the centre cell. The simulation shows transiently several types of patterns in the species biomasses: circular standing waves, patch structures and homogenous spread of dominant species. In the second, large-scale case study, the tree species’ spread since the last Ice Age in the Alpine region of the Valais is simulated, under temporally and spatially heterogeneous environmental conditions. The simulated spatio-temporal pattern consists of immigration waves of new species into empty or already forested areas, fast die-backs after sharp, strong temperature decreases, slower recolonization after temperature increases and spatial separation of the species according to the environmental conditions. The simulation indicates that the environment forms the basis for the endogenous dynamics, primarily migration and competition, which play a particular role during the transient phases after drastic changes in the boundary conditions (immigration and climate change).

We conclude that the forest-landscape model TreeMig is able to produce landscape patterns resulting from both, endogenous dynamics and exogenous drivers and is suitable for a range of different applications.

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* Corresponding author. Tel.: +41 1 739 3533; fax: +41 1 739 2215.
E-mail address: lischke@wsl.ch (H. Lischke).
1. Introduction

1.1. Patterns and processes in forest landscapes

Various traits of natural landscapes, e.g. vegetation type, coverage, species composition, biomass, show spatial patterns (Bolliger et al., 2003; O’Neill et al., 1988; Turner, 1990).

In natural forest landscapes, patterns may appear at different spatial scales: at the stand scale, e.g. as the mosaic of patches with tree groups of different age structures in temperate virgin forests (Koop and Hilgen, 1987; Korpel, 1995; Remmert, 1991), at the regional scale, as forest-vegetation belts along altitudinal or climatic gradients or treelines or at continental scales as different biomes along latitudinal and continentality gradients.

Landscape patterns are not static, but undergo more or less obvious changes, thus they are spatio-temporal or spatially dynamic. The drivers for landscape patterns and their changes arise from various processes that interact at different spatial and temporal scales. Such processes include, for instance, non-linear interactions and feedbacks, which act within the system boundaries and may be referred to as endogenous, whereas exogenous drivers include abiotic or biotic environmental factors (Bolliger et al., 2005, 2003).

Endogenous drivers for pattern generation at the single plant level include various demographic processes, such as reproduction (seed production, seed bank dynamics, germination), development (growth, maturation) and mortality (age-related). Interactions between individual plants at small spatial scales consist of competition for space or resources (nutrients, water, light), for instance, through shading or different use efficiency. Negative feedbacks exist in the form of intra-specific competition or specific antagonists. Positive feedbacks consist for example of reproduction or local modifications of the stand climate, e.g. by trees increasing temperature which in turn enhances tree growth. At the stand or community level, these endogenous plant level processes and interactions manifest themselves as gap dynamics and autogenic succession. At intermediate spatial scales, interactions between biotic landscape elements occur by movement, primarily dispersal (Clark and Ji, 1995; Neilson et al., 2005), either of plants or their antagonists, e.g. pathogens, herbivores or even higher order consumers (Malanson, 1997).

Landscape patterns can also be driven exogenously, i.e. by patterns of environmental factors such as nutrients, water, climate and anthropogenic forces. Environmental factors act either continuously (e.g. temperature), as rare extreme events or as disturbances (floods, droughts, fires, windstorms). Biotic factors such as pests, herbivores and pathogens also represent exogenous drivers for natural landscape patterns.

In most cases, natural landscapes are influenced by a combination of both endogenous processes and external factors and it is not clear how these interact. The relative importance of each driver for pattern generation is scale dependent. Endogenous drivers for landscape patterns may be considered more relevant at small spatial and temporal scales, as the environment may be considered constant. Exogenous drivers, however, dominate pattern generation at large spatial and temporal scales (e.g. ecosystem, biome).

