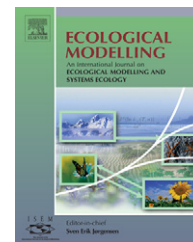


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Understanding alpine tree line dynamics: An individual-based model

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ABSTRACT

In addition to the effects of climate change, land use change is expected to trigger dynamic processes that may shift alpine tree lines upwards. To gain a conceptual understanding of the spatio-temporal processes shaping tree line patterns, we developed an individual-based and spatially-explicit model of spontaneous forest regeneration at the alpine tree line. Remote sensing data were integrated with the succession processes for individual trees in an object based image analysis approach. The model presented here predicts patterns of natural forest regeneration on a summer pasture in the Austrian Central Alps between 1954 and 2006. Different model scenarios are compared to the actual forest regeneration during the study period to validate the model's structure and its sensitivity to changing input parameters. The model's main process parameters are tested in four scenarios: A baseline scenario with the most likely input parameters derived from empirical studies in the literature; and three scenarios with differing parameters for seed production, seed dispersal kernel, and seedling competition with the ground vegetation. The tests largely confirm the model's formulation. The baseline scenario correctly predicts a significant upwards shift of the tree line elevation. Moreover it is demonstrated that (1) fecundity is a crucial factor in the expansion of forest into open land, (2) land cover and land use history have a significant impact on the emergence of forest regeneration patterns and (3) the dispersal kernel of Norway spruce has a long-distance component. We thus identified the key processes operating under environmental change from the characteristics of spatial changes in tree line patterns over the last 50 years.

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1. Introduction

The shift of the alpine tree line to higher elevations is a conspicuous indicator of the substantial landscape change that is currently going on in the alpine zone of the European Alps due to land use and climate change (Bolliger et al., 2007; Gehrig-

Fasel et al., 2007; Tasser et al., 2007). Spontaneous forest regeneration processes on less intensively used pastures have led to subalpine forest ecosystems extending their ranges to higher elevations, where the alpine tree line represents the leading edge. Despite its name, the tree line is actually a transition zone (=ecotone) to the treeless alpine grassland rather

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than a linear feature (Körner and Paulsen, 2004). There are major conservation concerns over the impact of environmental change on the alpine vegetation – specifically the loss of biodiversity and the decrease and fragmentation of habitats (Pauli et al., 2007). In the face of global and regional environmental change, a conceptual understanding of mountain ecosystem dynamics and species range shifts along elevation gradients is needed (Jeltsch et al., 2008).

The pattern of tree lines is the result of many biotic and abiotic factors operating at different spatial scales. At the global scale, the location of potential tree lines is closely correlated to climatic factors – most importantly to temperature (Körner, 1998; Alvarez-Uria and Körner, 2007; Kessler et al., 2007). With climate change, high-elevation trees currently react to rising temperatures by increased growth rates (Paulsen et al., 2000; Kessler et al., 2007). Consequently, the potential tree line has risen about 100–150 m higher than it was in the mid 19th century, the so called “Little Ice Age” (Nicolussi and Patzelt, 2006). However, on a regional scale, tree line dynamics in the European Alps are strongly influenced by land use changes – especially the abandonment of alpine summer pastures (Dirnbock et al., 2003; Gehrig-Fasel et al., 2007; Holtmeier and Broll, 2007; Pauli et al., 2007; Tasser et al., 2007). The centuries-long history of transhumant land use of alpine pastures has led to a significantly depressed tree line. Only since the last few decades, land use change has led to forest regeneration and to an upwards shift in the elevation of the alpine tree line (Gehrig-Fasel et al., 2007). Therefore, the term “forest regeneration” will be used in this paper for the establishment of new forest areas above the present tree line.

Last but not least, forest regeneration patterns are influenced at the local scale, as the forest advance is strongly related to dispersal characteristics of the current tree line species – that is, the production of viable seeds (Juntunen and Neuvonen, 2006), seed dispersal kernels (Clark et al., 1999; Dullinger et al., 2004), and seedlings competition with ground vegetation (Dullinger et al., 2004; Holtmeier and Broll, 2007; Tasser et al., 2007). The alpine tree line shift is thus driven by climatic gradients operating at global scales, by regional land use changes and by endogenous factors including dispersal, germination and mortality of individual trees at the local scale (Lischke et al., 2006).

In recent years a large number of ecological models have been developed to simulate spatial forest regeneration patterns in order to understand the natural dynamics of forest succession and to predict spontaneous forest regeneration (He et al., 1999; Hörsch, 2003; Dullinger et al., 2004; Yan and Shugart, 2005; Kupferschmid et al., 2006; Lischke et al., 2006; Rammig et al., 2006; Eerikainen et al., 2007; Tasser et al., 2007). Especially individual-based models (IBMs) are promising tools for getting a better understanding of natural dynamics and their underlying processes. Due to the scaling up approach, individual-based models can integrate factors operating at different spatial scales. Most importantly causal inferences of process–pattern relationships can be made, because with IBMs patterns evolve from simple rules on the individual level (Grimm and Railsback, 2005). Structurally realistic IBMs can be used as a virtual laboratory to experiment with real world data to improve the understanding of the processes that have

shaped a particular landscape. However, for shifting tree line ecotones, the information about processes resulting in tree line patterns has not been “decoded” yet in a systematic way.

In this study, we present a new, spatially explicit and individual-tree-based model of the forest dynamics at the alpine tree line to gain a better understanding of process–pattern relationships in response to land use and climate change. We focus on three parameters that are crucial for forest succession: fecundity, dispersal kernels and the influence of land cover and land use history on tree seedling germination. Remote sensing data are integrated with tree succession processes to model the natural forest regeneration during the last 50 years. Different scenarios are compared with the actual forest regeneration patterns to validate the model and to evaluate the sensitivity of the model to parameter modification.

2. Study area

The study area is located at the current tree line on an east-facing slope in the Austrian central Alps (Fig. 1). The modelled area comprises about 1 km² of the “Breitlehn Alm” – a pasture for cattle and sheep, with light summer use. It spans from the dense subalpine spruce forest at 1600 m a.s.l. to the alpine grassland at 2400 m a.s.l. The study period is from 1954 to 2006.

As in many parts of the Alps, the mid 1950s mark a turning point in land use practices within the study area. At the “Breitlehn” pasture the hay production was stopped in 1957 and the meadows were converted into pastures. Accordingly, the summer pastures have been used with decreasing intensity since then. Cattle numbers declined from 60 animals in the 1950s to 25 animals today (mostly heifers, three cows) and the number of sheep was more than halved from 450 to presently 200 head. Due to this fact, steep slopes and remote areas at high elevations were abandoned and the pasture is used more lightly in general.

