



Département d'Ecologie et Evolution

MODELLING TREE POPULATION DYNAMICS AT THE ALPINE AND BOREAL TREE-LINE ECOTONES IN RESPONSE TO CLIMATE AND LAND-USE CHANGE

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Summary

Ecotones are sensitive to change because they contain high numbers of species living at the margin of their environmental tolerance. This is equally true of tree-lines, which are determined by altitudinal or latitudinal temperature gradients. In the current context of climate change, they are expected to undergo modifications in position, tree biomass and possibly species composition. Altitudinal and latitudinal tree-lines differ mainly in the steepness of the underlying temperature gradient: distances are larger at latitudinal tree-lines, which could have an impact on the ability of tree species to migrate in response to climate change. Aside from temperature, tree-lines are also affected on a more local level by pressure from human activities. These are also changing as a consequence of modifications in our societies and may interact with the effects of climate change.

Forest dynamics models are often used for climate change simulations because of their mechanistic processes. The spatially-explicit model TreeMig was used as a base to develop a model specifically tuned for the northern European and Alpine tree-line ecotones. For the latter, a module for land-use change processes was also added. The temperature response parameters for the species in the model were first calibrated by means of tree-ring data from various species and sites at both tree-lines. This improved the growth response function in the model, but also led to the conclusion that regeneration is probably more important than growth for controlling tree-line position and species' distributions.

The second step was to implement the module for abandonment of agricultural land in the Alps, based on an existing spatial statistical model. The sensitivity of its most important variables was tested and the model's performance compared to other modelling approaches. The probability that agricultural land would be abandoned was strongly influenced by the distance from the nearest forest and the slope, both of which are proxies for cultivation costs. When applied to a case study area, the resulting model, named TreeMig-LAb, gave the most realistic results. These were consistent with observed consequences of land-abandonment such as the expansion of the existing forest and closing up of gaps.

This new model was then applied in two case study areas, one in the Swiss Alps and one in Finnish Lapland, under a variety of climate change scenarios. These were based on forecasts of temperature change over the next century by the IPCC and the HadCM3 climate model (ΔT : +1.3, +3.5 and +5.6 °C) and included a post-change stabilisation period of 300 years. The results showed radical disruptions at both tree-lines. With the most conservative climate change scenario, species' distributions simply shifted, but it took several centuries to reach a new equilibrium. With the more extreme scenarios, some species disappeared from our study areas (e.g. *Pinus cembra* in the Alps) or dwindled to very low numbers, as they ran out of land into which they could migrate. The most striking result was the lag in the response of most species, independently from the climate change scenario or tree-line type considered.

Finally, a statistical model of the effect of reindeer (*Rangifer tarandus*) browsing on the growth of *Pinus sylvestris* was developed, as a first step towards implementing human impacts at the boreal tree-line. The expected effect was an indirect one, as reindeer deplete the ground lichen cover, thought to protect the trees against adverse climate conditions. The model showed a small but significant effect of browsing, but as the link

with the underlying climate variables was unclear and the model was not spatial, it was not usable as such.

Developing the TreeMig-LAb model allowed to: a) establish a method for deriving species' parameters for the growth equation from tree-rings, b) highlight the importance of regeneration in determining tree-line position and species' distributions and c) improve the integration of social sciences into landscape modelling. Applying the model at the Alpine and northern European tree-lines under different climate change scenarios showed that with most forecasted levels of temperature increase, tree-lines would suffer major disruptions, with shifts in distributions and potential extinction of some tree-line species. However, these responses showed strong lags, so these effects would not become apparent before decades and could take centuries to stabilise.

Résumé

Les écotones sont sensibles au changement en raison du nombre élevé d'espèces qui y vivent à la limite de leur tolérance environnementale. Ceci s'applique également aux limites des arbres définies par les gradients de température altitudinaux et latitudinaux. Dans le contexte actuel de changement climatique, on s'attend à ce qu'elles subissent des modifications de leur position, de la biomasse des arbres et éventuellement des essences qui les composent. Les limites altitudinales et latitudinales diffèrent essentiellement au niveau de la pente des gradients de température qui les sous-tendent : les distances sont plus grandes pour les limites latitudinales, ce qui pourrait avoir un impact sur la capacité des espèces à migrer en réponse au changement climatique. En sus de la température, la limite des arbres est aussi influencée à un niveau plus local par les pressions dues aux activités humaines. Celles-ci sont aussi en mutation suite aux changements dans nos sociétés et peuvent interagir avec les effets du changement climatique.

Les modèles de dynamique forestière sont souvent utilisés pour simuler les effets du changement climatique, car ils sont basés sur la modélisation de processus. Le modèle spatialement explicite TreeMig a été utilisé comme base pour développer un modèle spécialement adapté pour la limite des arbres en Europe du Nord et dans les Alpes. Pour cette dernière, un module servant à simuler des changements d'utilisation du sol a également été ajouté. Tout d'abord, les paramètres de la courbe de réponse à la température pour les espèces incluses dans le modèle ont été calibrées au moyen de données dendrochronologiques pour diverses espèces et divers sites des deux écotones. Ceci a permis d'améliorer la courbe de croissance du modèle, mais a également permis de conclure que la régénération est probablement plus déterminante que la croissance en ce qui concerne la position de la limite des arbres et la distribution des espèces.

La seconde étape consistait à implémenter le module d'abandon du terrain agricole dans les Alpes, basé sur un modèle statistique spatial existant. La sensibilité des variables les plus importantes du modèle a été testée et la performance de ce dernier comparée à d'autres approches de modélisation. La probabilité qu'un terrain soit abandonné était fortement influencée par la distance à la forêt la plus proche et par la pente, qui sont tous deux des substituts pour les coûts liés à la mise en culture. Lors de l'application en situation réelle, le nouveau modèle, baptisé TreeMig-LAb, a donné les résultats les plus réalistes. Ceux-ci étaient comparables aux conséquences déjà observées de l'abandon de terrains agricoles, telles que l'expansion des forêts existantes et la fermeture des clairières.

Ce nouveau modèle a ensuite été mis en application dans deux zones d'étude, l'une dans les Alpes suisses et l'autre en Laponie finlandaise, avec divers scénarios de changement climatique. Ces derniers étaient basés sur les prévisions de changement de température pour le siècle prochain établies par l'IPCC et le modèle climatique HadCM3 (ΔT : +1.3, +3.5 et +5.6 °C) et comprenaient une période de stabilisation post-changement climatique de 300 ans. Les résultats ont montré des perturbations majeures dans les deux types de limites d'arbres. Avec le scénario de changement climatique le moins extrême, les distributions respectives des espèces ont subi un simple glissement, mais il a fallu plusieurs siècles pour qu'elles atteignent un nouvel équilibre. Avec les autres scénarios, certaines espèces ont disparu de la zone d'étude (p. ex. *Pinus cembra* dans les Alpes) ou ont vu leur population diminuer parce qu'il n'y avait plus assez de terrains

disponibles dans lesquels elles puissent migrer. Le résultat le plus frappant a été le temps de latence dans la réponse de la plupart des espèces, indépendamment du scénario de changement climatique utilisé ou du type de limite des arbres.

Finalement, un modèle statistique de l'effet de l'abrutissement par les rennes (*Rangifer tarandus*) sur la croissance de *Pinus sylvestris* a été développé, comme première étape en vue de l'implémentation des impacts humains sur la limite boréale des arbres. L'effet attendu était indirect, puisque les rennes réduisent la couverture de lichen sur le sol, dont on attend un effet protecteur contre les rigueurs climatiques. Le modèle a mis en évidence un effet modeste mais significatif, mais étant donné que le lien avec les variables climatiques sous-jacentes était peu clair et que le modèle n'était pas appliqué dans l'espace, il n'était pas utilisable tel quel.

Le développement du modèle TreeMig-Lab a permis : a) d'établir une méthode pour déduire les paramètres spécifiques de l'équation de croissance à partir de données dendrochronologiques, b) de mettre en évidence l'importance de la régénération dans la position de la limite des arbres et la distribution des espèces et c) d'améliorer l'intégration des sciences sociales dans les modèles de paysage. L'application du modèle aux limites alpines et nord-européennes des arbres sous différents scénarios de changement climatique a montré qu'avec la plupart des niveaux d'augmentation de température prévus, la limite des arbres subirait des perturbations majeures, avec des glissements d'aires de répartition et l'extinction potentielle de certaines espèces. Cependant, ces réponses ont montré des temps de latence importants, si bien que ces effets ne seraient pas visibles avant des décennies et pourraient mettre plusieurs siècles à se stabiliser.

1. Introduction

Ecotones and their value for environmental research

Ecotones are transition zones between adjacent ecosystem types, which follow environmental gradients (Risser, 1995). The two dominant factors controlling ecotone position are cold winter temperatures and water balance (Neilson, 1993). Because many species are already at the margin of their environmental tolerance, ecotones are particularly sensitive to climate change (Gosz and Sharpe, 1989; Risser, 1995), which makes them interesting for analyses of gradient changes. Additionally, there is a peak in species turnover - successive accumulation of marginal species - in ecotones (Oommen and Shanker, 2005). This is particularly true of transition zones along altitudinal gradients and to a lesser extent along latitudinal gradients, though the situation in the latter is more complex (McCain, 2005). This high species turnover renders ecotones suitable for early detection of change.

Changes in transition zones are often characterised by changes in either the dominant species or life-form (Gosz and Sharpe, 1989; Peters, 2002). The former corresponds to demographic change, while the latter is associated with ecosystem functional change (Neilson, 1993). Both types of change are likely to influence ecosystem processes and develop feed-back mechanisms (Gosz and Sharpe, 1989).

Tree-line ecotones

Tree-line ecotones mark the transition between ecosystems dominated by two different life-forms: herbs and trees. Because this transition is in most cases gradual, with increasing stand fragmentation and stunted growth of trees, the forest limit has been referred to as tree-line, timber-line or forest-line (Körner and Paulsen, 2004), with definitions varying between authors. Most of the literature on the subject refers to either the tree-line (isolated trees at least 3 m high) or the forest-line (both as defined by Körner and Paulsen, 2004). The forest model used in this study includes low tree densities and stunted growth forms, so the “tree-line” referred to in relation to the simulations corresponds to the same authors’ tree species line.