It is important to understand the mechanisms behind the formation of natural landscape patterns and their dynamics, because although today human land use is certainly the strongest driver of landscape change, it cannot be considered detached from the natural background. Disentangling the different natural causes of observed patterns in the past and present improves the understanding of the landscape system. More specifically, the analysis of landscape patterns is important for projecting future landscape development, particularly in the context of global change (e.g. for assessing species migration in the temperate and boreal zones), or testing scenarios of human intervention in landscape development, such as management and conservation activities. Analysing and projecting pattern dynamics at large scales involves the application of scaling (Lischke et al., in press-b). Understanding the mechanisms causing the patterns enhances the array of techniques for and the accuracy of such scaling approaches.

1.2. Dynamic landscape models

The aforementioned interactions at the ecosystem and landscape level, and the resulting spatio-temporal patterns, are complex and cannot be studied by observing characteristics of ecosystems or their proxies, such as pollen data, alone. In this situation, dynamic spatial models are useful instruments, because they incorporate essential processes, interactions and dependences on environmental factors.

Various modelling approaches are available to simulate forest-landscape dynamics, including: (i) cellular automata, (ii) individual-based position dependent forest models, (iii) interlinked gap models, (iv) frame-based models, (v) biogeography models, (vi) biogeochemical process models and (vii) dynamic global vegetation models (see reviews in Bolliger et al., 2005; Lischke et al., in press-a). The approaches differ significantly with respect to the aims they were designed for. Differences include the organizational levels (physiology, organ, individual, whole canopy) at which the models operate (Lischke, 2001), the level of detail in which the observed processes are modelled (inherent detail of mechanisms), the way they include information (empirical, process based) and the way they treat time (dynamic, static) and space (local, aggregated, distributed or spatially linked).

The inclusion of spatial interactions between landscape elements is a prerequisite for realistic dynamic landscape-pattern simulations. There are several existing dynamic spatio-temporal landscape models that include spatial interactions. Examples of these interactions are lateral shading, as in some individual-based, position-dependent forest models (e.g. SORTIE, Pacala et al., 1993; Picard et al., 2001; SILVA, Pretzsch, 2002), interaction rules, as in generic cellular automata (Bolliger, 2005; Bolliger et al., 2003), and seed dispersal processes, as in the models LANDSIM (Roberts, 1996) and LANDIS (He and Mladenoff, 1999; He et al., 1999), which are both based on presence/absence of tree age cohorts and also incorporate disturbances such as fire, wind, insects and forest management.

Several aspects have been identified as crucial in forest-landscape modelling: (a) structure, in terms of population densities of several species and within-stand horizontal and
vertical heterogeneity (Harvey, 2000; Löffler and Lischke, 2001; Moorcroft et al., 2001; Pacala and Deutschman, 1995; Strayer et al., 2003), (b) sufficient detail in population dynamics, particularly with respect to recruitment (seed production, dispersal and seed bank dynamics) (Finegan, 1984; Price et al., 2001) and (c) computational efficiency to simulate large areas at a sufficiently fine resolution. None of the spatio-temporal forest-landscape models existing to date fulfils all of these requirements simultaneously.

We present a new forest-landscape model named TreeMig, which is based on multi-species population dynamics, describes recruitment processes, includes spatial interactions by seed dispersal and efficiently accounts for within-stand heterogeneity. The model is designed for simulations of forest-landscape dynamics on scales ranging from single stand to continent.

Additionally, as a first step of model evaluation, we present a plausibility check to test the qualitative model behaviour. This implies that parameter values, boundary conditions and simulation results are within a plausible range, but do not necessarily reflect a specific real situation.

We investigate in two case studies which kind of forest-landscape patterns the model is able to produce at different scales. One case study works at fine spatial resolution with a constant environment and the other at coarse resolution under varying environmental conditions.

2. The TreeMig model

2.1. Requirements and concept

We chose a flexible model approach for TreeMig, to be able to adapt the model to new applications with their specific biotic and abiotic conditions by adjusting the drivers, parameters or single process functions, while the model structure remains.