The forest at the Breitlehn Alm is a subalpine spruce forest (*Vaccinio Piceion*) with mainly Norway spruce (*Picea abies*), mixed with about 10% European larch trees (*Larix decidua*) and patches of Green alder (*Alnus viridis*) in avalanche paths and along streams. The tree line lies around 1900 m a.s.l. and is comprised of forest patches embedded in a mosaic of alpine pastures, avalanche paths and previously cultivated land in

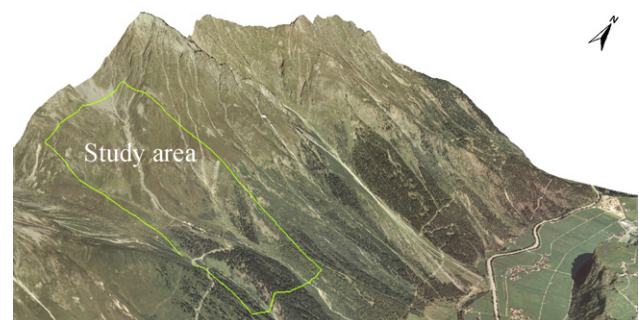


Fig. 1 – The study area in the mountain range above the village of Längenfeld, Ötztal valley in the Austrian Central Alps.

various stages of succession. At higher elevations above the current tree line, isolated pine trees (*Pinus cembra*) were also found in addition to spruce and larch. A European larch at 2309 m represented the highest elevation for a tree in the krummholz belt of the study area.

The model in this study focuses on Norway spruce (*Picea abies*), which currently is the dominant tree line species in the study area. This species is a shade tolerant conifer with wind distributed seeds. According to Ellenberg (1996), the maximum potential elevation for a closed spruce forest currently lies at about 2100 m in the Eastern Central Alps. Although under natural conditions Stone pines (*Pinus cembra*) would be expected to occupy the tree line in the Central Alps, no mature Stone pines were found in the study area. Consequently lacking of seed sources, Stone pines were not significant for the forest regeneration over the past decades and therefore were not included in the model.

3. Materials and methods

The presented model integrates landscape features, derived from an object based image analysis (OBIA) with ecological process parameters taken from the literature. Predicted forest regeneration patterns based on different scenarios are then compared with the pattern in 2006 derived from the remotely sensed data in order to validate the model and to assess the model's sensitivity to different parameters (Fig. 2).

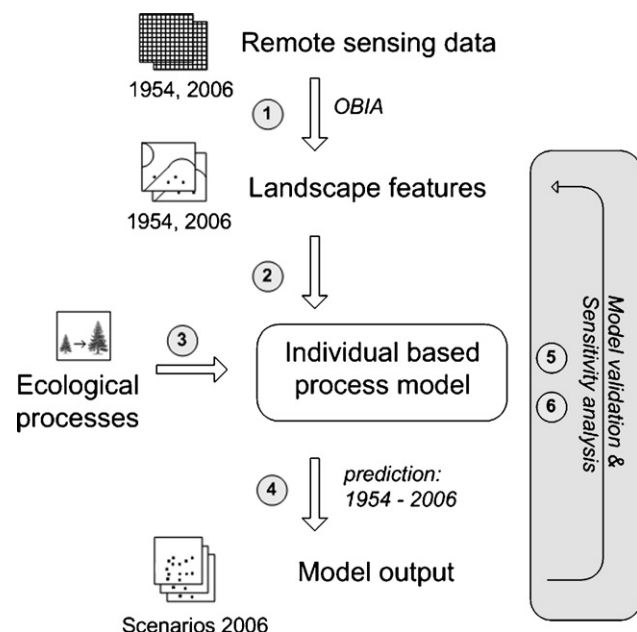


Fig. 2 – The construction of the presented model involves six steps: (1) deriving relevant landscape features from remote sensing data in an object based image analysis (OBIA) approach, (2) building the model, (3) parameterisation, (4) running the model for different scenarios, (5) model validation and (6) sensitivity analysis.

3.1. Remote sensing analysis

The model in this study is built on features and land cover classes that are derived from remote sensing imagery, i.e. aerial photos and LiDAR data. Two aerial photos of the study area provide a ground resolution, good enough to identify individual trees. For 1954 a black and white image with a ground resolution of 1 m (Fig. 3a) and for 2003 a RGB true colour image with a ground resolution of 25 cm is available (Fig. 3b). Additionally, high resolution LiDAR data for the same area were obtained for 2006, resampled to elevation and surface rasters with a 1 m resolution (Fig. 3d). All images were provided by the government of Tyrol.

In the first step land cover is classified, using an object based image analysis approach with the Definiens Professional 5.0 @software based on a rule-based, supervised classification. The OBIA method is used, because it delivers superior results for high resolution data compared to a pixel based classification (Burnett and Blaschke, 2003). Moreover the resulting map of an OBIA classification is comprised of object-polygons rather than pixels, directly applicable for further modelling in a GIS (Langanke et al., 2007). The land cover is segmented into homogenous land cover objects, which are then classified in a supervised approach. Expert knowledge regarding historic land use, especially to distinguish pastures and meadows, was collected in interviews with local farmers in the summer 2007. This information is integrated through a manual improvement of the classification for the respective land cover objects. This semi-automatic classification finally results in five land use/land cover (LULC) classes: hay meadow, lightly used pasture, dwarf shrub communities, bare ground, and closed forest (Fig. 3c).

In the second step, single trees are delineated manually from the 1954 image. Three height classes can be distinguished: small (≤ 6 m), medium (≤ 15 m), and tall trees. Tree heights are then assigned randomly within the class range to facilitate the modelling of growth for individual trees. For the recent forest a digital vegetation model (DVM) was calculated from the LiDAR data as the difference between the first and the last laser return (Fig. 3e). The tree top location and the tree heights are obtained from the DVM by automatic feature extraction with a finding local maxima algorithm. However, trees of less than 4 m height cannot be delineated with this method, because it is not possible to distinguish these small trees from green alder bushes. Moreover small trees in closed forest stands are not detected, where they are covered by higher trees.

3.2. Model concept and assumptions

Natural forest regeneration is modelled as the succession of individual trees, where each tree is represented as an attributed point. Time is handled in discrete annual time steps starting from 1954 until 2006. It is assumed that three core ecological processes and their response to environmental factors determine the spatio-temporal forest regeneration pattern: recruitment, growth, and mortality (Fig. 4).