The positions of both altitudinal and latitudinal tree-lines are primarily defined by temperature (Körner, 1998; MacDonald *et al.*, 1998; Jobbágy and Jackson, 2000; Körner and Paulsen, 2004). Traditionally, the temperature limit associated with tree-lines was the 10 °C July or summer isotherm (e.g. Lacoste and Salanon, 1969). However, this assumption has recently been challenged, at least where altitudinal tree-lines are concerned, and a new limit of 6-7 °C during the growing season has been suggested (Körner, 1998; Körner and Paulsen, 2004). As the day-length limit to the growing season differs between these two types of tree-lines, it is possible that trees may require higher temperatures to complete their growth cycle during the shorter, but more intense, boreal growing season. Continentality may also have an effect, as different mean July temperatures may correspond to similar night-time temperatures or yearly degree-day sums if the daily or seasonal temperature amplitudes differ. Despite varying opinions concerning the exact isotherm defining tree-lines, it is generally agreed that temperature is at least an important factor, if not the only one. On the other hand, the causes underlying this temperature effect remain unclear, even after decades of research on the subject (Grace *et al.*, 2002). There is a strong link between temperature and tree growth, which has made dendrochronology one of the leading methods for past climate reconstructions (Martinelli, 2004). One explanation is therefore that tree-lines

are a consequence of growth limitation by temperature (e.g. Grace and Norton, 1990), which slows down and eventually stops meristematic activity; this is known as carbon sink limitation (Körner, 1998; Paulsen *et al.*, 2000). The opposing theory is that of carbon source limitation, as the partial pressure of CO₂ in the atmosphere decreases with altitude. A recent study aimed at settling that debate gave an ambiguous answer, as the two species involved reacted differently to CO₂ enrichment (Handa *et al.*, 2005). Another well-supported hypothesis is that temperature limits seedling establishment, as trees seem more sensitive to cold during the first years of their life, so tree-lines could be due to an absence of regeneration (Kullman and Engelmark, 1997; Moiseev *et al.*, 2004; Gamache and Payette, 2005; Kullman, 2005). Other temperature-related factors such as frost damage, winter desiccation, snow mould or mechanical damage from snow may contribute to tree-line formation but are rarely considered critical (Körner, 1998).

Aside from temperature, a number of other factors may also play a role in shaping tree-lines, though their effects are often limited to a specific region. Esper and Schweingruber (2004) mention the presence of wind ecotones. Agro-pastoral activities in the Alps are also acknowledged to have produced a lowering of the tree-line by 100-300 m (Ellenberg, 1986; Tinner and Theurillat, 2003).

A sensitive, temperature-dependent ecotone such as the tree-line is expected to react strongly to the forecasted global warming (Holtmeier and Broll, 2005; Tinner and Kaltenrieder, 2005), either through altitudinal/latitudinal shifts or through densification of the existing forest (MacDonald *et al.*, 1998; Camarero and Gutiérrez, 2004). Because it marks the transition between two different life-forms, modifications of the tree-line would be accompanied by changes in ecosystem functions like carbon cycles. Warming and forest expansion could increase atmospheric carbon uptake, thus mitigating the effect of CO₂ emissions on climate. However, the carbon sink potential of forests and other ecosystems is still fairly uncertain, as estimates vary depending on the method used (Houghton, 2003). Some positive feed-backs which could accelerate the warming process have also been pointed out. Forests have a lower albedo (reflectivity) than grasslands, which leads to a warming effect on climate, particularly in areas with long snow-cover durations (Betts, 2000; Callaghan *et al.*, 2004). A study at the boreal tree-line also suggested that a change from tundra to birch forest could initially result in carbon from soil organic matter being suddenly released into the atmosphere due to changes in soil chemistry and decomposer activity (Sjögersten and Wookey, 2002). Forests are also major components of the water cycle (Beniston, 2003). Changes at the tree-line could result in increased water uptake, to compensate loss through evapotranspiration in a warmer climate or because of an increase in total forest area and tree density. On the other hand, if temperature increase gives rise to water stress, tree-lines could recede and the forest be replaced by steppe-like grassland (Gray, 2005).

Finally, from the point of view of biodiversity, tree-lines are important because of their richness in species and landscape elements. An abrupt change in climate could cause a loss of biodiversity (Tinner and Kaltenrieder, 2005), either because species are incapable of responding through migration or because of homogenisation of the landscape through forest densification, a phenomenon also associated with land-use change (Schöne and Schweingruber, 2001; Graf Pannatier, 2005).

There is therefore much interest in the rate at which the tree-line may advance in response to global warming (Grace *et al.*, 2002). This advance will not happen as a closed front, but will follow the initial colonisation of the most favourable sites through feed-back mechanisms (Alftine and Malanson, 2004; Holtmeier and Broll, 2005). These

processes are complex and tree-line ecotones are not linear indicators of climate change, as the response may be a succession of lagged and rapid changes (MacDonald *et al.*, 1998; Alftine and Malanson, 2004; Camarero and Gutiérrez, 2004).

Altitudinal tree-line: (Swiss) Alps

The altitudinal tree-line ecotone is relatively abrupt, because the temperature gradient is steep, decreasing by approximately 0.6 °C per 100 m vertical distance (e.g. Lacoste and Salanon, 1969; Theurillat and Guisan, 2001). However, despite the relatively short distances involved, species may not be able to migrate fast enough in the event of rapid climate change (Theurillat and Guisan, 2001; Tinner and Kaltenrieder, 2005). Other factors which may hinder migration or render it impossible are the increasing proportions of steep slopes - unsuitable for tree establishment - at higher altitudes or the absence of higher land into which to migrate on smaller mountains. In the Alps, and other regions with similar land-use history such as the Pyrenees, the pressure of human activities, such as grazing of livestock, in the areas above the current tree-line, is also likely to be an obstacle to upwards migration.

The case study area selected for simulations at the altitudinal tree-line is situated in the Upper Engadine region of Switzerland. From a vegetation point of view, it stretches from the montane to the nival zone. The bottom of the valley, which runs south-west to north-east, is divided between built-up areas (e.g. St Moritz), several small lakes and agricultural land. The lower mountain-sides are partly covered in forests, which gradually give way to other types of vegetation, such as mountain pastures, alpine meadows, etc. The mountain-tops are the bare rocks, snow-fields and glaciers of the nival zone. The main tree species at the tree-line are Swiss stone pine (*Pinus cembra* L.), European larch (*Larix decidua* Miller), with Norway spruce (*Picea abies* (L.) Karsten) usually found at slightly lower altitudes.

Latitudinal tree-line: Fennoscandia

The latitudinal tree-line ecotone stretches over a far greater distance than the altitudinal one, as the gradient shows a decrease of approximately 0.6 °C per 100 km. Species in boreal ecosystems will therefore require very high migration rates to keep up with the projected rate of climate change (Gray, 2005). Species migrating polewards in response to global warming will also have to adapt to the changes in light availability associated with higher latitudes. Although the number of days with 24 hours of light increases, this is also true of the number of light-less days, which limits the growing season. Furthermore, sun angles are lower, which limits the amount of energy received. Although population densities are by no means as high as in the Alps, human activities nevertheless influence forests at or near the tree-line. The main influence of humans is summer grazing by semi-domesticated reindeer (*Rangifer tarandus*), which is an important mortality factor for Downy birch (*Betula pubescens* Ehrhart) saplings (Suominen and Olofsson, 2000; Cairns and Moen, 2004). However, this negative impact of reindeer on tree-line migration may be mitigated by positive effects, such as a reduction in the vegetation cover, through trampling or winter feeding on ground lichen (*Cladina* spp.), which favours biodiversity and the establishment of tree seedlings (Suominen and Olofsson, 2000; Cairns and Moen, 2004). It is also debatable whether browsing by reindeer should be considered a disturbance, as they are a natural part of the ecosystem, though high reindeer population densities are an effect of reindeer husbandry (Suominen and Olofsson, 2000). Finally, other human activities which may

affect boreal forests in Fennoscandia, possibly at on a more local scale, include forestry and mining.

The case study area for simulations was situated in the Lake Inari region of Finnish Lapland, close to the Russian border. A large part of that area is covered in forests. The southern end is relatively low-lying, with some lakes and peat-bogs. The central part is hilly, with altitudes up to 700 m, and grasslands occupy the hill-tops. Finally, the northern end goes down to altitudes around 100 m by the shores of Lake Inari, which lies to the north-west of the study area. The main built-up area is the village of Ivalo. Aside from Downy birch, which has already been mentioned, the main tree-line species are Scots pine (*Pinus sylvestris* L.) and Norway spruce. The latter is usually found in moister areas and its distribution does not extend as far north as those of the other two species.

Climate and global change

The issue of climate change is subject to much debate, a striking example of which is the controversy over the climate reconstruction by Mann *et al.* (1999), the so-called “hockey stick”. This showed a dramatic rise in temperature since the beginning of the 20th century, far greater than any of the fluctuations which occurred during the previous 900 years, such as the Medieval Warm Period (800-1400 AD) or the Little Ice Age (1600-1850 AD). The magnitude of the recent warming trend was attributed to anthropogenic climate forcing, because climate models run using natural forcing (volcanic and solar) alone did not reproduce the “hockey stick” pattern. The main source of anthropogenic forcing is the emission of green-house gases, such as CO₂, which have increased radically since the Industrial Revolution of the 19th century (IPCC, 2001). Over the last few years, this climate reconstruction has been challenged (e.g. McIntyre and McKittrick, 2005). Most climate reconstructions agree on a warming trend in the 20th century (e.g. Esper *et al.*, 2002; D'Arrigo *et al.*, 2006; Osborn and Briffa, 2006), but differ as to its relative importance compared to the Medieval Warm Period. If past climate variability is greater than previously thought, then the respective weights of natural versus anthropogenic forcing as causes for the recent warming trend may have to be reconsidered (Esper *et al.*, 2005). However, although its underlying causes and magnitude are debated, the global warming trend of the last 100 years is generally acknowledged.

These climate reconstructions are important to understand the changes we are experiencing (Esper *et al.*, 2005), so that we can attempt to forecast future climate trends. The IPCC (2001) projections of climate change for the coming century are perhaps the most commonly-used forecasts. They give a range of values based on various scenarios for future green-house gas emissions (IPCC, 2000), which has made them a target for adversaries of Mann *et al.*'s (1999) climate reconstruction, who argue that they are unreliable, given that the recent warming trend is not as important as previously thought (Khandekar *et al.*, 2005). However, a recent study (Scheffer *et al.*, 2006) looking at feed-back between warming and CO₂ concentrations concludes that on the contrary, the IPCC predictions may be too optimistic by 15-78 % on the scale of a century.

Aside from a general increase in temperature, other climate factors which can be expected to change in the coming decades are precipitation and climate variability. Both of these could affect tree-line ecotones. For instance, Camarero and Gutiérrez (2004) predict that an increase in temperature variability would prevent the altitudinal tree-line in the Pyrenees from rising in response to global warming.

