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Simulation of Dynamic Tree Species Patterns in the Alpine Region of Valais (Switzerland) during the Holocene

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Abstract: The spatio-temporal forest landscape model TreeMig is presented. It is based on a forest dynamics model that incorporates spatial variability by frequency distributions for tree densities and light intensities. It also takes into account seed production, intra-specific density regulation and seed dispersal. As a case study, the change of the tree species patterns in the Central-Alpine region of Valais was simulated with the model, using climate anomaly and immigration scenarios. The simulations were run on a grid with 1km x 1km resolution and with a yearly time step during the Holocene in the highly structured and heterogeneous environment of the valley of Valais in the Alps. As input, a scenario of temperature anomalies in the Holocene, spatially interpolated climate data, and times of species immigration into the simulation area were used. The results show a vivid pattern of species spread, changes of dominance, and up and down shifts of the timberline, which are triggered by the variability of the external factors but exhibit endogenous dynamics, i.e. migration and succession, after drastic changes of the boundary conditions, such as immigration of species into the simulation area or strong climate changes. However, on the observation scale no purely endogenous effects such as pattern formation can be observed.

Keywords: Spatially explicit model; spatially linked model; process- model; tree species migration; seed dispersal; TreeMig; landscape pattern

1. INTRODUCTION

Spatio-temporal patterns in a landscape can arise from purely endogenous processes, like feedbacks and nonlinear interactions, such as shown in many studies with simple abstract models. In nature, however, ecosystems are influenced by external factors and their heterogeneity, and it is not clear how in such natural systems external forcing and intrinsic dynamics interact, i.e. in which situations patterns are predominantly formed endogenously, and when patterns are determined mainly by the environment.

One example for an ecological process exhibiting complex landscape patterns, is the spatio-temporal vegetation development since the last glacial, such as preserved in pollen records. Such vegetation changes are interesting, since in the context of present and anticipated future rapid climate changes, the question of whether ecosystems are able to follow fast enough to shifts in the local site conditions is crucial [see e.g., Kirschbaum and Fischlin, 1996]. How will for instance tree species spread in a structured environment, such as the European Alps under changing environmental conditions? Particularly the potentially delayed immigration of species to new habitats is important. Such a migrational lag can cause a considerable delay of natural afforestation beyond the current timberlines and thus of carbon sequestration, as compared to the assumption that the species are already present and only limited by low temperatures.

Tree species migration is influenced by a variety of factors and interacting processes: by the spatial interaction through seed dispersal limiting the maximum speed of spread, by the nonlinear dynamics of the local forest communities with processes such as growth, birth, and death, interactions like (hierarchical) competition or self regulation through shading, by environmental factors influencing all these processes, and by the heterogeneity of this environment. Due to these complicated interactions, the processes and patterns cannot be studied by analyzing the pollen data alone. Models are required which incorporate the essential processes, interactions and dependencies on environmental factors of tree migrations to understand the past and to assess the future response of vegetation to climate change.

In this study, we present the model TreeMig, which is suitable to simulate the migration of tree species in a structured environment and under changing environmental conditions. In a regional case study in the European Alps during the Holocene, the patterns resulting from simulations with this model are evaluated with respect to internal processes and external forcing.

2. MATERIAL AND METHODS

2.1. The spatio-temporal tree migration model TreeMig

The model is originally based on the forest gap model ForClim [Bugmann, 1994, Bugmann, 1996], in which birth, growth and death of individual trees of many different species are followed on a set of small patches. The process functions depend on light, climate and other site conditions. Since birth and mortality are stochastic in these models and the simulated areas and subpopulations are small the dynamics on the different patches differ. This results in a horizontal structure. The differential growth of the individuals results in a certain vertical structure. Since the fate of single trees is followed and many replicates of the stochastic dynamics have to be calculated to obtain reliable mean values, gap models are very computing time consuming, and thus not suitable for large-scale applications. Therefore, ForClim was aggregated to the distribution based, height structured population model DisCForM [Lischke, Löffler et al., 1998b, Löffler and Lischke, 2001]. DisCForM describes the dynamics of the population densities of trees in each tree height class. The variability from patch to patch is described by assuming the trees in each height class to be randomly distributed over the patches, which results in a Poisson distribution of the tree population densities. From this distribution, frequency distributions of the light intensity and of the light dependent establishment, growth and death rates are calculated. By this, competition through shading and its spatial variability is included. This approach produces a purely deterministic description of the dynamics, which still reflects the variability in a forest, but is much faster than the stochastic gap model.