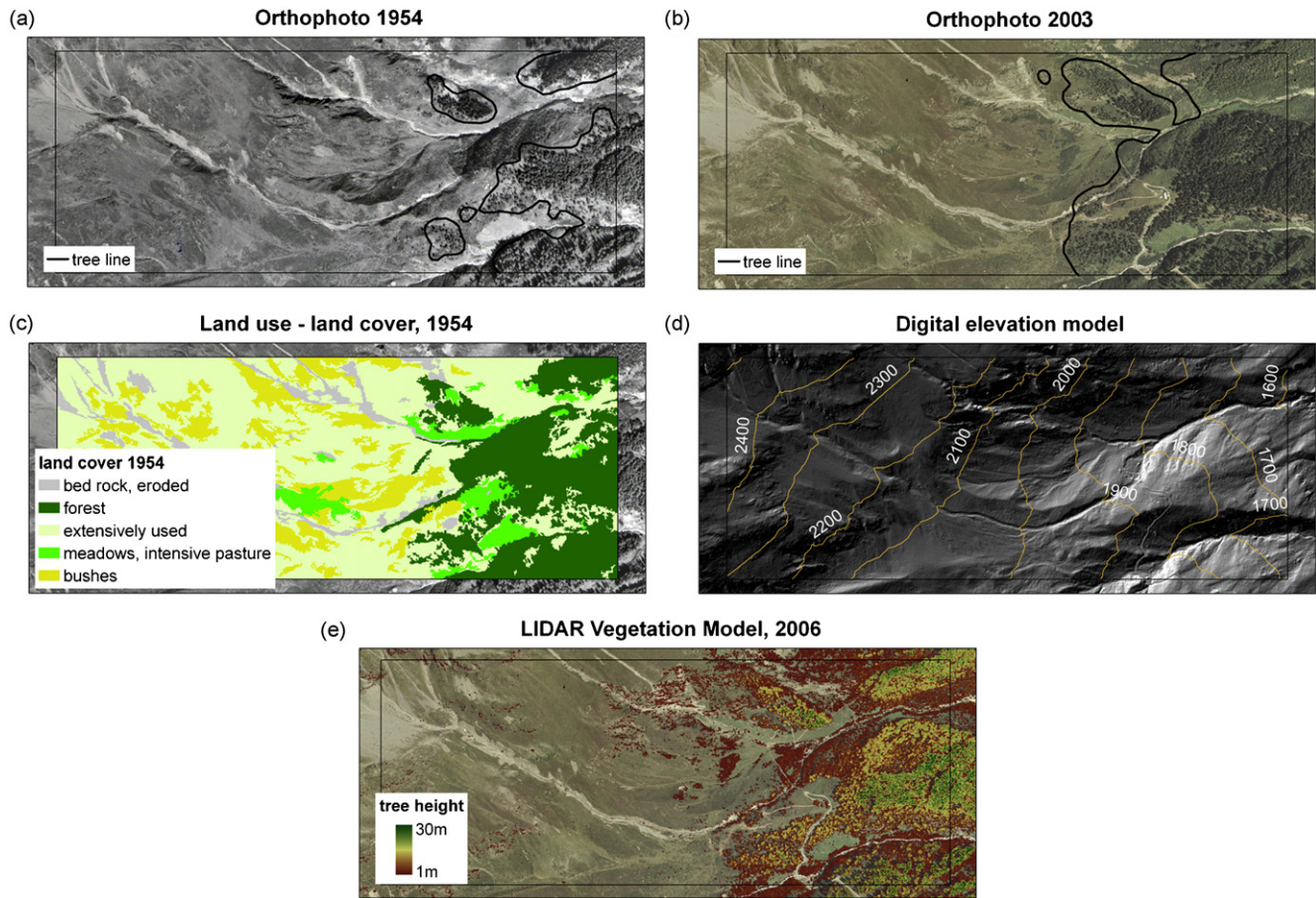


Fig. 3 – The remote sensing data, which are used for the model in this study: (a) aerial photo 1954 (b) aerial photo 2006 (c) land cover – land use classification for 1954 (d) digital elevation model from airborne LiDAR data (e) LIDAR, digital vegetation model.

3.2.1. Recruitment

The successful establishment of seedlings is composed of the processes seed production, seed dispersal and germination. The amount of seeds drives the quantity of germinated seedlings. Wind distributing conifers produce a large amount of seeds, up to several thousands per seed tree and year (Sagnard et al., 2007). However, not all seeds are viable and only a fraction germinate in the extreme environmental conditions of the alpine tree line (Hofgaard, 1993). In the presented model the initial location, where the seeds are placed is random. To take account for the strong temporal variation in seed tree fecundity in subalpine forests, every seventh year is modelled as a mast year with an increased seed production (Mencuccini et al., 1995; Kupferschmid et al., 2006). The spatial seedling distribution pattern is modelled via the germination process, by comparing a seed's random fitness value with the germination probabilities in a particular land cover class. Only seeds that successfully germinate are passed on to the next step. Three factors are detrimental to germination: great distance to seed trees, unfertile or too densely vegetated land cover types, and high elevations (Dullinger et al., 2004; Rammig et al., 2007; Tasser et al., 2007). The germination probabilities in dependence on these factors are modelled as follows:

- (a) Distance to seed trees: Spruce seeds usually fall to the ground at about one or two tree lengths from the seed tree, heavier seeds of better quality are usually dispersed over even shorter distances (Hanssen, 2003). However, secondary dispersal through strong winds can carry the seeds farther away (Sagnard et al., 2007). Seed germination thus is a composite process of dispersal over near and far distances, which can be modelled as the overlay of seed distribution functions (Clark et al., 1999):

$$\text{Prob}_{\text{germ}}(\text{dist}) = ae^{-0.5(\text{dist}/c_1)^{d_1}} + be^{-0.5(\text{dist}/c_2)^{d_2}} \quad (1)$$

where $\text{Prob}_{\text{germ}}$ is the probability of successful germination for each seedling, dist is the distance to the nearest seed tree, a and b are normalisation constants, c_1 and c_2 are distance parameters and d_1 and d_2 are shape parameters. For $d_1 = d_2 = 2$, the function is Gaussian.

- (b) Land cover type: Land cover and historic land use has a long-term influence on spatial forest regeneration pattern. For shade tolerant species as Norway spruce high solar radiation can rapidly lead to fatal seedling desiccation (Germino et al., 2002). The best microsite conditions outside closed forests are characterised by herbaceous cover, which is taller than the seedling to protect it from direct