Finally, global change is not restricted to climate or even the underlying anthropogenic forcing. Changes in human societies affect the environment directly and none so visibly as land-use change. This can have an impact on biodiversity (e.g. Reidsma *et al.*, 2006) and other ecosystem services (Schröter *et al.*, 2005; Metzger *et al.*, 2006), for example water supply. At the altitudinal tree-line in the Alps, the main change in land use is agricultural land-abandonment, often due to rural depopulation, which started with the Industrial Revolution but has increased since the end of World War II (Baldock, 1996; MacDonald *et al.*, 2000; DLG, 2005). The consequences of this, namely the gradual closing up of former pastures and homogenisation of the tree-line ecotone, has been observed to result in loss of biodiversity (Schöne and Schweingruber, 2001; Graf Pannatier, 2005). Changes in human activities at the boreal tree-line in Fennoscandia have resulted in quite the opposite trend, as modern reindeer herding practices have increased the grazing pressure by increasing population densities (Väre *et al.*, 1996; Suominen and Olofsson, 2000). These anthropogenic changes may interact with climate change, either positively or negatively, as for instance reforestation, which results in a greater carbon uptake.

Forest gap models and their descendants: from JABOWA to TreeMig

Forest succession models, such as gap models, are a useful tool for studying the responses of forest composition and biomass in a changing climate (Loehle and LeBlanc, 1996; Sykes *et al.*, 1996), whether for reconstructing past forest dynamics (e.g. Heiri *et al.*, 2006) or projecting the effects of future climate change (e.g. Prentice *et al.*, 1993). The main reason why these models are considered adequate for climate change simulations is that they are mechanistic, i.e. they simulate responses based on processes, rather than correlations with climate data. However, several limitations of these models have been pointed out. These include the way in which the growth equations are derived (Loehle and LeBlanc, 1996; Sykes *et al.*, 1996), the difficulties in applying these models over large areas, partly because seed-dispersal is not explicitly included (Loehle and LeBlanc, 1996; Perry and Enright, 2006) and the absence of socio-economic factors such as land-use change when the models are applied on the landscape level (Perry and Enright, 2006). Some of these limitations have been addressed recently, while others remain open to improvement.

The first forest gap model was JABOWA (Botkin *et al.*, 1972), which was based upon the following assumptions: (1) the forest stand is abstracted as a composite of many small patches of land, each of which can have a different age and succession stage; (2) patches are horizontally homogeneous, i.e. tree position within a patch is not considered; (3) the leaves of each tree are located in an indefinitely thin layer (disc) at the top of the stem; and (4) succession processes are described on each patch separately, i.e. there are no interactions between patches (Bugmann, 2001). All later models can be traced back to JABOWA and most are still based on one or more of these assumptions.

The four basic assumptions of JABOWA have been challenged and scrutinised, resulting in alternative formulations in specific gap models. For instance, representing the leaves as a disc at the top of the stem is especially critical at higher latitudes, where sun angles are low (Bugmann, 2001). The FORSKA model (Prentice and Leemans, 1990; Prentice *et al.*, 1993), designed for boreal forests, therefore represents the crown as a cylinder rather than a disc.

Although most gap models have been developed for forests, they have also been applied to grasslands (STEPPE, Coffin and Lauenroth, 1990) and shrublands (Higgins *et al.*,

1996) ecosystems. The ECOTONE model (Peters, 2002) was developed to study the grassland-shrubland transition zone.

The DisCForM model (Lischke *et al.*, 1998) was derived by aggregation from its parent model, ForClim (Bugmann, 1994, 1996). The main innovations in DisCForM are: (1) the continuous height distribution of the trees is replaced by a discrete height structure; and (2) the entire forest is simulated at once in each time step. All trees of a certain height are assumed to be randomly distributed over the forest, which results in a Poisson distribution (Lischke *et al.*, 1998). Simulating the entire forest in one run shortens computing time considerably. Additionally, the model is formulated as a system of coupled ordinary differential equations rather than Monte-Carlo algorithms, which allows the numerical application of mathematical methods such as stability analysis (Lischke *et al.*, 1998).

TreeMig (Lischke, 2005; Lischke *et al.*, 2006), which is used as a basis for the model development in this thesis, is a spatially-explicit version of DisCForM, aimed at simulating tree migration. For this purpose, it explicitly simulates seed production, seed dispersal, seed bank dynamics and the recruitment and development of seedlings and saplings (Lischke, 2005; Lischke *et al.*, 2006). The inflow I of seeds into a model grid cell is the sum over all species i of the number of seeds S produced in all the other cells multiplied by the dispersal kernel k for that species (Eq. 1.1). The dispersal kernel is a probability density function, dependent on the distance z and combining two negative exponentials, one for short-distance and the other for long-distance transport.

$$I = \sum (S_i \cdot k_i(z)) \quad (1.1)$$

These inflowing seeds are added to the seed bank S_b , which also depends on the seed bank at the previous time step and the local seed bank dynamics L_{sb} (Eq. 1.2)

$$S_{b,t+1} = S_{b,t} + L_{sb} + I_t \quad (1.2)$$

The local seed bank dynamics consists of seed loss D through predation and loss of germinability and of seed germination B (Eq. 1.3). Germination depends on the seed bank and the shading resulting from the number of trees N in all height classes j above 0 (i.e. adult trees). The newly-germinated seedlings enter the local tree dynamics in height class 0 (seedlings and saplings).

$$L_{sb} = -D - B(S_b, N_{j>0}) \quad (1.3)$$

The local tree dynamics uses the functions found in DisCForM and ForClim. The parameters for the various functions such as growth, mortality, response to environmental conditions, etc. were mostly derived from the literature, as described by Bugmann (1994). They include 30 tree species found in the forests of Central Europe.

State of the art and general research goals

While the scientific community mostly agrees on the existence of climate change, its intensity and the effects it might have on ecosystems is the subject of much speculation. Estimates of the severity of climate change have been produced using climate models (e.g. HadCM3 - Gordon *et al.*, 2000; Pope *et al.*, 2000) and are constantly being updated in the light of new findings (e.g. Khandekar *et al.*, 2005; Scheffer *et al.*, 2006). The impact of climate change on ecosystems can be simulated using different types of models, such as dynamic global vegetation models (DGVMs, e.g. Cramer *et al.*, 2001), niche-based models (NBMs, e.g. Thomas *et al.*, 2004; Thuiller *et al.*, 2006), gap models (e.g. Peters, 2002) or landscape models (e.g. Schumacher and Bugmann, 2006).

These vegetation models vary with respect to their spatial, temporal and taxonomic resolutions. Some are mechanistic (i.e. they simulate processes), others are statistical. Their capacity to take into account various factors influencing plant distribution, such as human impact, also varies. NBMs are commonly used for climate change modelling, but they are purely statistical and only simulate one point in time, so they cannot take into account processes such as seed dispersal and species migration, which may be crucial for sessile species in a changing climate. The latter is usually assumed to be either unlimited or impossible (Thomas *et al.*, 2004; Thuiller *et al.*, 2006), though it may be constrained to an estimated migration zone around the current distribution. However, NBMs can include various types of input data, so human factors such as land use change, based on socio-economic scenarios, can easily be included alongside climate variables. These models therefore predict changes in habitat suitability, rather than species' distributions. DGVMs include vegetation dynamics, but have a coarse spatial resolution and therefore only include vegetation types, not plant species. Results from these models need to be complemented by simulations of vegetation dynamics on smaller scales, where factors such as human pressure or regional precipitation patterns can be included (Cramer *et al.*, 2001).

Landscape models and spatially-explicit dynamic (gap-type) models are both used to simulate vegetation dynamics at the landscape level, but they differ by their scales and levels of aggregation. Landscape models work on a large scale and are typically rather aggregated (Perry and Enright, 2006). Gap models simulate plant species, although plant functional types could also be used. Because they are mechanistic and have a fine resolution, it is possible to study rates of change at both the leading (colonisation) and trailing (disappearance) edges of species' distributions during migration. These have not received much attention so far, as models often assume that species disappear immediately when climate becomes unfavourable, thus removing the competition effect on the colonisation by new species. Another ongoing debate, in which hypotheses might be tested using spatially-explicit gap models, is the question of whether tree species' distributions are governed by limitations to growth (Hättenschwiler and Körner, 1995; Körner and Paulsen, 2004) or to recruitment (Woodward, 1988; Kullman and Engelmark, 1997; Moiseev *et al.*, 2004; Kullman, 2005).

Although gap-type models are well suited to answering questions about climate change at the regional level, they sometimes suffer from having been built on previous models without re-evaluation of the theory behind the equations or the way in which the parameters were derived. Some equations can be traced back to the original JABOWA model (Botkin *et al.*, 1972) and have not been updated to follow advances in physiology or match other improvements made to gap models since. Parameters have often been derived from distribution maps of species or literature sources (e.g. Botkin *et al.*, 1972; Kienast, 1987; Bugmann, 1994). This brings back some of the same problems encountered with niche-based models, such as the inability to simulate growth outside species' current realised niches. Additionally, gap-type models generally do not include the impact of human factors on tree growth and distribution.

General research goals

- Improve the spatially-explicit forest dynamics model TreeMig by fine-tuning some of its growth equations and parameters. This includes basing the equations on more recent theoretical knowledge and using tree growth measurements to try and capture growth processes.

- Investigate the potential of growth versus establishment as the main factor underlying species' distributions.
- Expand the TreeMig model so that it includes human influence. As socio-economic models are themselves very complex, this will involve some degree of simplification so that it can fit in the forest model.
- Finally, investigate by means of the new model the impact of different climate change scenarios on the position of tree-lines and the species composition of forests near the tree-line. Rates of change and possible lags in the responses of some or all of the species will be of particular interest, rather than just the composition resulting from equilibrium with the new climate.

Thesis structure, aims and research questions

This work was split into four chapters (n° 2-5), three main ones which are (or will be) the subject of full-length scientific publications and one smaller study which will be submitted as a short communication.

2. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data

Rickebusch, S., Lischke, H., Bugmann, H., Guisan, A. and Zimmermann, N.E., submitted to Forest Ecology and Management on 9 May 2006.

The aim was to understand the limitations to tree growth and species distribution in cold environments, by analysing tree-ring width data, in order to test and improve the theoretical basis upon which the growth equations in the TreeMig model lie. This was designed to overcome some of the draw-backs mentioned by Loehle and LeBlanc (1996) about forest dynamics models as a tool for climate change simulations, such as drought stress being taken into account twice. The ultimate goal was to calibrate the model for Alpine and Fennoscandian tree-line species, as a basis for the work in the following chapters.

- What are the effects of cold temperatures on the growth of different tree species and are they correctly calibrated in the model? Are there any other effects of temperature which may affect tree-line forests?
- Is tree-ring data a useful tool for deriving these parameters and can they be used to adapt the model for species in a different ecosystem?