One requirement we put in first place was the applicability of TreeMig at a range of spatial scales. For example, species migration operates at spatial extents ranging from region to continent and over centuries to millennia, whereas stand dynamics is restricted to a few hectares for a couple of decades to centuries. The spatial resolution has to capture the spatial heterogeneity of the relevant environmental factors, intrinsic processes and resulting patterns. TreeMig allows to adapt it to the heterogeneity of the area to be simulated. For example, in a rugged terrain such as the Alps, the grain should not be much above 1 km, which is the standard resolution of TreeMig. In addition to the forest population processes (growth, mortality, competition and establishment) TreeMig includes processes and interactions essential for landscape dynamics, i.e. reproduction, including seed production, seed density regulation and, most importantly, seed dispersal. Furthermore, within-stand heterogeneity, in terms of species and vertical and horizontal stand structure, is included. Other factors, such as bioclimatic, are usually assumed to be homogenous within each cell. The state variables, i.e. the mean tree densities, are also assumed to be homogenous within a cell, which introduces a discretization error.

Finally, the model has to include the explicit dependence on external drivers relevant for the systems studied. Since climate, and its change, is a primary driver for the formation of patterns and shifts in species composition, the basic model processes are formulated as temperature and precipitation dependent. Additionally, nutrient supply and disturbances are accounted for.

TreeMig (Fig. 1) is formulated as a set of time discrete difference equations with a yearly time step. The state variables are the population densities of seeds in the seed bank $S_{bs,x,y,t}$ and of trees $N_s,i,x,y,t$ in height class $i$ (of height $h_i$) of species $s$ in cell $(x, y)$ at time $t$. The change in $N$ and $Sb$ between $t$ and $t+1$ consists of local dynamics $L$ and $L_{sb}$ (Eq. (3)–(5)) and spatial interactions, i.e. seed inflow $I$ (Eq. (6)). (For a detailed model description and the parameter values see the online appendix.)

\[ N_{s,i,x,y,t+1} = N_{s,i,x,y,t} + I_{s,i,x,y,t} \]

\[ S_{bs,x,y,t+1} = S_{bs,x,y,t} + I_{sb,s,x,y} + I_{s,x,y,t} \]

2.2. Local dynamics

The local tree dynamics of TreeMig is based on the distribution-based, height-structured tree population model DiscForM (Lischke et al., 1998; Löffler and Lischke, 2001), which in turn uses the process functions and parameters of the well-tested gap model ForClim (Bugmann, 1994).

The local dynamics $L$ is determined by ingrowth $IG$ into height class $i$ from the height class below, outgrowth $OG$ into the next class above and fatalities $D$.

\[ L_{s,i,x,y,t} = IG_{s,i,x,y,t}(N_{s,i-1,x,y,t}, N_{jz,i-1,x,y,t}) - OG_{s,i,x,y,t}(N_{s,i,x,y,t}, N_{jz,i,x,y,t}) - D_{s,i,x,y,t}(N_{s,i,x,y,t}, N_{jz,i,x,y,t}), \quad i = 1, \ldots, 15 \]

Outgrowth and fatalities of height class $i$ are proportional to the population density in this height class, while ingrowth is proportional to the population density of the height class below. Growth and survival are reduced due to shading by all higher trees $N_{jz,i,x,y,t}$ of all species. All process rates depend on the bioclimatic variables degree-day sum (above 5.5 °C), minimum of monthly mean temperatures and drought stress index. They are calculated in advance according to the ForClim-E (Bugmann and Cramer, 1998).

To include within-stand variability, the distribution-based approach assumes that the trees in each height class are randomly distributed over the stand, which results in a Poisson distribution of tree population densities per unit area (833 m²); frequency distributions of light intensity and light-dependent establishment, growth and mortality rates in each height class are calculated from the tree distributions of all higher height classes (Lischke et al., 1998; Löffler and Lischke, 2001). In this way, competition through shading and its spatial variability is included.