Model architecture

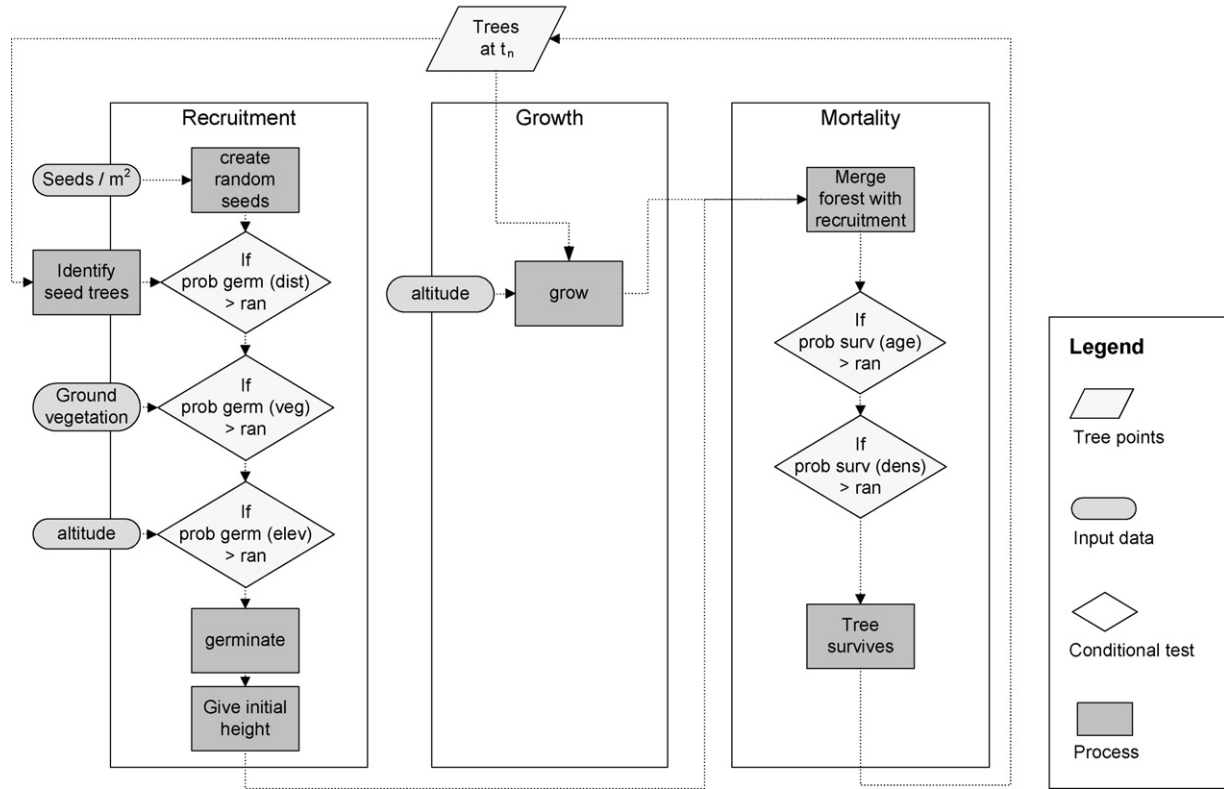


Fig. 4 – The model iterates each year through the processes of recruitment, growth and mortality. A new seedling establishes if the germination probabilities ($\text{prob}_{\text{germ}}$) in dependence to the distance to the nearest seed tree (dist), the ground vegetation (veg) and the elevation (elev) are greater than random seedling fitness values (ran). At the end of each year a tree dies, if the surviving probabilities ($\text{prob}_{\text{surv}}$) in dependence to the tree age and the tree density (dens) are smaller than random mortality values (ran).

sunlight (Germino et al., 2002). However, a very dense grass cover constitutes a physical barrier to emerging roots and thus prevents successful germination (Sagnard et al., 2007), because the tiny spruce seeds do not have sufficient reserves to penetrate thick turfs before they reach the substrate. The germination probability for Norway spruce seedlings in dependence on the land cover is derived from regressing newly established forest stands against historic land cover types in the Eastern Central Alps (Tasser et al., 2007). It is assumed that the germination probabilities stay constant over the study period, because the investigated time span is comparatively short in terms of ground cover succession processes (Irvani et al., 2007). In Table 1 the germination probability parameters are summarised for the land cover classes in the study area.

- (c) Elevation: The probability of germination decreases with higher elevations. Besides restrictions in seed production, recruitment is oppressed by seedling mortality, especially at early stages (Juntunen and Neuvonen, 2006). The influence of germination success and seedling mortality are subsumed under the germination probability along the elevation gradient described by Tasser et al. (2007). The germination probability declines along a sigmoid curve with

increasing elevation:

$$\text{Prob}_{\text{germ}}(\text{elev}) = 1 - \frac{1}{1 + e^{-(\text{elev}-i)/\text{const}}} \quad (2)$$

where $\text{Prob}_{\text{germ}}$ is the germination probability, elev is the elevation, i is the inflection point and const is a normalising constant.

3.2.2. Growth

At each time step trees grow in a sigmoid curve in dependence to their own height, the elevation, and a stochastic component. The tree height at the time t can be expressed with the growth rate equation proposed by Rammig et al. (2007):

$$H(t+1) = H_{\text{max}} \left(1 - \left(1 - \left(\frac{H(t)}{H_{\text{max}}} \right)^{1/3} \right) e^{-g} \right)^3 \quad (3)$$

where H is the tree height, t is the tree age, H_{max} is the maximum height and g is the growth rate. At a young age trees grow slowly until a certain height is reached and the growth rate accelerates. When tree heights come close to the maximum height, the growth rate slows down again.

Table 1 – The model components and the main input parameters for the baseline scenario

| Model component | Parameter values | Source |
|--|--|---|
| Maximum seedling density | 0.003 seedlings/m ² year | Hofgaard (1993), Rammig et al. (2007) |
| Tree height threshold for maturity | 7 m | Juntunen and Neuvonen (2006) |
| Prob _{germ} (dist) (formula 1) | Normalisation constants, $a = b = 0.5$ Distance parameter, $c_1 = 15$ m Distance parameter, $c_2 = 110$ m Shape parameter, $d_1 = d_2 = 2$ (Gaussian function) | Clark et al. (1999), Tasser et al. (2007) |
| Prob _{germ} (elev) (formula 2) | Inflection point, $i = 1550$ m Normalising constant, $const = 155$ | Tasser et al. (2007) |
| Prob _{germ} (veg) | Forest: 100% Shrub land: 34% Lightly used pasture: 32% Frequent stocking: 2% Bare ground; built up area: 1% | Tasser et al. (2007) |
| $H(t+1)$ (formula 3) | Maximum tree height, $H_{max} = 35$ m Growth rate, g : random variable | Rammig et al. (2007) |
| Prob _{surv} (age) (formula 4) | (for age ≤ 6 years) • Constant, $const = 10$ • Constant, $a = 104.63$ • Exponent, $b = 0.639$ (for age ≥ 7 years) • Prob _{surv} (age) = 0.99 | Hanssen (2003) |
| Prob _{surv} (dens, age) (formula 5) | Maximum weighted tree density, $dens_{max} = 0.06$ Tree age sensitivity threshold, $age_{sens} = 100$ years | Empirical data |

The first two components are fecundity parameters. The germination probabilities (Prob_{germ}) are modelled in dependence on the distance dist to the nearest seed tree (1), the elevation elev (2), and the ground vegetation type veg. The tree height $H(t+1)$ (3) is a stochastic equation that takes a random growth parameter. The last two survival probability functions (Prob_{surv}) describe the mortality at the end of each time step depending on the tree age (4) and on the joint tree density (dens) and age values (5).