3. Combining probabilistic land-use change and forest dynamics modelling to simulate global change responses at the Alpine tree-line

Rickebusch, S., Gellrich, M., Lischke, H., Guisan, A. and Zimmermann, N.E., submitted to Ecological modelling on 2 June 2006.

We aimed to implement a statistical model for agricultural land-abandonment (Gellrich *et al.*, 2007; Gellrich and Zimmermann, 2007) into the newly-calibrated version of TreeMig, to produce a new model (TreeMig-LAb) and to test the combined model on theoretical landscapes and our Alpine case study area. Including land-use management into the forest model was an aim of the PINE project and abandonment of agricultural land is an important socio-economic issue in the Alps, one which has a direct impact on the tree-line.

- How can a statistical model including socio-economic and environmental variables be integrated in a forest dynamics model, including feed-back effects between the two?
- How does this combined approach compare to simpler ways of simulating land-abandonment?

4. **Climate change effects and interactions with human land use at the Alpine and northern European tree-lines**

Rickebusch, S., Zimmermann, N.E., Lischke, H. and Guisan, A., in preparation.

This chapter aimed to investigate the impacts of a) combined climate and land-use change on the altitudinal tree-line and b) climate change on the latitudinal tree-lines, using different scenarios spanning the range of the IPCC (2001) forecasts.

- Are tree species able to migrate in response to climate change and are there lags in this response?
- Does it depend on the type of tree-line and/or the rate of change?

5. **Effect of reindeer browsing on Scots pine growth in Northern Finland**

Article in preparation. Diploma project for the post-graduate diploma in applied statistics at the ETH, Zürich.

This small study aimed to develop a statistical model of the effect of the browsing of ground lichen by reindeer on tree growth at the boreal tree-line, with a view to including human management effects in the forest dynamics model for that ecotone.

- Is there an effect of reindeer browsing (depletion of the lichen cover) on Scots pine growth?
- Is that effect linked to any climatic variables, which might affect the trees in the absence of the protective lichen cover?

A fifth publication, to which the work for this thesis also contributed, was added as an appendix.

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

Lischke, H., Zimmermann, N.E., Bolliger, J., Rickebusch, S. and Löffler, T. J., 2006. Ecological Modelling, 199: 409-420.

This paper is the main reference for the TreeMig model. Aside from some input in the text, my contribution consisted mainly in drawing figures for the user's guide, available as an online appendix to the article. Parts of this online appendix are also included here, in particular the description of the species parameters.

Project frame: PINE

This thesis was part of the European Union 5th Framework project "Predicting Impacts on Natural Ecotones" (PINE - contract number EVK2-CT-2002-00136). This interdisciplinary project aimed to investigate the impact of land-use management decisions on European tree-line ecotones under different climate change scenarios, using a novel multi-proxy approach. One key expected output was a predictive model enabling stake-holders to view the possible consequences of these impacts, in order to help decision-making processes. The project was built around four main disciplines:

- a) Socio-economic analysis and development of potential land-use management scenarios.
- b) Dendroecology, including analysis of ring-width and wood density, height increment and needle production, cambium dynamics and stable carbon isotopes.
- c) Pollen analysis and reconstruction of Holocene migration.
- d) Modelling.

All of these analyses were conducted at various sites across Finnish and Swedish Lapland for the latitudinal tree-line and in the Alps (Austria, Italy, Slovenia, Switzerland) for the altitudinal tree-line.

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2. Understanding the low-temperature limitations to forest growth through calibration of a forest dynamics model with tree-ring data

Submitted to Forest Ecology and Management

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Abstract

The sensitivity of altitudinal and latitudinal tree-line ecotones to climate change, particularly that of temperature, has received much attention. To model the possible effects of climate change and improve our understanding of the factors affecting tree-line position and movements, we used the spatially-explicit dynamic forest model TreeMig. Although well-suited because of its landscape dynamics functions, TreeMig features a parabolic temperature growth response curve, which has recently been questioned, and the species parameters are not specifically calibrated for cold temperatures.

Our main goals were to improve the theoretical basis of the temperature growth response curve in the model and to develop a method for deriving that curve's parameters from tree-ring data. We replaced the parabola with an asymptotic curve, calibrating this for the main species at the subalpine (Swiss Alps: *Pinus cembra*, *Larix decidua*, *Picea abies*) and boreal (Fennoscandia: *Pinus sylvestris*, *Betula pubescens*, *Picea abies*) tree-lines.

After adjustment of its parameters, the new growth curve fitted the field measurements (tree-ring widths) better. For the subalpine species, the minimum degree-day sum was lowered by around 100 degree-days; in the case of *Larix*, the maximum ring-width was increased to 5.19 mm. At the boreal tree-line, the minimum degree-day sum for *Pinus sylvestris* was lowered by 210 degree-days and its maximum ring-width increased to 2.943 mm; for *Betula* (new in the model) the minimum heat sum was set to 325 degree-days and the maximum ring-width to 2.51 mm; the values from the only boreal sample site for *Picea* were similar to the subalpine ones, so the same parameters were used. However, adjusting the growth response alone did not improve the model's output concerning species' distributions and their relative importance at tree-line. Minimum winter temperature, which controls seedling establishment in the model, proved more important for determining distribution. *Picea*, *P. sylvestris* and *Betula* did not have minimum winter temperature limits, so these values were set to -7, -11 and -13 respectively.

In a case study for the Alps, the original and newly-calibrated versions of TreeMig were compared with data from the National Forest Inventory (NFI). Both models gave similar, reasonably realistic results.

In conclusion, this method of deriving temperature responses from tree-rings works well. However, regeneration and its underlying factors are probably more important for controlling species' distributions than previously thought, whereas the growth response seems secondary. More research on regeneration ecology, especially at the upper limit of forests, is needed to improve predictions of tree-line responses to climate change further.

Keywords: TreeMig, degree-day sum, minimum winter temperature, tree-line, growth, establishment, regeneration

Introduction

When analysing the effects of climate change, transition zones, such as the subalpine or boreal tree-line ecotones (as defined by Körner and Paulsen, 2004), are of particular interest because their fine balance, with species living at the extreme limit of their tolerance, makes them more sensitive to change (Theurillat and Guisan, 2001; Kullman, 2005). Furthermore, climate-induced timber-line shifts can significantly influence the global carbon budget (Solomon and Kirilenko, 1997; Neilson *et al.*, 2005). Although other factors, such as wind, may also play a significant role (Esper and Schweingruber, 2004), temperature is believed to be the most important factor governing forest growth at tree-line (Körner, 1998; Jobbágy and Jackson, 2000; Körner and Paulsen, 2004). Therefore, in any model used to investigate the impact of climate change on these ecotones, the temperature growth response, especially around its lower extremity, should be based on sound theoretical knowledge, preferably supported by evidence from field studies.

Dynamic forest gap models are often used to study the effects of climate change on the species composition and structure of forests under a range of change scenarios. In the original JABOWA forest gap model (Botkin *et al.*, 1972) and many of its descendants, the temperature growth response curve (yearly diameter increment versus degree-day sum) has a parabolic shape. In some of these early models, the growth decline at higher temperatures (right-hand side of the parabola) can be interpreted as an indirect representation of drought, which is not modelled separately. However, the parabolic degree-day growth response curve was retained in many subsequent models, despite the introduction of drought as a separate variable. Although the shape of the curve may have little effect on species' distributions under current climate, it can cause artificial die-back effects when the model is run under changing climate conditions (Bugmann, 2001). Several approaches have been used to replace the parabolic growth response curve by one which reflects the effect of temperature alone, such as an asymptotic function (e.g. Bugmann and Solomon, 2000; Lexer and Hönninger, 2001).

Apart from the shape of the curve, the other prerequisite for a realistic model is the set of parameters defining the curve's boundaries (minimum, asymptote) for each species. The difficulty lies in finding the parameters for potential, rather than realised growth: model curves express the former, but it is rarely observed in the field and experiments under controlled conditions are difficult with large, long-lived species such as trees. Loehle and LeBlanc (1996) suggest using dendroclimatic analysis to improve the climate response functions in forest simulation models. Although tree-rings are an expression of realised, rather than potential growth, if one factor (in this case temperature) primarily influences the response, potential growth can be estimated provided enough data is available.

Another aspect of forest response to temperature is the establishment and survival of seedlings. There have been studies of the effects of temperature on regeneration at tree-line, for instance in the mountains of North America (Lloyd and Graumlich, 1997; Germino *et al.*, 2002), the Southern Urals (Moiseev *et al.*, 2004) or Scandinavia (Kullman, 1986, 2005), but only a few in the Alps (Motta and Nola, 2001). The values for the minimum winter temperature allowing recruitment in a species vary greatly amongst authors (e.g. Kienast, 1987; Prentice and Helmisaari, 1991; Bugmann, 1994). The minimum winter temperature is the limit below which actual damage is caused to the trees and it can be represented by the coldest month's mean temperature, as a surrogate for the absolute minimum temperature (Sykes *et al.*, 1996). On the other hand, some species have winter chilling requirements. These are mostly related to the length of the chilling season, although the maximum temperature of the coldest month has also been used as a measure of winter chilling. A longer chilling season is thought to protect species with a low tolerance to late frost by delaying bud-burst; in deciduous species, chilling may also be necessary to trigger abscission (Sykes *et al.*, 1996).

The spatially-explicit dynamic forest model TreeMig (Lischke, 2005; Lischke *et al.*, 2006) is well adapted to simulating the effects of climate change, as it includes processes for landscape dynamics (e.g. seed production and dispersal) as well as the usual climate-dependent forest population processes (e.g. growth, competition). It is also designed to be flexible and its parameters can be adapted for different applications. TreeMig is derived from the distribution based model DisCForM (Lischke *et al.*, 1998), itself scaled-up from an early version of the gap model ForClim (Bugmann, 1994, 1996), and uses the traditional parabolic growth response curve with ForClim's parameter set. The impact of low temperatures on forests is also included as a minimum winter temperature limit on regeneration in the model, but TreeMig, like most of its gap model predecessors, does not address the issue of winter chilling requirements (Price *et al.*, 2001).

In their review of the suitability of forest models for assessing the effects of climate change, Loehle and LeBlanc (1996) concluded that dynamic forest models were the best solution, provided some improvements were made. These included realistic reproduction and dispersal functions, based on the trees present in the model, and competition for light, all of which have been addressed in the TreeMig model (Lischke and Löffler, 2006). The other aspects requiring improvement were the growth-response functions, in particular the replacement of the temperature-response parabola by a curve representing the fundamental niche of each species, and mortality functions, including disturbance regimes.