2.2.1. Reproduction

TreeMig explicitly simulates seed production, seed dispersal, seed bank $Sb$ dynamics and the recruitment and development of seedlings and saplings $N_{s,0,x,y,t}$ (Lischke and Löffler, 2006) (5). The number of seeds $S$ produced per year by each tree depends on its height, species and mast seeding period. The seed inflow
Fig. 1 – Concept of the TreeMig model. It is implemented on a rectangular grid. In each grid cell, trees in different height classes germinate, grow, die and produce seeds. In each height class, a theoretical distribution of tree densities across the entire stand is calculated, based on the average population density per height class. The resulting light distribution determines the process rates and the dynamics of all trees within this height class. The seeds are dispersed to the same or other grid cells, where they enter the seed bank. Seed bank dynamics includes a species-specific density regulation.

\[ I_{b,s,x,y,t} = -D_{b,s,x,y,t} - B_{s,x,y,t} \left( S_{bs,x,y,t}, N_j \geq 0, x, y, t \right) \] (4)

We introduced species-specific seed antagonists (e.g. seed predators or pathogens) or alternatively an intra-specific competition term, which results in a limitation of the seed number of each species (Lischke and Löffler, 2006). As default, the intra-specific competition formulation is used. The seedlings germinating (8) from the seed bank add to the number of saplings \( N_{s,0,x,y,t} \), which grow and die similarly to the adult trees. The yearly change of the saplings is given by \( L_{s,0,x,y,t} \):

\[ L_{s,0,x,y,t} = B_{s,x,y,t} \left( S_{bs,x,y,t}, N_j \geq 0, x, y, t \right) - OC_{s,0,x,y,t} \left( N_{s,0,x,y,t}, N_j \geq 0, x, y, t \right) - D_{s,0,x,y,t} \left( N_{s,0,x,y,t}, N_j \geq 0, x, y, t \right) \] (5)

Parameters for the reproduction model were compiled from various sources (see references Tables 1a and 1b, online appendix). The carrying capacity limiting species-specific seedling numbers was roughly estimated to 1000 seeds/833 m² by comparing the simulated biodiversity and species composition to those observed in data of the Swiss National Forest Inventory (Lischke and Löffler, 2006).

2.3. Spatial interaction

To obtain the landscape model, the local model is implemented on a grid of square cells, the size of which can be varied (default: 1 km × 1 km). The forests in the different cells interact through seed dispersal.

\[ I_{s,x,y,t} = \sum_{lat,lon,i} S_{i, lat, lon}, k_s(z). \]

\[ k_s(z) = (1 - \kappa_s) \frac{1}{\alpha_{s,1}} e^{-z/\alpha_{s,1}} + \kappa_s \frac{1}{\alpha_{s,2}} e^{-z/\alpha_{s,2}} \] (6)

The seed inflow \( I \) into a cell is defined as the seeds \( S \) of a species produced in all other cells and heights, multiplied by the dispersal kernel \( k_s \), which is the probability density function for a seed dispersed from source cell \((\xi, \nu)\) to land in a target cell \((x, y)\) in two-dimensional space. The kernel depends on the distance \( z \) between the two cells and on
the species’ mean dispersal distance $\alpha_s$. The direction is not taken into account. Due to the modular formulation of the model code, the dispersal kernels can easily be exchanged. Currently, a combination of two negative exponentials, one for short-distance transport (e.g., ballistic, normal wind, small animal transport) and one for long-distance transport (e.g., by birds, large mammals, uplifting by wind) is implemented. The species-specific values of $\kappa_s$, $\alpha_{s1}$, and $\alpha_{s2}$ were roughly assigned (Tables 1a and 1b of the online appendix), for the wind-dispersed species based on terminal velocities and wind speed distributions (Lischke and Löffler, 2006). These values range from 25 to 200 m. The seed transport, defined by seed production and the dispersal kernel, can be simulated either deterministically or stochastically. For stochastic transport, the number of seeds reaching a sink cell from a source cell is sampled from a binomial distribution.