3.2.3. Mortality

Two factors can cause a tree's death in the model at the end of each time step. Firstly the seedlings' mortality decline with increasing age, which can be described with a negative exponential function (Hanssen, 2003):

$$\text{Prob}_{\text{surv}}(\text{age}) = \text{const}(a \times \text{age})^{-b} \quad (4)$$

where Prob_{surv} is the survival probability for each tree at the end of the time step, const and a are constants, age is the tree age and b is the exponent of the exponential equation.

Secondly the model accounts for density induced competition effects with other trees, if stands get too dense. The forest density is calculated locally with a 50 m moving window kernel, weighted with the crown radius to account for the increased shadowing effect of larger crowns. The maximum forest density of mature subalpine spruce forest stands is derived from the 2006 LiDAR scene of the Ötztal mountain range, outside the study area. In stands that have reached maximum densities, younger trees are modelled to have a higher probability to die than older trees, adding to their age dependent mortality rate. Trees older than a certain sensitivity threshold are not affected by dense forest stands.

$$\text{Prob}_{\text{surv}}(\text{dens}, \text{age}) = 1 + \left(1 - \left(\frac{\text{dens}}{\text{dens}_{\text{max}}}\right)\right) + \frac{\text{age}}{\text{age}_{\text{sens}}} \quad (5)$$

where Prob_{surv} is the tree survival probability, dens is the tree density weighted with the crown radius, age is the age of an individual tree, $dens_{max}$ is the maximum tree density, weighted with the crown radius observed in the mature forest stands in 2006 and age_{sens} is the age sensitivity threshold.

3.3. Parameterisation and sensitivity analysis

The described process model architecture builds the basis for several simulation runs with different parameters. In the first step, a baseline scenario is calculated with the most likely input parameters derived from empirical studies in the literature (Table 1).

In the second step, the parameters of the baseline scenario are changed in their range of possible values to estimate the model's sensitivity to changing its key process parameters. We focus on three processes that are important for forest regeneration: fecundity (Hofgaard, 1993), seed dispersal (He and Mladenoff, 1999; Albani et al., 2005; Brooker et al., 2007; Sagnard et al., 2007), and seedling competition with the ground vegetation (Berger et al., 2008).

3.3.1. Fecundity

Fecundity is modelled as the seed density in mature forest stands. The germination success in mature forest stands in the montane zone was assumed to be near 100%. Rammig et

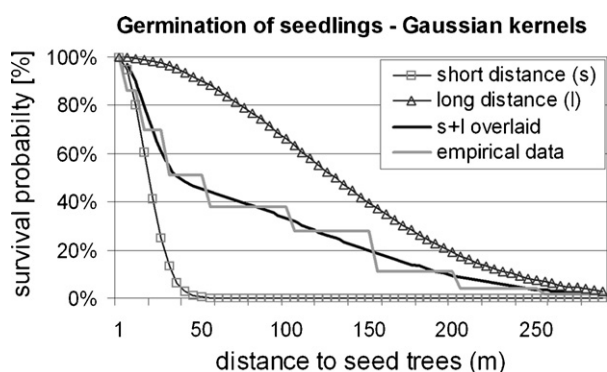


Fig. 5 – The probability of new seedling establishment declines with the distance to a seed tree. The probability function can be modelled as two overlaid Gaussian functions that describe the combined dispersal processes over short and long distances, respectively.

al. (2007) found one germinated seedling per 33 m² and year for a reforesting windblow site at 1400 m a.s.l. in the Swiss Alps. The amount of seeds between regular and mast years has a ratio of about 1:30 (Hofgaard, 1993). In the baseline scenario one seed is placed in 150 m² and every 7th year is modelled as a mast year with one seed in 5 m², resulting in an average of about one seed in 30 m² per year.

However, for a declining forest at the northern tree line in Norway Hofgaard (1993) found an average density of only one germinated seedling per 165 m² and year. This value is taken to simulate the reduced fecundity scenario, such that one seed is placed in 840 m² in regular years and mast years are modelled with one seed per 28 m².

3.3.2. Seed dispersal

The seedling density was taken as joint dispersal and germination probability in dependence on the distance to the nearest seed tree. The maximum number of germinated seedlings represents the aggregated seedlings density that was found empirically in closed forest stands. Successful seedling establishment was modelled with two overlaid Gaussian functions, representing the short and the long-distance distribution component (Fig. 5). The maximum distance of young growth from historic forest stands is about 200 m (Tasser et al., 2007).

Seed trap experiments, however, state that the maximum distance of dispersed seeds from Norway spruce trees is not more than 60–100 m from the seed tree (Bolli et al., 2007), but typically less than 25 m (Sagnard et al., 2007). These data suggest that the long-distance distribution is negligible. To test the model for its sensitivity to an altered seed dispersal kernel, the secondary distribution over far distance was omitted completely in a low-wind scenario. Primary dispersal is modelled by only one Gaussian distribution function, describing the short-distance dispersal as

$$\text{Prob}_{\text{germ}}(\text{dist}) = e^{-0.5(\text{dist}/20)^2} \quad (6)$$

where $\text{Prob}_{\text{germ}}$ is the germination probability at the distance dist.

3.3.3. Seedling competition with ground vegetation

Five classes can be distinguished on the basis of the aerial photo of 1954: hay meadow, lightly used pasture, dwarf shrub communities, bare ground, and closed forest. To quantify germination probabilities for the five land use – land cover classes, newly reforested areas are regressed against historic land cover with the data from an empirical study in the Eastern Central Alps (Tasser et al., 2007). The values range between 1% for solid rock and built up area and 100% for forest stands (Table 1).

The baseline scenario does not account for the successional change of the ground cover itself. This simplification is valid for intensively used grassland, as the succession from meadows to Mountain pine forests takes about 450 years, where in the first 300 years hardly any natural forest regeneration takes place (Iravani et al., 2007). However, for tall grass pastures the succession into a mountain pine forest is significantly shorter. Iravani et al. (2007) state that the germination probability in lightly used pastures and in shrubby areas increases up to 30% over the period of 50 years, whereas the formerly mown areas stay fairly impenetrable for seeds. To test, which impact the simulation of a later successional state has on the model output, a scenario with a decreased seedling competition with the ground vegetation is modelled. For this scenario the germination probability is increased by 30% for lightly used pastures and shrubby land.

3.4. Model validation

In the model validation multiple patterns found in the 2006 image are compared with the forest patterns of the modelled scenarios in order to validate the model structure and its parameterisation (Mulligan and Wainwright, 2004; Grimm et al., 2005). A range of patterns that are relevant for describing forest regeneration are chosen as basis for the comparison: the extent of forested area, the location of the tree line, the location and distribution of single trees, the forest distribution along the elevation gradient and the forest distribution on LULC 1954 classes. For the visualisation and the comparative analysis of the spatial distribution of forest patches, the trees are aggregated into three forest density classes: dense forests, sparse forests and open land with single trees (Fig. 6). The thresholds for dense and sparse forests are determined visually from the forest density maps computed on the basis of the 2006 image. In total six datasets are compared, the actual situation in 1954 and in 2006, as well as the predicted scenarios for 2006, i.e. the baseline scenario and the three scenarios with modified parameter values. The overall spatial prediction accuracy is calculated as the number of correctly identified pixels, divided by the correct pixels plus the error pixels of commission (number of pixels that have been predicted an incorrect class) and omission (number of pixels that have been incorrectly included in the class).