To obtain the migration model TreeMig [Lischke and Löffler, 2004], DisCForM has been implemented on a grid of square grid cells of 1km x 1km. TreeMig simulates explicitly seed production, seed dispersal and the development of seedlings/saplings. The number of seeds produced per year by each tree depends on its height, species and mast seeding period. The seed inflow into a cell is then defined by the seeds produced in all other cells multiplied with the dispersal kernel, which is a distance dependent probability density function, given by the combination of two negative exponentials ($\exp(-x/\alpha)$) for short- and long-distance transport. The values of α range from 25 m and 200 m. The seeds arriving at a cell build up the local seed bank, which is decreased by loss of germinability, predation and germination. Tests with several formulations of the reproduction submodel revealed that it was necessary to limit the seed number of each species separately to get a realistic biodiversity [Lischke and Löffler, 2004]. This was achieved by introducing an intra-specific competition term or species-specific antagonists (e.g. seed predators or pathogens). The seedlings germinating from the seed bank add to the saplings,

which grow and die similarly to the adult trees. The local behavior of TreeMig has been tested against Swiss National Forest Inventory data representing different climatic conditions and stand ages [Bolliger and Lischke, 2004]. Parameters for the reproduction model have been compiled from various sources [Lischke and Löffler, 2004]. The parameter limiting species-specific seedling numbers was fitted by eyeball to a subset of the data. The overall correspondence between model and the entire data set was satisfying for most species and conditions.

2.2. Input data

The study area (Figure 1) encompasses the central Alpine region of Valais, which spans a large range of environmental conditions, altitudes from 400 m to 4000 m, yearly mean temperatures between -1 °C and 11 °C, and yearly precipitation sums between 350 mm in the eastern parts of the valley and 2000 mm in the high altitudes. The central Alps separate the main valley from the glacial refuges of many species in the south and east. This region has defined paths where species could immigrate, namely the northern opening of the valley and several lower mountain passes in the southeast. An area of 50 km^2 was chosen, simulation were carried through on $1 \text{ km} \times 1 \text{ km}$ grid cells, from the end of the last glacial about 14000 before present (BP) to present. Four test sites were chosen to evaluate the temporal simulation pattern, characterized by their western-eastern position and their altitude. Site 2 is situated in the central part of the valley bottom (670 m), site 1 at the timberline (2390 m), site 3 below timberline (1990 m) close to the Simplon pass, an site 4 in medium altitudes (1475 m).

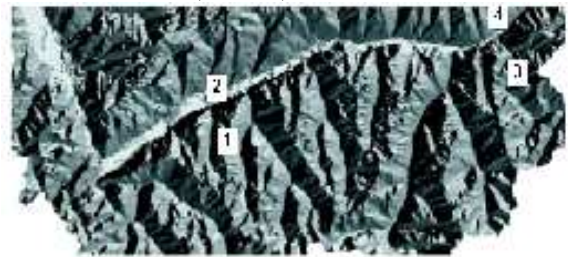


Figure 1: Simulation area in the Valais, Switzerland. The numbers refer to selected sites, where temporal courses of the simulation are evaluated.

The model uses as input the bioclimatic variables day degree sum (above 5.5 °C), lowest monthly temperature mean and a drought stress index (between 0 and 1). They were derived according to the model ForClim-E [Bugmann and Cramer, 1998] for each cell in the simulation area and each year in the simulation period. The bioclimatic variables were based on monthly temperatures and precipitations interpolated from climate station values and on a temperature anomaly scenario, reconstructed from chironomids in an Alpine lake [cf fig. bottom, Heiri,

Lotter et al., 2003]. The species were assumed to immigrate from the Northwest, i.e. from the lake Geneva and from the Southeast over the lowest pass, i.e. the Simplon (2000 m altitude). In the simulation,

at 14000 BP no trees were present. The approximate immigration years for the species arriving from the North were assessed from pollen records from the pollen database for the European Alps