### 3. Case studies

We present here two case studies to test the model’s ability to form patterns in different situations. Under the assumption that patterns depend on spatial resolution, one comparatively fine and one coarser resolution were chosen for the two case studies. Moreover, in order to test the influence of endogenous versus exogenous drivers on patterns, the first case study is set up in a temporally and spatially constant environment, the second one in a strongly heterogeneous and variable environment.

#### 3.1. Case study 1: “local pattern formation”

The first case study represents a theoretical model application, which tests the influence on the simulated patterns of the model processes alone.

The simulation was run for 800 years on a grid consisting of 50 $\times$ 50 cells of 100 m side length. The bioclimatic drivers were kept constant in space and time, at values corresponding to a temperate, humid climate (degree-day sum of 1564 $\circ$C, minimum winter temperature of $-2.7\circ$C and absence of drought stress). The simulation was run with the 30 most important Central European species (for a list see Tables 1a and 1b of the online appendix). It was initialized in a spin-up run of 5 years, during which all cells were empty, except the centre one, where the simulation was run with a constant seed supply but without seed dispersal. In this way, all species that can establish under these conditions form an initial low forest in the centre cell. After the spin-up, the model was switched to its standard configuration, i.e. seed production, seed loss (predation, loss of germinability, germination) and stochastic seed dispersal were activated and the constant seed supply was disabled.

The simulation results are presented in Fig. 2 as contour plots of species biomasses for selected time steps (for an animation of the simulation, see online appendix).

The spatio-temporal pattern is determined by: (a) complementary quasi-standing waves of Betula pendula, Populus tremula and Populus nigra in the first 100–200 years, (b) outliers and fringe spread of species with few seeds (Quercus petraea, Sorbus aucuparia, Fagus silvatica) and (c) homogenous spread of dominant species that produce large seed quantities (Picea abies). The patterns of less dominant species are overlaid by those of more dominant species. The patterns are not stable throughout the whole simulation, but eventually reach a more or less homogenous spatial distribution of all species towards the end of the simulation, with P. abies and F. silvatica dominating the other species.

The wave-like pattern formation is due to the interaction of similar early-successional tree species with slightly different competitive behaviour. While P. tremula is slightly stronger in the competition for resources, B. pendula disperses more seeds. At distant locations, the latter is thus able to escape the competition with aspen by building up new populations. Closer to the source cell, the amount of seeds is limited by the carrying capacity, which gives a competitive advantage to P. tremula. When the trees of the first cohort of a species reach the age of first seed production, B. pendula forms a new colonization ring, whereas P. tremula follows behind in another ring. These initial ring structures persist for a long time, but eventually vanish, i.e. the wave pattern is not stable. Even in a simulation (not shown) with only P. tremula and B. pendula, both species end up coexisting homogenously in space.

A transient patch structure is created by the stochastic long-distance transport of the comparatively fewer seeds of Q. petraea, S. aucuparia, A. incana and F. silvatica. New satellite populations establish away from the main population centre, originating from a few seeds that arrive there at random. The satellite populations then again spread regularly and merge with the original population after several hundred years of simulation. These species obviously produce too few seeds (compared to their seed dispersal capability) to dominate homogenously across the newly invaded areas.

This simplified case study demonstrates the ability of the TreeMig model to produce a number of different endogenously driven patterns as a result of seed production, dispersal and regeneration, as well as species competition for resources and mortality.

#### 3.2. Case study 2: “Holocene tree-species migration in an Alpine region”

The topic of the case study is the potential spatio-temporal vegetation development in the Alpine region of the Valais since the last Ice Age. It is an example of large-scale spatio-temporal landscape dynamics. The region has defined immigration paths for each tree species, which is important for simulating migration. Furthermore, the strong climatic heterogeneity, due to the topography and continentality gradients, makes it particularly suitable for evaluating the combined effects of external drivers and model processes on spatio-temporal patterns.