4. Results

4.1. Model validation

Fig. 6a and b shows the forest distribution in the years 1954 and 2006, and Fig. 6c–f maps the modelled scenarios. All sce-

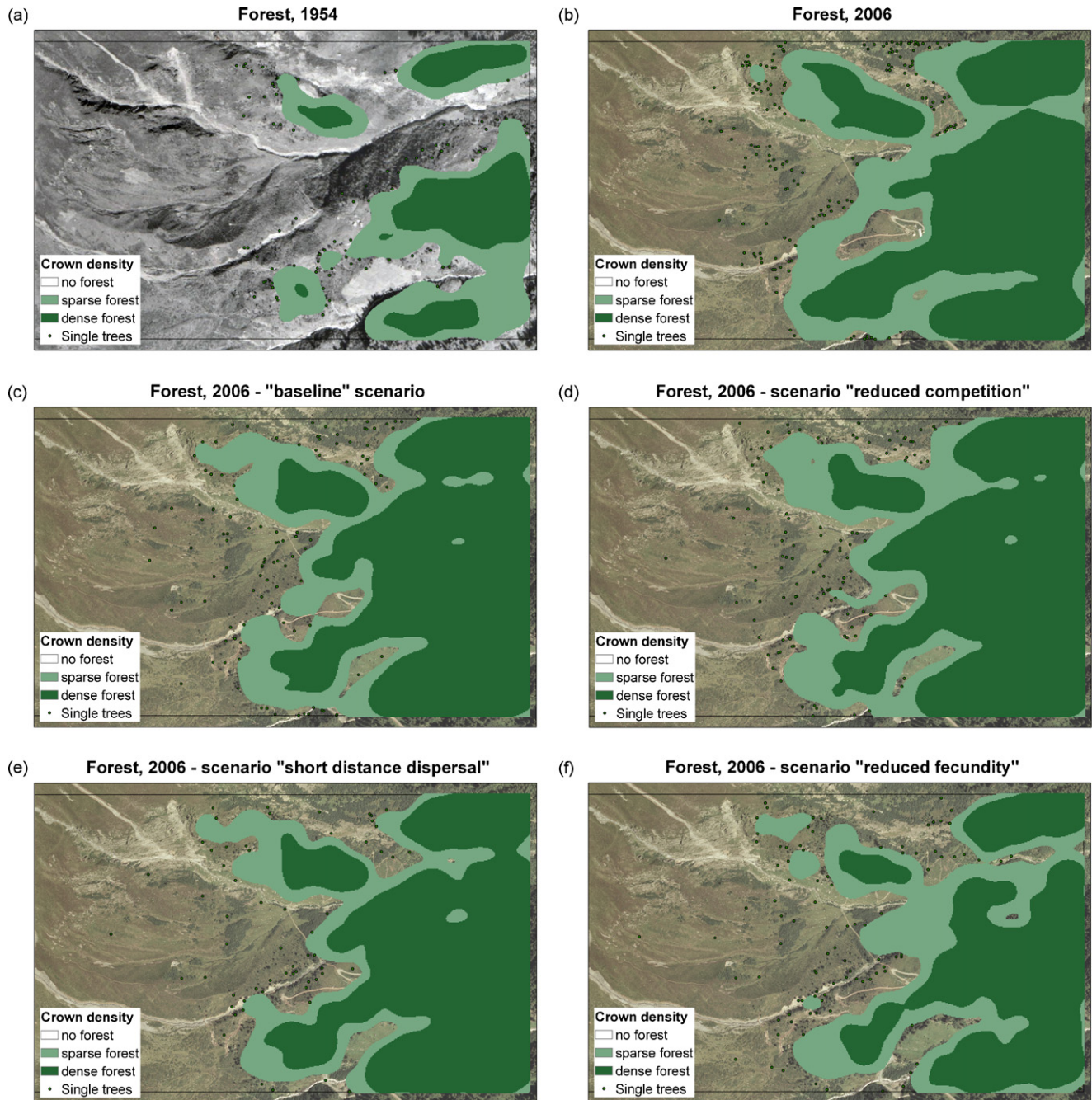


Fig. 6 – The delimitation of dense and sparse forest for (a) 1954 (b) 2006 and the model output for (c) the baseline scenario (d) the scenario with a reduced seedling competition with the ground vegetation (e) the scenario with a dispersal kernel over short distances only and (f) the scenario with the reduced fecundity.

narios predict the observed forest regeneration trend and the upwards shift of the alpine tree line. However, the “reduced competition” scenario best fits the real situation in 2006 not only quantitatively but also in respect to the forest location and multiple forest patterns. This scenario almost precisely predicts the extent of the forested area in quantitative terms (Fig. 7a). The “reduced competition” scenario has 95.1% overall spatial prediction accuracy for the three forest classes, “no”, “sparse” and “dense forest”, which represents the greatest spatial accuracy of all scenarios (Fig. 7b).

Table 2 summarises key figures, describing multiple forest regeneration patterns for the scenarios compared to the observed forest patterns. A characteristic forest pattern at the alpine tree line is the decreasing forest cover along the elevation gradient. The “reduced competition” scenario correctly predicts the relative area covered with forest, which decreases sharply from 71% around 1850 m a.s.l. to 8% around 2000 m a.s.l. (Fig. 8). Moreover, the forest pattern shaped by historic land use is also best reflected by this scenario (Table 2). Last but not least, the location and distribution of pioneering, single