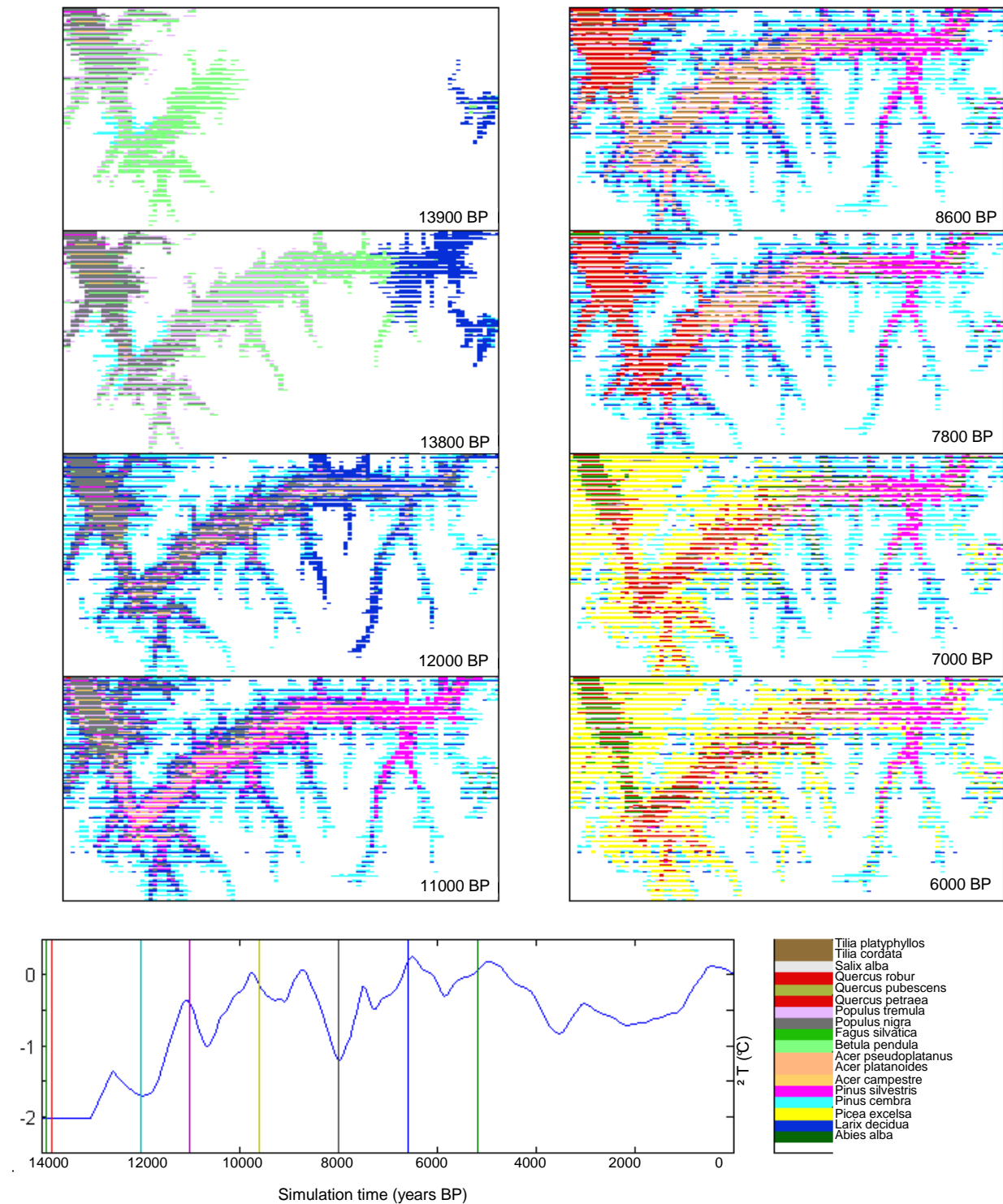


Figure. 2: TreeMig simulation of tree species spread on a 1 km * 1 km grid over 100 km * 50 km in the region of Valais, Switzerland. In each cell the species biomasses (t/ha) are drawn as stacked columns. A completely filled cell corresponds to 450 t/ha total biomass. The graph at the bottom indicates the assumed temperature anomaly along with the times corresponding to the maps shown above (vertical lines).

[van der Knaap and Ammann, 1997] from the southern part of the Swiss Central Plateau; those of the species immigrating over the Simplon were assessed from a pollen record from Simplon.

Simulation experiments

The simulations were run with the described time series of bioclimate and species immigration. Species-specific biomasses were stored for every cell and every 200 years and displayed as a movie and as a series of maps. To separate the influence of succession and migration (intrinsic dynamics) from that of the environment, at selected timepoints the model was run into equilibrium keeping the bioclimate constant at the values of these times. All species which had immigrated before into the simulation area were allowed to be present everywhere. The simulated equilibrium species biomasses $eq_{x,y,s}$ were compared to the species biomasses $y_{x,y,s}$ with transient climate and migration with a similarity index $S = 1 - \frac{\sum_{x,y,s} |y_{x,y,s} - eq_{x,y,s}|}{\sum_{x,y,s} (y_{x,y,s} + eq_{x,y,s})}$.