The central Alpine region of the Valais (Fig. 3) spans a large range of environmental conditions, with altitudes stretching from 400 to 4600 m, yearly mean temperatures between $-10$ and $11\circ$C and yearly precipitation sums between 350 mm in the eastern parts of the valley and clearly above 2000 mm at high altitudes. The central Alps separate the main valley from the glacial refuges of many species in the south and east. The few paths where species could enter the region are the northern opening of the valley and several lower mountain passes.
in the south-east. The simulation was carried out on an area of 50 km × 110 km (Fig. 3) with 1 km × 1 km grid cells and ran from the end of the last Ice Age, ∼14,000 before present (BP), to present.

The scenario of past climate change used in this study was derived from current climate data and assumptions about the temperature anomalies. Bioclimatic variables (degree-day sum above 5.5 °C, minimum of monthly mean temperatures and a drought stress index (between 0 and 1)) were generated for each cell and each year in the simulation period. For this we used current monthly temperature and precipitation values, interpolated from climate stations (Zierl, 2001). Past climate throughout the simulation period was obtained by adding an anomaly scenario to current temperature values.

The temperature anomaly (Fig. 4) has been reconstructed using chironomids in Alpine lakes for the period from 11,000 BP to present (for details, see Heiri et al., 2005). This record is one of the few continuous quantitative climate reconstructions for the Central Alps. The smoothed, 62-sample July air temperature reconstruction (as described in Heiri et al., 2003) was used with the revised age-scale for the Hinterburgsee sediment record (described in Heiri et al., 2004) to produce
a Holocene temperature scenario for the present study. For the late glacial period (14,000–12,500 BP), cold conditions were assumed, followed by even lower temperatures during the Younger Dryas (12,500–11,000 BP), according to reconstructions from different proxies (e.g. Ammann et al., 1996; Labeyrie et al., 2003; Lister et al., 1998). The reconstruction of precipitation anomalies is much more uncertain than that of temperature, particularly if pollen-derived scenarios cannot be used to avoid circularity and leave open the potential for comparison with pollen data. Thus, one has to rely on a range of different scenarios. In the simulation presented here, precipitation was set to current values.

We assumed that no trees were present at 14,000 BP. The species were assumed to immigrate from the north-west, i.e. from Lake Geneva, and from the south-east over the lowest pass, the Simplon (2000 m altitude). The approximate immigration years for the species arriving from the north-west were taken from stratified, time calibrated pollen records of the south-western part of the Swiss Plateau, less than 80 km from the valley opening (pollen database for the European Alps, van der Knaap and Ammann, 1997), by estimating the earliest appearance above 0.5% in the pollen records. Species’ immigration times over the Simplon were derived from a pollen record collected slightly below the Simplon pass (van der Knaap and Ammann, 1997).

The results (Figs. 5 and 6, see also animation in the online appendix) show a distinct pattern of species spreads, changes in dominance and vertical fluctuations of the timberline, all triggered by the variability of the external factors but enforced by endogenous dynamics, namely migration and successions, after drastic changes in the boundary conditions, such as immigration of species into the simulation area or strong climate changes.