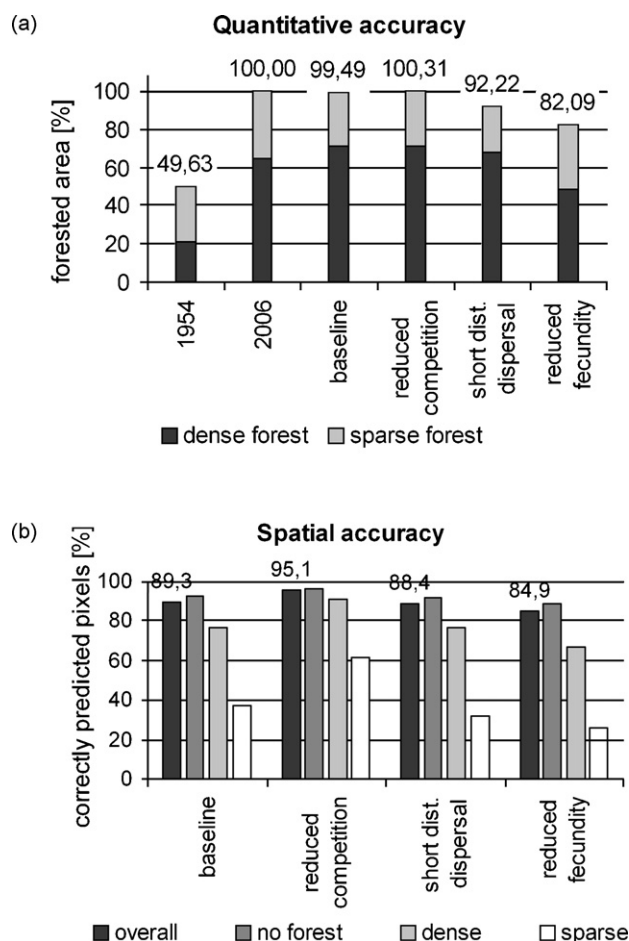


Fig. 7 – Accuracy assessment of the modelled scenarios: (a) a quantitative assessment in terms of predicted forested area compared to the observed forest extent in 2006 in percent (b) a spatial prediction accuracy assessment based on a pixel per pixel comparison.

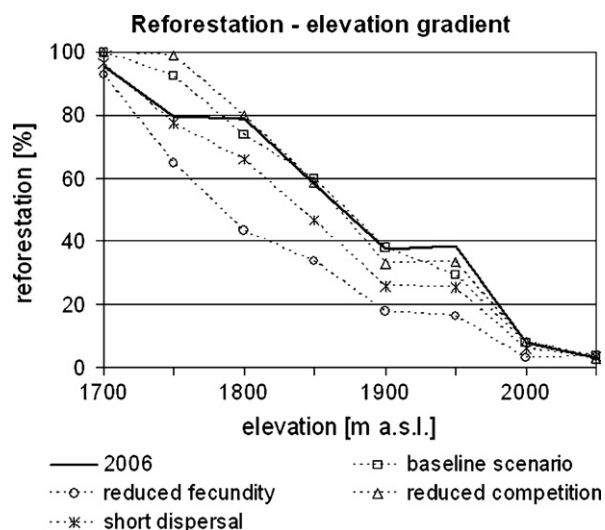


Fig. 8 – Forest regeneration of open land along the elevation gradient for the actual situation (solid line), the baseline scenario (dashed line) and the three scenarios with changed parameters (dotted lines).

trees outside the forest stands are crucial for the forest regeneration process. By 2006 the amount of trees outside forest stands has doubled from 80 trees to 167, the median distance of single trees to the forest edge increased from 12 m to 20 m (Table 2). This indicates that the zone between the tree and the timberline increases and that young growth can establish further away from forest stands. The “reduced competition” scenario picks up this trend, predicting 132 trees, and a median distance of 24 m.

4.2. Sensitivity analysis

In the sensitivity analysis the model is tested for its boundary conditions in terms of three key processes, firstly seed production, secondly germination and thirdly dispersal. The

Table 2 – The main results comparing the actual and the predicted forest regeneration pattern

| | 1954 | 2006 | Baseline scenario | Reduced fecundity | Short dispersal | Reduced competition |
|---|--------|--------|-------------------|-------------------|-----------------|---------------------|
| Forested area (m ²) | 173311 | 349236 | 347444 | 286700 | 322064 | 350301 |
| Forest cover, 1675–1725 m (%) | 61.9 | 98.4 | 100.0 | 97.2 | 98.6 | 100.0 |
| Forest cover, 1825–1875 m (%) | 29.7 | 70.6 | 71.9 | 53.3 | 62.5 | 71.1 |
| Forest cover, 1975–2025 m (%) | 0.0 | 7.9 | 7.7 | 3.2 | 6.0 | 8.2 |
| Forest cover, LULC class “forest” (%) | 65.0 | 96.0 | 97.4 | 92.1 | 95.1 | 97.5 |
| Forest cover, LULC class “shrubland” (%) | 0.0 | 2.2 | 1.6 | 0.4 | 0.6 | 1.9 |
| Forest cover, LULC class “lightly used” (%) | 4.6 | 19.4 | 18.7 | 12.6 | 16.0 | 19.3 |
| Forest cover, LULC class “intensive” (%) | 13.5 | 47.6 | 52.3 | 30.5 | 47.4 | 49.4 |
| Forest cover, LULC class “bare ground” (%) | 0.8 | 11.0 | 6.9 | 3.6 | 5.0 | 6.7 |
| Dense forest (%) | 41.5 | 64.7 | 71.5 | 59.2 | 73.6 | 70.3 |
| Tree line, maximum elevation (m) | 1948 | 2093 | 2086 | 2089 | 2093 | 2060 |
| Tree line, mean elevation (m) | 1793 | 1881 | 1899 | 1867 | 1878 | 1896 |
| Single trees (frequency) | – | – | 494 | 224 | 283 | 575 |
| Single trees ≥4 m (frequency) | 80 | 167 | 127 | 102 | 64 | 132 |
| Median distance of single trees ≥4 m to the nearest forest edge (m) | 12.4 | 19.6 | 22.8 | 21.1 | 19.6 | 23.8 |

main results of the comparison between the scenarios and the actual forest regeneration pattern are summarised in Table 2.

4.2.1. Scenario “reduced fecundity”

This first scenario, where the amount of yearly seeds is reduced to about a fifth of the baseline value, results in significantly less trees compared to all other scenarios: after the modelled time span of 52 years, the different seed quantity results in only a third of the trees predicted by the baseline scenario, 3483 compared to 11 350 trees respectively. Consequently, the resulting forest density is generally low, and the proportion of sparse forest to the total forest area is with 41% the highest of all scenarios (Table 2). Moreover, the tree line is clearly lower over the entire elevation gradient compared to the actual forest regeneration and all the other scenarios (Fig. 8).

Although the extent of forested area increases from 173 311 m² to 286 700 m², the increase in the amount of trees and the forest expansion into open land is comparatively small. On lightly used grasslands only 44 100 m² are predicted to be reforested compared to actually 82 200 m². The percentage of trees outside forests is the highest of all scenarios: 6.4% compared to 4.3% for the baseline scenario.

4.2.2. Scenario “short-distance dispersal”

This second scenario, where the maximum distance for seed dispersal is reduced from 250 m to 60 m, has a comparatively high ratio of dense forest stands (74% compared to 71% in the baseline scenario). The short-distance dispersal scenario thus has the highest proportion of dense forests of all scenarios and also overestimates the actual situation (Table 2). On the other hand, the modification of the dispersion shape results in 8.3% less trees, i.e. 10 404 trees compared to 11 350 trees in the baseline scenario and the forested area for the short-distance scenario extends over a 7.3% smaller area than in the baseline scenario (322 064 m² compared to 347 444 m²). Lightly used grasslands and scrublands at medium distances can hardly be reached by the seed rain and the forest regeneration of these land cover classes is accordingly low. In the short-distance dispersal scenario forests cover only 43% compared to actual 53% of the total area around the current tree line between 1825 m a.s.l. and 1975 m a.s.l. The difference in the amount of trees beyond the tree line is even more accentuated: short-distance dispersal results in 2.7% compared to 4.3% of the total amount of trees in the study area for the baseline scenario.