The growth parameters in ForClim, also used in TreeMig, were originally derived for Central European forests in general (Bugmann, 1994), but not specifically adapted to studying the sensitive tree-line ecotone under climate change. The aim of the present study was to improve our understanding of tree growth and distribution in response to temperature, therefore providing a better basis for the formulation and parameterization of the TreeMig model. In particular, we wanted to (1) take into account criticisms of the shape of the temperature-related growth function (Loehle and LeBlanc, 1996; Bugmann and Solomon, 2000), (2) capture the physiological limitations to growth for the main tree-line species through the use of tree-ring data (Loehle and LeBlanc, 1996), (3) calibrate TreeMig for Alpine and Fennoscandian tree-line species, and (4) evaluate the new model in a case study in the Alps.

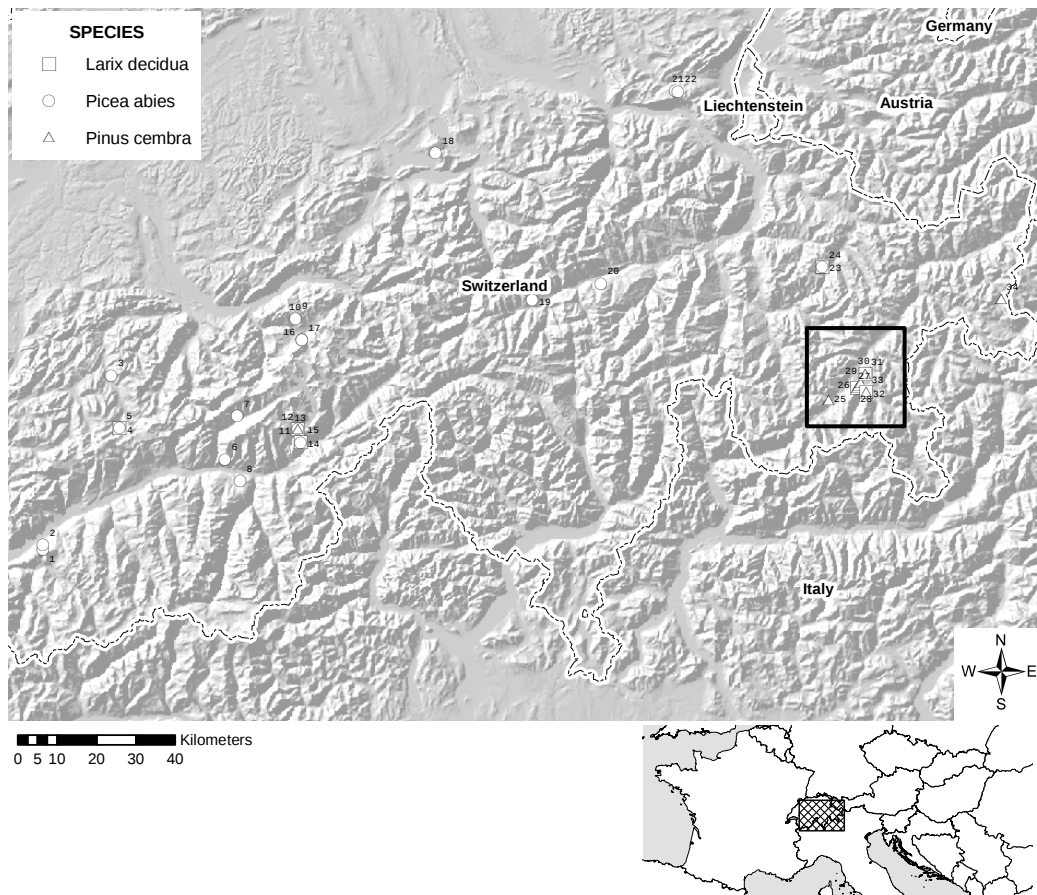


Figure 2.1. Location of the tree ring-width data sites in the Alps. The symbols indicate the species sampled at each site. The numbers refer to those in Table 2.1, which contains information on the sites and datasets used. The black square shows the extent of the case study area in the Upper Engadine (Switzerland).

Material and methods

To calibrate the temperature response in TreeMig, we used dendrochronological (ring-width) data for the three main subalpine tree-line species at locations throughout the Swiss Alps, collected from various literature sources (Fig. 2.1, Table 2.1). Preference was given to sites (or groups of neighbouring sites) for which data had been collected at different altitudes, although some isolated sites were included to increase the range of altitudes and climatic regions in the dataset. The species were: European larch (*Larix decidua*), Norway spruce (*Picea abies*) and Swiss stone pine (*Pinus cembra*).

Similarly, the temperature response curves of Scots pine (*Pinus sylvestris*), Downy birch (*Betula pubescens*) and Norway spruce (*Picea abies*) were calibrated using dendrochronological data from the boreal tree-line in Fennoscandia (Table 2.1). A separate calibration was necessary, as the species compositions of both tree-lines differ: *Larix decidua* and *Pinus cembra* do not occur in Fennoscandia, while *Pinus sylvestris* and *Betula pubescens* are present in the Alps but do not form the tree-line. Even when a species is present in both regions, like *Picea abies*, a separate calibration may be necessary if different ecotypes were involved.

Table 2.1. Dendrochronological data sites. For sites in Switzerland (1-34), locations can be found on the map (Fig. 2.1). Wherever trees were sampled along a transect, the altitude range is given. The species are: *Picea abies* (Pa), *Larix decidua* (Ld), *Pinus cembra* (Pc), *Pinus sylvestris* (Ps) and *Betula pubescens* (Bu).

Nb.	Name	Coordinates	Altitude	Species
1	Bisse de Saxon ^a	7.18 E, 46.12 N	1570	Pa
2	Creux du Dailley ^a	7.18 E, 46.13 N	1200	Pa
3	Gyrs ^a	7.40 E, 46.52 N	1900	Pa
4-5	Iffigenalp ^a	7.43 E, 46.40 N	1900	Ld, Pa
6	Tatz Stockwald ^a	7.78 E, 46.33 N	1850	Pa
7	Lötschental ^a	7.82 E, 46.43 N	1900	Pa
8	Bürchen Bielwald ^a	7.83 E, 46.28 N	1740	Pa
9	Grindelwald S2 ^b	8.01 E, 46.66 N	2060	Pa
10	Grindelwald S3 ^b	8.01 E, 46.65 N	1960	Pa
11-13	Riederalp Aletschwald ^a	8.02 E, 46.40 N	2000	Ld, Pa, Pc
14-15	Binna ^a	8.03 E, 46.37 N	1800	Ld, Pa
16	Grindelwald N3 ^b	8.03 E, 46.60 N	1700	Pa
17	Grindelwald N2 ^b	8.03 E, 46.60 N	1760	Pa
18	Rigi Klösterli ^a	8.48 E, 47.03 N	1400	Pa
19	Sedrun ^c	8.80 E, 46.69 N	1900	Pa
20	Obersaxen ^a	9.03 E, 46.73 N	1580	Pa
21	Churfürsten U2 ^d	9.29 E, 47.17 N	1580	Pa
22	Churfürsten U1 ^d	9.30 E, 47.17 N	1640	Pa
23-24	Davos ^e	9.77 E, 46.76 N	1970	Ld, Pa
25	Silvaplana ^f	9.78 E, 46.46 N	2140	Pc
26-27	Muottas da Schlarigna AM ^g	9.88 E, 46.48 N	2260-2390	Ld, Pc
28	Muottas da Schlarigna RN ^f	9.88 E, 46.49 N	2180	Pc
29	Celerina ^f	9.89 E, 46.49 N	1840	Pc
30-31	Tschainas ^g	9.91 E, 46.51 N	2250-2410	Ld, Pc
32-33	Muottas da Puntraschigna ^g	9.91 E, 46.47 N	2255-2385	Ld, Pc
34	Tamagur ^f	10.36 E, 46.68 N	2210	Pc
101	Abisko ⁿ	18.82 E, 68.35 N	365	Bu
102	Jebren ⁱ	18.88 E, 68.43 N	370	Bu
103	Nikkaluokta ^j	19.10 E, 67.90 N	475	Ps
104	Kiruna ^j	20.30 E, 67.85 N	470	Ps
105	Karesuando ^k	22.25 E, 68.47 N	350	Ps
106	Muonio ^l	23.37 E, 68.13 N	255	Ps
107	Pallastunturi ^a	24.10 E, 68.03 N	270	Pa
108	Kevo ⁱ	27.02 E, 69.75 N	80	Bu
109	Kevo F ^m	27.08 E, 69.67 N	110	Ps
110	Kaamanen ⁿ	27.25 E, 69.12 N	155	Ps
111	Laanila P1 ^o	27.27 E, 68.51 N	230	Ps
112	Laanila P2 ^o	27.47 E, 68.50 N	225	Ps
113	Laanila P3 ^o	27.48 E, 68.50 N	220	Ps
114	Laanila F ^m	27.50 E, 68.50 N	220	Ps

Data sources: (a) WSL Dendro Database, Switzerland. www.wsl.ch/dendro; (b) Meyer and Bräker (2001); (c) Bolli (2004); (d) Hitz (2003); (e) Heiri (2002); (f) Niederer (2003); (g) Mütterthies (2002); (h) Karlsson *et al.* (2004); (i) S. Karlsson, H. Grudd (unpublished); (j) H. Grudd. Stockholm University Dendro database; (k) M. Lindholm, J. Meriläinen. International Tree-Ring Data Bank, IGBP PAGES/World Data Center for Paleoclimatology, NOAA/NCDC Paleoclimatology Program, Boulder, Colorado, USA; (l) R. Jalkanen (unpublished); (m) McCarroll *et al.* (2003); (n) Jalkanen and Tuovinen (2001); (o) H. Grudd, M. Tuovinen (unpublished).

Climate data processing

The climate data for the different tree-ring collection sites was derived from mapping daily minimum and maximum temperatures (T_{min} , T_{max}) using the DAYMET simulation model (Thornton *et al.*, 1997). In this, all the stations in a defined neighbourhood contribute to predict the local temperature through a distance-weighted regression which follows a Gaussian curve. For Switzerland, the available maps cover a 38-year time-span (1961 to 1998) and have a 250 m resolution (grid of square cells). The annual degree-day sums for those years at each of the sites in Table 2.1 were calculated using the double sine-wave method described by Allen (1976), with a lower threshold of 5.5 °C and no upper threshold.