The spatial patterns resulting from the simulation are shown as maps of species composition at selected time points (Fig. 5). During the initial colonization (14,000–12,600 BP), fast migrating species such as birch (B. pendula) and aspen (P. tremula) spread rapidly at low altitudes, poplar (P. nigra) and pine (Pinus silvestris) follow. Swiss stone pine (Pinus cembra) spreads into the valley at higher altitudes. Larch (Larix decidua) is trapped south of the Simplon pass because of the low temperatures. During the cold period of Younger Dryas (12,700–11,700 BP), only Swiss stone pine remains within the Valais. With the rapid warming between 11,700 and 11,000 BP (corresponding to –0.8–1 °C/century), poplar spreads again and pine colonizes the dry valley bottom. Larch has managed to cross the Sim- plon pass and spreads westward along the subalpine belt. The timberline, with Swiss stone pine, has shifted upwards tremendously. By 7800 BP, maple has spread throughout the valley, while oak follows at a slower pace (9000 and 7800 BP). They outcompete pine, which retreats to the eastern dry areas of the Valais. A few firs (Abies alba) have passed the Simplon and spread into the valley, along the slopes, from the east. Spruce (P. abies) and beech (F. silvatica) enter the valley from...
Fig. 5 – TreeMig simulation (13,800–11,000 BP) of tree species spread on a 1 km × 1 km grid, over a 100 km × 50 km area in the region of the Valais, Switzerland. In each cell, the species biomasses (t/ha) are drawn as stacked columns. A completely filled cell corresponds to 435 t/ha total biomass. For an animation of the spatio-temporal pattern, see “HoloceneTreeMigration.avi” in the electronic appendix.

the north-west. By 6000 BP, spruce and beech have spread almost throughout the Valais. Many species still coexist at their eastern limits, in the valley. This spread of spruce and beech continues until present, when spruce dominates in the region, particularly on the slopes. It reduces fir, oak and beech to low biomasses at medium altitudes and pushes Swiss stone pine and larch up to high elevations. Only in the valley bottom do pine, oak and beech co-exist. Pine dominates in the dry eastern region. This pattern corresponds largely to the current species composition in the Valais, as recorded on the plots of the first Swiss National Forest Inventory (EAFV, 1988), which show beech and oak in the west and pine in the east of the valley bottom, spruce at medium to high altitudes, some fir at intermediate altitudes on the northern slopes and larch with
some Swiss stone pine at the timberline. The main deviation between simulation and data lies in the under-representation of larch and fir (particularly in the north).

The large-scale spatio-temporal pattern is dominated by five aspects: (1) the initial colonization of the empty habitats, (2) the disappearance of most species during the very cold Younger Dryas, (3) the recolonization after Younger Dryas, (4) the immigration waves of various new species with the invaders partly co-existing (Pinus, Populus and Quercus) and partly outcompeting the formerly established trees (Picea and Fagus) and (5) the spatial separation of the species according to environmental conditions. The importance of each of these factors differs between times and locations. The dynamics and spatial patterns of the exogenous drivers influence the simulated patterns directly (aspects (2) and (5)) and initiate transient phases of strong spatio-temporal endogenous pattern formation (aspects (1), (3) and (4)). At this coarse scale (grain = 1 km × 1 km), no pattern types such as those in the local, fine-scale case study (quasi-standing waves, patches) could be observed. This might be because the resolution is
too coarse with respect to the interaction ranges and because of the strong gradients of the environmental variables.

The same simulation with a different temperature anomaly (up to 5.5°C higher temperatures in the first period (14,000–11,000 BP), ca. 0.35°C lower temperatures afterwards, Lischke, 2005), differs mainly in the species composition and spread until 11,000 BP. There, Larix manages to pass the Simplohn already in the first centuries, spreads and dominates on the slopes, before being suppressed by Swiss stone pine. The climatic bottleneck at the pass is therefore not as narrow as in the simulation presented here. Later, oak immigration is slower and that of spruce faster than in the simulation we present here. This is probably due to the slightly cooler climate influencing migration speed through growth and competition, which affect mean annual seed production. The final species composition, however, is nearly identical between the two simulations. This indicates that the (spatial) transient behaviour is more sensitive to changes in driving variables than the equilibrium state and corroborates the conclusion in Lischke (2005), that changes in boundary conditions have a particularly strong influence, via species’ migrations, on the spatio-temporal pattern.