3. RESULTS

The spatial patterns resulting from the simulations are shown as maps of species composition at selected time points (Figure. 2), the similarity to the equilibrium composition in Table 1. During the initial colonization (14000 to 13800 BP), fast migrating species such as birch (*Betula pendula*) and aspen (*Populus tremula*) spread rapidly, poplar (*Populus nigra*), pine (*Pinus sylvestris*), Swiss stone pine (*Pinus cembra*) and larch (*Larix decidua*) (from the East) follow slower. The vegetation is far from equilibrium (Table 1, 13900, 13800). At 12000 BP, the low and medium elevations of the central valleys are completely populated, in the valley by poplar and pine, at the slopes by larch and at the timberline by Swiss stone pine, which drives back larch from the east and from the west. At 11000 BP, the timberline has shifted upwards, Swiss stone pine has mostly displaced larch, a small population of fir has developed south of the Simplon-pass, and in the eastern part of the valley, which is characterized by low precipitation sums, pine dominates. The vegetation resembles more to the equilibrium composition but still migration goes on. Until 8000 BP, maple has spread far through of the valley, oak follows slower (9600 BP, 8000 BP). They push pine back to the very dry areas. A few firs have passed the Simplon-pass, and spread in the valley and at the

Years BP	Similarity index
13900	0.16
13800	0.24
12000	0.48
11000	0.54
9600	0.56
8000	0.60
6600	0.61
5200	0.69

Table 1 : Similarity between simulated biomasses in transient simulation (Figure. 2) and equilibrium simulation .

slopes from the east. Spruce (*Picea abies*) and beech (*Fagus sylvatica*) enter the valley in the north. At 6600 BP, spruce and beech have spread from the west. At their eastern limit, still many species coexist. At 5200 BP, spruce dominates in the region. It has outcompeted fir, oak, and beech at the medium altitudes, and pushed Swiss stone pine back to high elevations. At this time the simulated vegetation is close to equilibrium which itself is determined by the climate.

Figure 3 shows the temporal pattern of the species composition at the four selected sites. The long-term climate pattern is manifested most strongly at the high timberline site 1, by the slow initial increase of biomass at 11000 BP and by the gaps at about 8000 BP and between 4000 and 1500 BP. Species biomasses fluctuate at all sites, which reflects the temperature fluctuations given by the climate anomaly but also by the stochastic climate generator. However, the fluctuations are strongest at the borders of the distribution ranges of the species, such as at the high timberline site (1), or at the higher border of the distribution range of pine (site 2) or spruce (site 3, after 7000 BP). At the lower timberline site (3), the fluctuations are small until spruce appears, which competes with Swiss stone pine in warm periods, resulting in strong fluctuations also in this species. Such switches between two competing species (Swiss stone pine and pine) appear also at site 4, where Swiss stone pine is driven by the fluctuations of pine. The immigration of species is reflected mainly by the appearance of spruce. Larch and Swiss stone pine seem to appear later in the west (site 1) than in the east (site 3). However, the spatio-temporal simulations, particularly the movie, reveal that both species are present in the region of site 1 already around 12600 BP. Thus, this apparent migration lag is due to too cold temperatures.

4. DISCUSSION

The large-scale spatio-temporal pattern is dominated by three aspects:

1) the initial colonization of the empty habitat, 2) the immigration waves of the various species with intermediary species intermingling and outcompeting of residents, if the immigrants such as spruce or beech are dominant, and 3) the spatial separation of the species according to the environmental conditions. The relative importance of these factors differs between times and locations. The influence of the spatio-temporal pattern of the environmental factors is especially strong at the borders of species ranges. The environment forms the stage for the endogenous dynamics, i.e. migration and competition, which play particularly in transient phases after drastic changes of the boundary conditions, i.e. immigrations.

At the studied scale (grain = 1 km * 1 km) no endogenous pattern formation can be observed. This is partly because the resolution is too coarse with respect to the interaction ranges and the gradients in the

environmental variables. Furthermore, the simulations are rarely in equilibrium due to the constantly changing climate and the pulses of immigration.