Mean monthly temperatures (T_{mm}) for each site were calculated from the daily minimum and maximum values (Eq. 2.1, with n the number of days in the month in question). The minimum winter temperature ($MinWiT$) for each year (y) was then calculated as the lowest of the mean monthly temperatures for the three winter months (Eq. 2.2).

$$T_{mm} = \Sigma[(T_{min} + T_{max}) / 2] / n \quad (2.1)$$

$$MinWiT_y = \min(T_{mm}_{Dec, y-1}, T_{mm}_{Jan, y}, T_{mm}_{Feb, y}) \quad (2.2)$$

The methods for calculating degree-day sum and minimum winter temperature follow those described by Bugmann (1994) for the ForClim model, which are also used in TreeMig. However, we applied the sine-wave method for degree-day sum directly to daily temperatures, rather than use monthly values and an empirical correction factor, by definition only applicable to the region for which it was derived, which might diminish the portability of the model.

Growth curves and parameter adjustment

First, we examined the calibration of the temperature constraints on tree growth, particularly near its cold-induced limit. To achieve this, for each site and species (Table 2.1), all the tree ring-width values falling within the time-span of the climate data were assigned their corresponding degree-day sum. The ring-widths were then sorted according to this sum and grouped into 25 degree-day “windows”. In each window, we calculated the mean of the 10 % largest ring-widths, i.e. those that were supposed to be constrained primarily by temperature. Figure 2.2 shows an example for *Picea abies* at site n° 9 (Grindelwald S2); the mean values (■) correspond to one data series on that species’ plot (Fig. 2.3b). This procedure was repeated for each of the sites and species in Table 2.1, to obtain the temperature-related potential growth of each site/species combination. The reason for using the 10 % largest ring-widths, rather than the single largest value, is that individual trees have inherently different growth potentials and the overall maximum ring-width only reflects the potential of the fittest tree. Additionally, it buffers the effect of local temperature peculiarities, which are not captured by the climate maps we used and could lead to over-optimistic results if the largest ring-widths alone were taken into consideration. A percentage of the largest values should therefore give a more realistic estimate of the average growth potential in a tree population.

The potential growth values at all the sites for one species were plotted together (Fig. 2.3). The original parabolic growth curve of TreeMig and the asymptotic curve (Eq. 2.3), proposed by Bugmann & Solomon (2000) and used in the model ForClim V2.9, were also plotted.

$$gDDGF_s = \max(1 - \exp((kDDMin_s - uDD) \cdot a), 0) \quad (2.3)$$

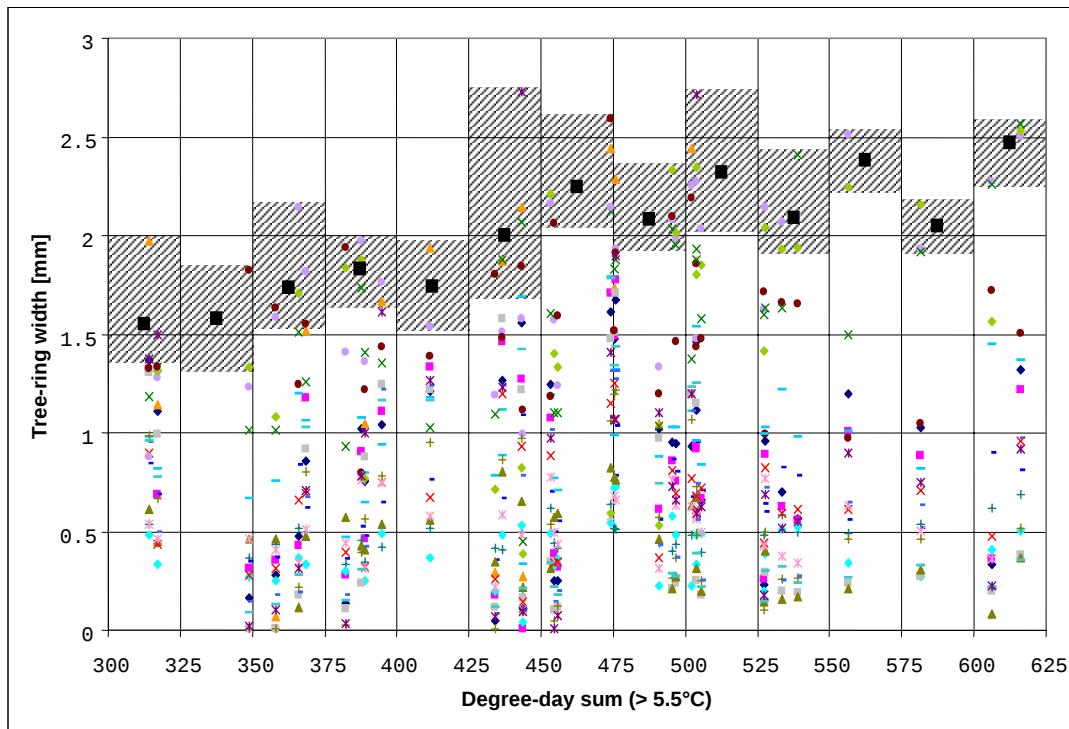


Figure 2.2. Tree growth (ring-width) versus degree-day sum (above a 5.5 °C threshold). The data for all the trees sampled (represented by different symbols) was grouped into 25 degree-day sum “windows”. Within each of these, the mean (■) of the 10 % largest ring-width values observed (shaded area) was calculated. These means represent potential tree growth, at that particular site and for each degree-day sum window, when individuals are constrained by temperature alone. The smaller ring-width values are probably the result of temperature combined with other factors, such as competition or tree age, and were therefore not included in the calculation. The example given here is *Picea abies* at site n° 9 (Grindelwald S2).

According to this equation, the growth response to degree-day sum ($gDDGF_s$) is a function of the minimum degree-day sum allowing growth for species s ($kDDMin_s$), the current degree-day sum (uDD) and a parameter describing the slope of the curve (a). This last was determined so that growth was equal to 75 % of its optimum when $uDD = kDDMin_s + 1000$ for any species (Bugmann and Solomon, 2000).

The asymptotic curve was then adjusted according to the rules described below in order to fit the dendrochronological data. The aim was to draw an envelope through the highest values (sites with the best conditions) in each window, so as to capture the temperature-related response. The first, general adjustment was to make the curve steeper by modifying the slope parameter a so that 75 % of the maximum growth was reached when the degree-day sum was 250 degree-days (instead of 1000) above the minimum for species s ($kDDMin_s$). Different values were tested visually and 250 degree-days gave good results for all the species in this study, but species-dependent values could be used for other species. The species parameters ($kDDMin_s$ and maximum ring-width) were then adjusted individually for each species. The minimum degree-day sum was set to the lower limit of the coldest 25 degree-day sum window (in other words, the lowest degree-day sum value in the data set was rounded down to the nearest 25 degree-days). The maximum ring-width was set to the highest mean of 10 % maximum ring-width value for that species, unless it was lower than the original model parameter, in which case the latter was retained. This was done on the assumption that if

the highest value in the field data is lower than the model parameter, the field data sample might simply have missed the highest potential value, whereas if the field data yields a higher maximum than the model, then the real potential is at least as high as the field data. Maximum ring-width is not directly a parameter in the model, but is determined by the species' growth factor (kG_s) via the model's growth equation (Eq. 2.4, Bugmann, 1994, 1996; Lischke *et al.*, 2006), so it was in fact this last factor which was adjusted.

$$\frac{\Delta D}{\Delta t} = \frac{kG_s \cdot D \cdot \left(1 - \frac{H}{Hm_s}\right)}{274 + (Hm_s - 137) \cdot \left(\frac{6D}{Dm_s} - \frac{4D^2}{Dm_s^2}\right)} \cdot f(e) \quad (2.4)$$

where D and H are the current diameter and height, respectively, Dm_s and Hm_s the maximum diameter and height for the species, $f(e)$ a modifying function of environmental factors such as temperature, light, etc.; the constant value of 137 represents "breast height" (in centimetres) and is also the minimum height for an "adult" tree in TreeMig.

Minimum winter temperature for seedling establishment

Next, we examined the temperature effect on seedling establishment. In the model, the latter is constrained by minimum winter temperature, in addition to degree-day sum. The tree chronologies used did not indicate birth years (or even pith age, as there was no guarantee it had been hit every time) and birth numbers were also not available for the same reason and because of selective sampling. To determine the minimum winter temperature allowing seedling establishment ($kWiT_s$), the minimum winter temperature ($MinWiT$) values for all years at each of the tree-ring data collection sites were used in conjunction with the knowledge that regeneration had been possible at these sites, at least in some years. The coldest site for each species was selected and the $kWiT$ was estimated as the 95th percentile of $MinWiT$ for that site, rounded up to the next degree. This means that regeneration is assumed to occur on average once every 20 years at the most unfavourable site. Although 20 years is an arbitrary value, it meant that the new $kWiT_s$ value matched the existing parameters for Larch and Swiss Stone Pine. The sites used were Grindelwald S2 (*Picea abies*) and Tschainas (*Larix decidua* and *Pinus cembra*). The latter is an altitudinal transect and the highest plot (2410 m) was used.

Parameters for the boreal tree-line

The same methods were used to determine the model parameters for the three main boreal tree-line species in Finland and Sweden, namely Scots pine (*Pinus sylvestris*), Downy birch (*Betula pubescens*) and Norway spruce (*Picea abies*). Fewer chronologies were available, especially for birch and spruce (Table 2.1). The climate maps, also derived using the DAYMET simulation model (Thornton *et al.*, 1997), cover a time-span of 30 years (1973-2002) and have a 600 m resolution (grid of square cells). The methods for calculating the degree-day sums and minimum winter temperatures were the same as for the Alps, as were the criteria used to determine the species parameters ($kWiT$ and kG) for *Pinus sylvestris* and *Betula pubescens*. The sites used for calibrating $kWiT$ were Muonio and Kevo, respectively. In the case of *Picea abies*, for which we only had one site, the resulting potential curve was added to the subalpine sites' plot, as a way of checking whether the subalpine calibration might be used.

Downy birch was a new species in the model and the other parameters were derived from various sources in the literature, according to the method described by Bugmann (1994) for the subalpine species (for details of the Downy birch parameters and literature used, see Appendix II).

Model setup and evaluation - case study Alps

Comparing both the original and the new growth curves graphically against tree-ring data provides some insight into their ability to model tree-line forests realistically. However, the effect of the changes in the parameters on the model output was further investigated through a case study in the Alps. The test area was a 100x100 cell raster of 250 m resolution, situated in the Upper Engadine valley, Switzerland (Fig. 2.1). This was chosen because it was large enough to cover a range of different conditions (altitude, exposition), but at the same time offered a good compromise between resolution and computing time. Altitudes in the grid range from 1369 to 3723 m, but the lowest points in the Engadine valley itself are around 1630 m, while the lowest points in the grid are situated in a valley to the north-west, which belongs to a different catchment area. The bottom of the Engadine valley is only sparsely covered by forests, as most of it is either built-up, lakes or agricultural land. The forests are found mainly on the lower to middle mountain sides. Above the forest there is herbaceous vegetation and higher up bare rock, snow and ice.