4. Discussion of the model

The forest-landscape model TreeMig accounts for within-cell structure in terms of horizontal and vertical heterogeneity within the forest stand and in terms of species. Reproduction is modelled in a detailed way, including seed production by adult trees, seed dispersal, seed bank dynamics, germination and sapling development. The case studies demonstrate that the model can successfully be applied to various situations, with, for instance, different spatial (region to continent) or temporal (centuries to millennia) scales. Additionally, the case studies illustrate that the model can produce several types of patterns, including regular or stochastic patchy patterns on the small scale and a combination of exogenously and endogenously generated patterns in the large-scale simulation on the other hand.

4.1. Comparison with other spatially dynamic landscape modelling approaches

TreeMig is similar to some other landscape model approaches, in that it simulates multi-species forests which are spatially linked. It differs in the way the population dynamics and reproduction are implemented and particularly in the within-cell heterogeneity.

In the model LandClim, Schumacher et al. (2004) replaced the presence/absence of species cohorts of the LANDIS model with species biomass dynamics. However, this model includes only presence/absence of seeds and does not link seed numbers to adult tree density and maturity. Thus, it biases the inter-specific competition. Pennanen et al. (2004) and Pennanen and Kuuluvainen (2002) also developed LANDIS further. As in TreeMig, seed production and dispersal were linked to seed sources. Similarly to the intra-specific seed density regulation of TreeMig, this model limits the seed numbers of strong seed producers. The limitation is modelled by a rule which forces shade intolerant species to establish in open gaps only. Also similarly to TreeMig, the landscape model LandMod (Garman, 2004) was scaled up from a gap model to accelerate the computation. It includes seed production and dispersal. Growth and mortality functions, as well as bioclimatic values, were fitted by meta-modelling (Urban et al., 1999) to gap model simulations. In contrast to TreeMig however, none of these models account for within cell variability. As demonstrated in simulations with LandMod (Garman, 2004), this can lead to a significant underestimation of the density of shade-intolerant species.

4.2. Potential and limitations of the model

TreeMig is a model for studying vegetation dynamics at a broad range of spatial and temporal scales, ranging from stands to regions with resolutions of 100–1000 m. Because the essential process functions are included, the model is general in the sense that it can be used for different topics and in different regions without changing its structure. Beyond that, most parameters and functions of this model are interpretable and measurable.

The inclusion of antagonists or a carrying capacity for seeds makes the model formulation similar to that of traditional gap models: the supply of saplings of each species is limited. However, in TreeMig this supply depends on the presence or absence of parent trees, as in the spatial gap-model MOSEL (Malanson, 1996). Moreover, the seed supply in TreeMig increases continuously depending on the number of parent trees, i.e. the positive feedback “more seeds–more trees–more seeds” acts, as long as the number of seeds produced remain below the carrying capacity.

The flexibility of TreeMig is demonstrated by the different applications for which the model is currently being used as a basis: the simulation of riparian forest dynamics in the context of the restoration of the Rhone river (Glenz et al., submitted for publication), land use and climate change at the Alpine and boreal treelines and the assessment of human influence on vegetation composition in the Holocene by comparing the model simulations to pollen sequences.

TreeMig is computationally efficient in comparison with models of a similar level of ecological and environmental detail, thus it allows simulations at the regional scale. The simulation time is about 2/30 ms per grid cell and year on a Sun Blade 1000 workstation with an UltraSparc III cu 900 MHz CPU with 1 GB RAM, what amounted to 48 h for the Holocene study, which encompasses 6050 grid cells and 14,000 years.

The computing time will be limiting if very large areas, e.g. the entire Alpine Arch or entire Europe, are to be simulated with a fine resolution. Increasing the grain to values greater than 1 km would however increase discretization errors, due to assumptions about the distribution of species inside cells. The spatial resolution of the model should also not be smaller than 100 m, otherwise the distribution-based approach, which assumes a theoretical distribution over patches of 833 m². For such resolutions an individual-based, position-dependent approach is more suitable.

Some uncertainties remain in the model, including the final shape of the dispersal kernel. Most parameters for the tree dynamics were taken from a well-tested gap model (For-
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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.ecolmodel.2005.11.046.

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