4.2.3. Scenario “reduced competition with ground vegetation”

The main distinction of this third scenario, where the probability of germination on lightly used pastures and scrubland is raised to simulate a later successional state of the ground vegetation, is reflected in the amount of trees above the tree line. The reduced competition results in 16% more trees than in the baseline scenario (575 trees compared to 494). The forested area increases marginally by less than 1% from 347 444 m² in the baseline scenario to 350 301 m² (Table 2). However, higher germination probabilities enhance the forest regeneration on lightly used grassland and scrubland in relation to other LULC classes. The relative forest regeneration rates per land cover

class are predicted slightly more accurately than in the baseline scenario (Table 2).

5. Discussion

5.1. Model prediction and validation

The validation results show that the “reduced competition” scenario predicts not only quantitative measures correctly, but also match actual forest regeneration over a range of different aspects of spatial distribution, such as forested area per elevation and land cover class, the ratio between dense forests, sparse forests and single trees, and the point pattern of single trees outside forest stands. It can thus be concluded that the model concept is plausible and that it may represent the real system behaviour (Grimm et al., 2005).

5.2. What drives forest regeneration at the alpine tree line?

5.2.1. Fecundity

Fecundity is a crucial factor for forest expansion into open land. Whereas the forest expansion in the baseline scenario correctly predicts the actually observed upwards shift of the tree line, the reduced fecundity scenario clearly does not match the observed forest regeneration pattern. The reduced fecundity scenario is parameterised with a particularly low seed density described for a declining forest with a broad transition zone at the northern tree line (Hofgaard, 1993), which is consistent with the clearly reduced expansion trend generated in the reduced fecundity scenario.

5.2.2. Dispersal kernel

The short-distance dispersal scenario can be interpreted as a low wind scenario. This scenario results in a distinct pattern, which does not match the observed forest regeneration pattern. The resulting pattern in the low wind scenario is twofold, firstly the forest expands into comparatively lower elevations and secondly the tree line itself is sharper, due to the quick decline in the amount of seeds with increasing distance to a seed tree. Consequently, the forest regeneration process is slowed down, when the long-distance dispersal component is missing. However, the comparison with the actual forest regeneration shows that dispersal kernels of Norway spruce at the alpine tree line also have a clear long-distance component with maxima of 250 m. Strong thermal alpine winds regularly blow upslope and thus contribute to long-distance upslope dispersal (Bolli et al., 2007). Nathan et al. (2002) demonstrate that one fraction of wind distributed seeds are uplifted aerodynamically above the forest canopy and further distributed over long distances, whereas the other fraction falls to the ground near the seed source. This finding confirms the bimodal seed dispersal over short and long distances. The long-distance component is particularly important, because isolated single trees resulting from long-distance dispersal serve as forest regeneration cells outside closed forest stands (Holl et al., 2000). Gömöry et al. (2006) state that Norway spruce is not only a typical climax species, but also behaves successfully as pioneer, because of its dispersal kernel: single trees can estab-

lish in suitable sites at medium distances from the forest edge and a strong seed dispersal at short distances allows the early colonisers to expand further into open land.

5.2.3. Broad scale factors: land use change versus climate change

Land cover and historic land use proved to be highly influential for the emergence of forest regeneration patterns. In 1954 the mean tree line elevation was at 1793 m a.s.l., which is more than 300 m below the potential tree line for spruce forests (Ellenberg, 1996). The almost full forest regeneration of the avalanche path shows that climatic factors do not limit the general upwards shift of the depressed tree line ecotone in the study area over the last 50 years. Accordingly, in their study about the driving factors of tree line shifts Gehrig-Fasel et al. (2007) come to the conclusion that land use change is the clearly dominant factor for the establishment of new forest areas in the Swiss Alps. As the current mean elevation in the study area still lies about 220 m below the potential tree line, the upslope forest advance can be expected to proceed. Körner (1998) shows that the tree line upwards shift induced by climate warming reduces growth limitation. Climate change with further increasing temperatures is likely to become a more important factor, especially at higher elevations and when longer time spans are considered (Gehrig-Fasel et al., 2007).

On a finer scale, historic land cover and land use, strongly influence the forest regeneration pattern. Whereas islands of former meadows remain open, all scenarios correctly predict an almost full forest regeneration of the avalanche path at the same elevation. Iravani et al. (2007) observed a similar phenomenon for the Swiss National Park. Grassland islands stayed open for decades after abandonment, although they were surrounded by dense forests. The impact of land cover on forest regeneration can be explained with microsite characteristics of the ground vegetation that strongly influence seedling emergence and survival (Germino et al., 2002; Dullinger et al., 2004; Kupferschmid et al., 2006).

Furthermore, the slightly better fit of the reduced competition scenario compared to the baseline scenario indicates dynamic changes of land cover classes due to the succession of ground vegetation after land use change. In the field a high abundance of dwarf shrub patches in the pastures was observed in the summer 2007, which confirms an advanced successional state (Tasser and Tappeiner, 2002).

5.2.4. Unpredicted clustering

The actual forest regeneration in 2006 shows a clustering of trees above the current tree line, which is not predicted by the scenarios. This unpredicted pattern indicates that the model does not account for a driving force, which shapes the pattern of pioneering trees above the current tree line. Visual inspection of the 2006 image suggests that this pattern might be explained with topographic properties. Hörsch (2003) states that the spatial pattern of forest alliances can be explained to a great extent through topographic features, which substitute a range of abiotic factors like temperature, moisture, wind and disturbance factors. This finding is confirmed by Tasser et al. (2007), who found a significant correlation between forest regeneration and topography.

6. Conclusion

We identified the main properties of key forest regeneration processes at the alpine tree line operating under environmental change. The forest regeneration model developed in this study was validated and correctly predicts a significant upwards shift of the alpine tree line. The impact of three key factors for forest regeneration was tested by comparing the spatial characteristics of the actual tree line patterns to the modelled scenarios. Firstly fecundity proved to be a crucial factor for forest expansion into open land. Secondly land cover and land use history has a significant impact on the emergence of forest regeneration patterns. Thirdly it is shown that the dispersal kernel of Norway spruce has a long-distance component. However, the actual forest regeneration in 2006 shows a clustering of trees above the actual tree line, which is not predicted by any of the scenarios. Future research should be directed towards the explanation of the factors for this clustered tree distribution and the impact of landform properties on the spatio-temporal succession pattern of pioneering trees.

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