The original version of TreeMig and the new one were run on that grid for 500 years under current climate conditions. The climate input data (degree-day sum, minimum winter temperature and drought stress) was generated, using the algorithms of ForClim-E and TreeMig (Bugmann, 1994, 1996; Lischke *et al.*, 2006), from the DAYMET climate maps (monthly mean temperature and precipitation sum, 1961-1998) and the bucket size found in the Swiss soil suitability map (SFSO, 1992). The bucket size is the difference between field capacity and the permanent wilting point, expressed as centimetres of water in the rooting zone. For the new version of TreeMig, additional maps of daily minimum and maximum temperatures (1961-1998) were used and the ForClim-E algorithms modified to calculate the degree-day sum with Allen's (1976) sine-wave method. The algorithms for minimum winter temperature and drought stress were unchanged.

In both cases (original and new TreeMig), trees were only allowed to grow on cells classified as "forest", as defined by Gellrich *et al.* (in revision). This rather broad definition includes scrubland, bushes/shrubs and groups of trees, as well as the various closed and open forest categories from the Swiss Area Statistics (SFSO, 2001). The tree-line ecotone, where trees are increasingly sparse and small, mostly falls into either open forest or one of these other categories, which are not strictly forests but contain woody vegetation. Seeds of all species were assumed to be present in the soil for the first 10 years (spin-up), after which normal forest dynamics, including seed production and dispersal, were allowed to run, i.e. forest composition was determined by growth, competition, regeneration of species within each simulated cell and migration between cells. The model output after 300 years, which showed no major differences with the 500-year output, was used to represent present-time forest, because most forests in Switzerland are managed and rarely exceed 300 years of age. The model output was expressed as biomass (total for all height classes) per species and grid cell. This was compared with the data from the first Swiss National Forest Inventory (NFI, Bachofen *et al.*, 1988). As there are far fewer NFI plots than forest cells in the model test area, NFI plots from the entire Engadine valley were used, provided they were within the

same altitudinal range as the study area (Table 2.4). This re-establishes the balance somewhat and is justified as the abiotic conditions (climate, soil, etc.) are similar throughout the valley. Only the model results from within the Engadine valley itself were used and the output from the small area situated in a different valley was excluded because of the possibility of different climatic influences.

The NFI data and the output from the two versions of TreeMig were plotted individually to show the respective proportions of larch, spruce, pine and other species (grouped) within 100 m altitudinal bands. The results per species and altitudinal band from the two model runs were also plotted against the NFI data.

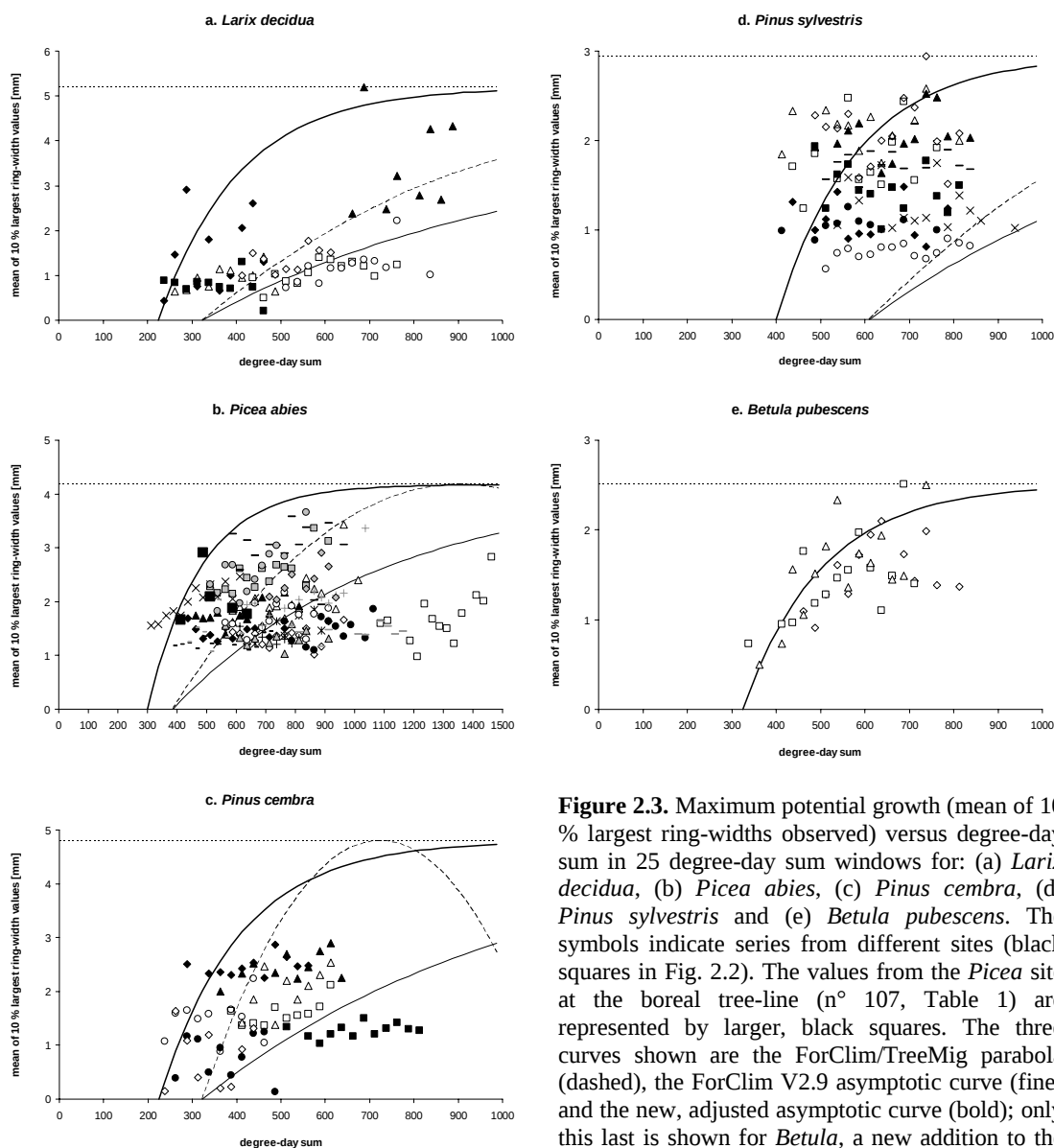


Figure 2.3. Maximum potential growth (mean of 10 % largest ring-widths observed) versus degree-day sum in 25 degree-day sum windows for: (a) *Larix decidua*, (b) *Picea abies*, (c) *Pinus cembra*, (d) *Pinus sylvestris* and (e) *Betula pubescens*. The symbols indicate series from different sites (black squares in Fig. 2.2). The values from the *Picea* site at the boreal tree-line (n° 107, Table 1) are represented by larger, black squares. The three curves shown are the ForClim/TreeMig parabola (dashed), the ForClim V2.9 asymptotic curve (fine) and the new, adjusted asymptotic curve (bold); only this last is shown for *Betula*, a new addition to the model. The new curve is adjusted to approximately form an envelope around the data, representing maximum potential growth. The dotted line shows the maximum ring-width (original value for *P. abies* and *P. cembra*, new one for the other three species).

Results

Growth curves and parameter adjustment

The potential growth values calculated from the tree chronologies show considerable differences between the sites for all species (Fig. 2.3). The only exception is *Betula pubescens*, for which all three sites show similar growth patterns (Fig. 2.3e). In the case of *Picea abies* (Fig. 2.3b), there are large differences between the subalpine sites; however, the single boreal site (represented by large black squares) does not stand out, although it must be noted that it contains only a few data points.

Neither the traditionally-used parabola nor the ForClim V2.9 asymptotic curve captured the observed growth very well. In fact, although conceptually an improvement, the latter was systematically too flat, whereas the slope of the parabola was adequate in some cases, for example *Pinus cembra* (Fig. 2.3c). The *kDDMin* value (lowest annual degree-day sum allowing growth) had to be reduced for all three species (i.e. trees grow at colder temperatures than the original parameters suggest). The difference was slightly larger for *Larix* and *Pinus cembra* than for *Picea*, but the biggest change occurred for *Pinus sylvestris* (boreal tree-line). The maximum ring-width (asymptote of the new function) was set to the largest value across all sites for larch, Scots pine and birch by modifying the growth parameter (*kG*). The original model maximum was kept for spruce and Swiss stone pine, as in both cases it was higher than the largest measured value in our data.

The new minimum degree-day sum and growth parameters for all five species are given alongside the original values in Table 2.2 (*kDDMin* and *kG*). For *Betula pubescens*, only the new values are given as it was not part of the original set of species in the model. The growth rates are linked to the maximum ring-widths (Fig. 2.3) by means of Eq. 2.4, so the relation between the two depends on the species' maximum height and diameter.

Table 2.2. Minimum degree-day sum (*kDDMin*), growth factor (*kG*, with corresponding maximum ring-width *maxRW* in mm) and minimum winter temperature (*kWiT*, in °C) parameters for three Alpine and two boreal tree-line species in the original and new versions of TreeMig.

Species	original			new		
	<i>kDDMin</i>	<i>kG</i> (<i>maxRW</i>)	<i>kWiT</i>	<i>kDDMin</i>	<i>kG</i> (<i>maxRW</i>)	<i>kWiT</i>
<i>Larix decidua</i>	323	170 (4.029)	-11	225	219 (5.190)	-11
<i>Picea abies</i>	385	171 (4.178)	-999	300	171 (4.178)	-7
<i>Pinus cembra</i>	323	115 (4.803)	-11	225	115 (4.803)	-11
<i>Pinus sylvestris</i>	610	119 (2.683)	-999	400	131 (2.943)	-11
<i>Betula pubescens</i>	-	-	-	325	180 (2.510)	-13

Minimum winter temperature for seedling establishment

The summary statistics and 95th percentile of the minimum winter temperature at the coldest site for each species are shown in Table 2.3, along with the parameter value derived from the 95th percentile (see also Table 2.2, *kWiT*).

In the two cases where there was a winter temperature limit to regeneration in the original model (*L. decidua* and *P. cembra*), the new parameters are equal to the old ones. *P. abies* and *P. sylvestris* have been given minimum winter temperature limits,

Table 2.3. Minimum winter temperature (minimum of December, January and February monthly means) at the coldest site for each species.