The simulations demonstrate that single local data sets, such as pollen records are difficult to interpret with respect to spatio-temporal patterns: The clear pattern of spread in the spatial simulations is hardly detectable in the single site trajectories. Taking further into account the uncertainties in pollen data, climate scenario and immigration scenarios related to dating and interpretation [Lischke, Guisan et al., 1998a] it becomes even more evident that an analysis of the processes in the past leading to such data sets is impossible without models – and that for a thorough model testing many pollen data sets are required which additionally stem from a less complex area than the Alps.

The presented simulations are a first step towards analyzing past and assessing future tree species migrations under a changing climate. The presented simulations serve to demonstrate the generic behavior of the model in quasi-realistic situations. However, some traits of the simulations are rather unrealistic,

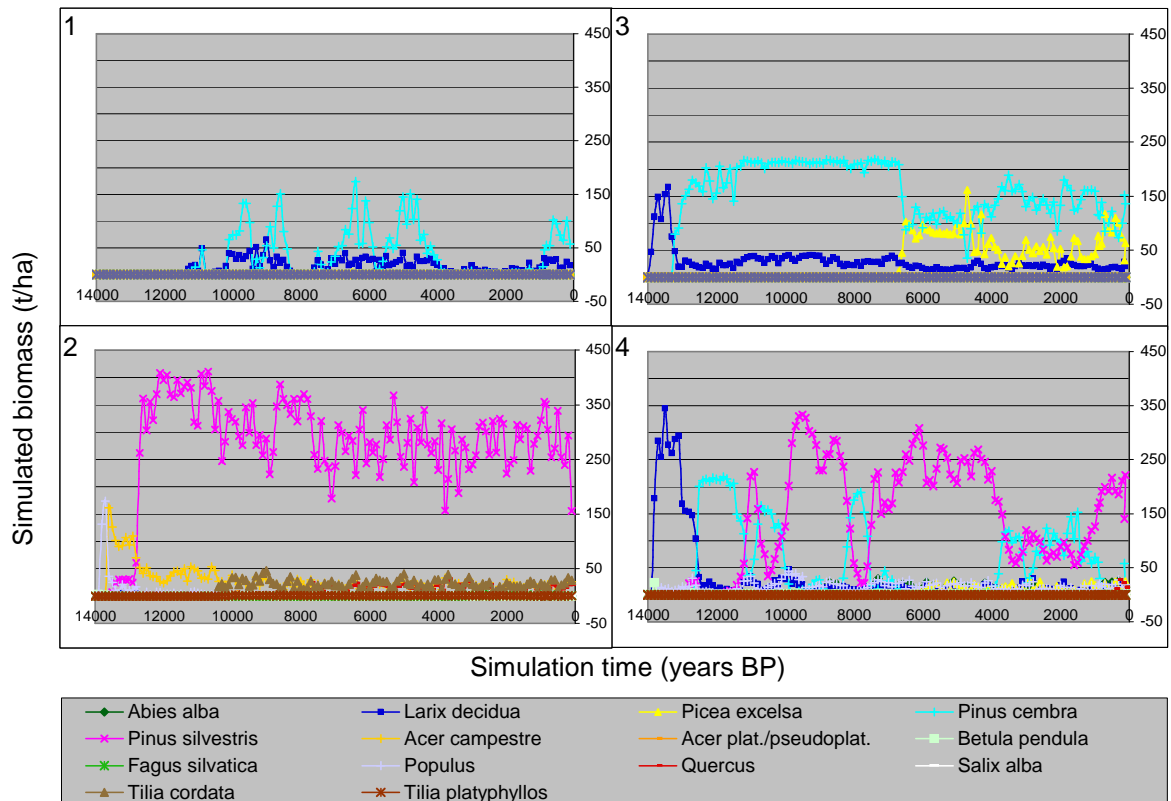


Figure 3: Simulated species biomasses at selected sites with different altitudes (1 and 3 close to timberline, 2 low, 4 medium) and different longitudes (1,2 west, 3,4 east).

e.g. the overwhelming dominance of spruce. The simulated species composition for current conditions resembles that at 5200 BP, i.e. is dominated by spruce, oak, and beech in the low altitudes, and pine at the very dry sites. The current forests in Valais such as recorded in the Swiss National Forest Inventory [EAFV, 1988], have much less spruce and more fir and larch. This deviation is probably to a large extent due to the oversimplified climate change scenario we used, which assumes that precipitation was the same as today, whereas it was probably considerably drier in the late glacial and early Holocene [Guiot, Harrison et al., 1993]. In future simulations, various combinations of climate anomaly scenarios shall be tested.

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