Species	Site	min.	mean	median	95 th percentile	kWiT
<i>Larix decidua</i>	Tschainas	-19.2	-15.0	-15.0	-11.4	-11
<i>Picea abies</i>	Grindelwald S2	-15.0	-10.8	-10.9	-7.5	-7
<i>Pinus cembra</i>	Tschainas	-19.2	-15.0	-15.0	-11.4	-11
<i>Pinus sylvestris</i>	Muonio	-24.9	-17.3	-17.5	-11.1	-11
<i>Betula pubescens</i>	Kevo	-24.6	-19.4	-19.5	-13.7	-13

instead of the “no limit” value (-999). For Spruce, the new value matches the minimum January temperature (often equivalent to *kWiT*) given by Kienast (1987). The *kWiT* value for *B. pubescens* is the lowest of all the species in this study, which is unsurprising as it has the most northerly distribution of the boreal tree-line species.

Model evaluation - case study Alps

Comparing the tree biomass in the TreeMig simulations with that in the NFI data shows that both model versions tend to err on the high side (Fig. 2.4a). This is mostly due to the over-optimistic representation of spruce (Fig. 2.4c), although this is marginally better in the new version. At altitudes up to 2000 m, the new calibration improves the results for larch (Fig. 2.4b). At higher altitudes however, the new TreeMig version clearly over-estimates *Larix*'s biomass, although the lack of NFI plots above 2300 m makes comparison difficult. The third species shown is *Pinus cembra* (Fig. 2.4d), for which both models underestimate the biomass at lower altitudes. In the highest band where NFI data exists (2200 m), the new model gives good results and above that it continues the trend (increasing biomass with altitude) before evening out and decreasing sharply at 2500 m. The original TreeMig version results in a similar pattern but with larger biomass values around 2200-2400 m, which are possibly a bit too high.

Finally, several other species are present in smaller quantities in the NFI data and the TreeMig simulation results. In the forest inventory plots, we find mainly *Pinus sylvestris* (up to 2000 m) and *Pinus mugo* ssp. *uncinata* (above 1600 m). The original model results in very small quantities of these two species, along with other species (e.g. *Alnus incana*, *Populus tremula*, *Sorbus aucuparia*) also found as traces (<1 t/ha on average) in the NFI data. The new version of the model gives better results for *Pinus sylvestris*, although it is still under-represented on average. The results of the two models differ only marginally for *Pinus cembra* and the other species.

Table 2.4. Number of National Forest Inventory plots and TreeMig forest cells per 100 m altitudinal band. The NFI plots are located in the whole of the Engadine valley, whereas the TreeMig cells come from the study area only.

Altitude	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500
NFI plots	22	33	46	53	39	15	3	0	0	0
TM forest cells	12	133	302	277	253	203	113	32	7	2

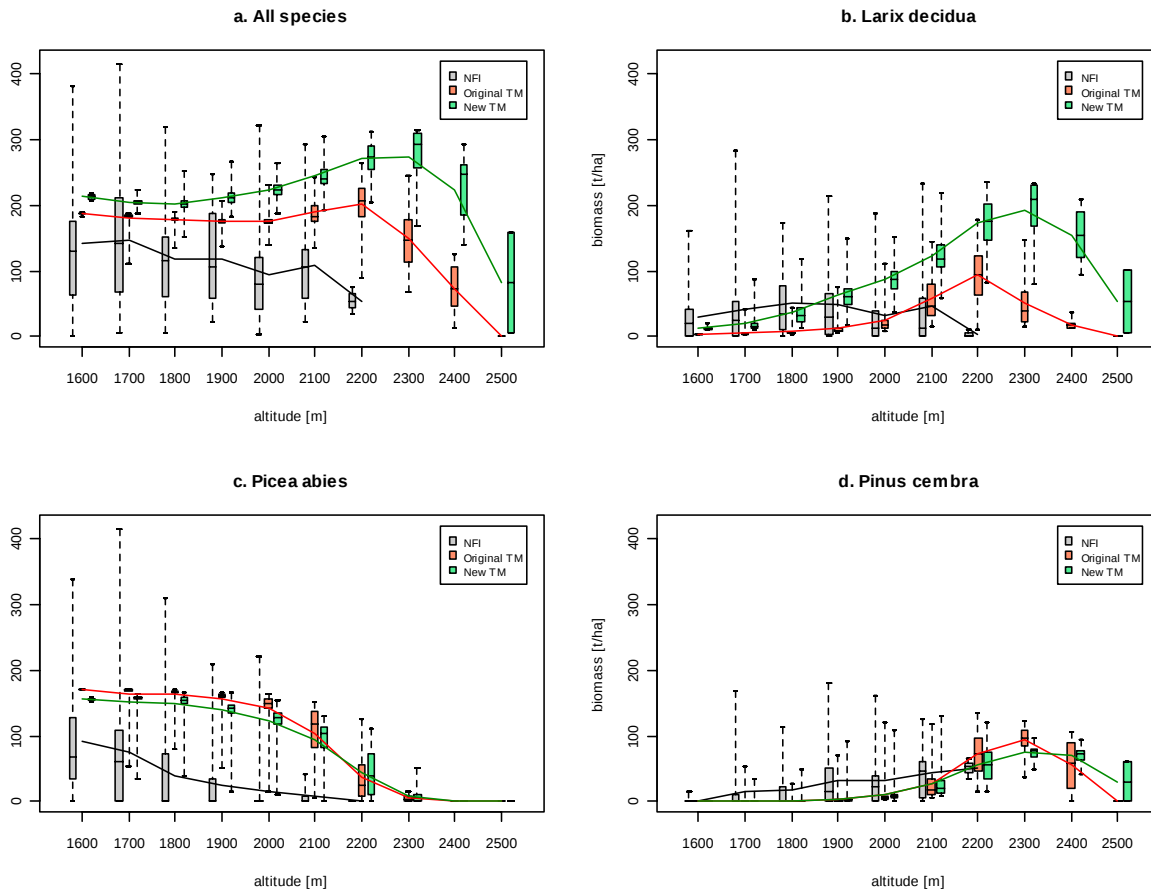


Figure 2.4. Boxplot of the biomass [t/ha] per 100 m altitudinal band found in the National Forest Inventory data and the results from simulations with the original and new versions of TreeMig (Lischke *et al.*, 2006). The total biomass (a) is given, as well as the values for the three main tree-line species: *Larix decidua* (b), *Picea abies* (c) and *Pinus cembra* (d). The boxes denote the 25th and 75th percentile, with whiskers extending to the minimum and maximum values. The full lines indicate the mean biomass in each case and are aligned, whereas the boxes had to be placed side by side for clarity's sake. The values on the x-axis indicate the lower end of each altitudinal band. The number of NFI plots and TreeMig forest cells per altitudinal band is given in Table 2.4.

Discussion

Growth curves and parameter adjustment

The difference in the maximum growth observed at the various tree-ring sampling sites indicates that in some cases local conditions, such as drought frequency or soil type, may affect growth more than air temperature does. The increase in CO₂ levels over the last few decades may also affect growth and therefore mask the temperature response signal (Nicolussi *et al.*, 1995; Rathgeber *et al.*, 2003), though this response may be temporary, depend on the tree type (evergreen or deciduous) or interact with defoliation events (Handa *et al.*, 2005). The direct effect of CO₂ on growth may also be counteracted by the associated indirect effect of drought stress due to increased temperature (Martinelli, 2004). This shows the importance of using many sites, as well as a large number of trees, when attempting to establish growth potential from tree rings. We were only able to use that part of the tree-ring data which fell within the time-

span of the climate maps, but our sample included trees of different ages, so the age-related variability was also taken into account.

For all the species in this study, the first adaptation necessary to fit the new growth curve to the tree-ring data was a sharp increase of its slope. This concurs with the findings by Paulsen *et al.* (2000), that radial tree growth declines rapidly within the tree-line ecotone. The asymptotic curve shape, with a sharp increase in growth at the lower end of the temperature range, would also explain why these authors found a decrease in correlation between ring-width and altitude throughout the 20th century, particularly during the warmest phases (1920-1950 and 1980 onwards): during warmer periods, the whole range of degree-day sum values within the altitudinal gradient is situated in the “flat” part of the growth response curve, so there is little correlation between growth and altitude; in colder periods on the other hand, the same sites have heat sums which correspond to the steeper part of the curve.

The minimum degree-day sum parameters had to be lowered for all species. The largest adjustment of *kDDMin* occurred for *Pinus sylvestris*, which was expected as the model was originally developed for Central Europe whereas the tree-ring data came from Fennoscandia, so it may be put down to different ecotypes. It is also possible that the original calibration reflects the realised niche because Scots pine is out-competed by other pine species and larch towards the tree-line in Central Europe. *Pinus sylvestris* is not excluded from the subalpine tree-line by temperature, but by the lower resistance to desiccation and higher light requirements of its seedlings, in comparison with those of *Pinus cembra* (Hättenschwiler and Körner, 1995). On the other hand, the spruce measurements from the boreal tree-line fell within the range of those from the subalpine sites. Although we cannot draw firm conclusions from a single site, it does indicate that the spruce parameters from the Alpine calibration may be adequate for simulations in northern Europe. Finally, the birch chronologies allowed us to get a reasonable estimate of the growth parameters for that species and add it to the model. However, those parameters should still be used with caution because of the small amount of data from which they were derived.

The growth rate (*kG*) of *Larix decidua*, which was originally similar to that of *Picea abies*, was increased in the new model version to match the larger values found in the tree-ring data. This supports the findings of Dullinger *et al.* (2005), that larch grows faster than spruce on average. For *Picea abies* and *Pinus cembra*, the growth rates remained the same, as the tree-ring data did not yield higher values than the original maximum; for the latter species, the measured values were actually considerably lower, indicating that the data used may not have captured the full growth potential. For *Pinus sylvestris*, the measured growth was only slightly larger than expected and *kG* was adjusted accordingly.

Although the tree-ring-based parameter estimates could still be improved, particularly in species for which little data was available, the new growth curves are a step in the right direction. They not only match the field data (tree-ring widths) better but are based on a more solid theoretical background: drought is no longer accounted for twice, as was the case when a parabolic growth response curve was used in a model which accounted for drought effects *per se*.

Fitting growth curves to the tree-ring data involved some trial and error, as this had to be done visually for want of adequate statistical methods. In particular, some guesswork was needed in determining the steepness of the slope or the minimum degree-day sum, as sufficient amounts of data were not always available for full range of temperatures

and differences between field sites sometimes masked the temperature response. However, the new curves definitely fit better than the original ones.

Minimum winter temperature for seedling establishment

One of our key findings was that regeneration seems to be the principal factor limiting tree distribution at the cold forest limits, as changing the growth curve alone did not improve the model results when compared to the NFI data, even when the uncertainties contained in the latter, such as stand age or management, were taken into account. On the contrary, changing the growth response to degree-day sum but not the minimum winter temperature (which limits regeneration) would have resulted in an even greater over-estimation of spruce's biomass, well above the altitude at which it is currently observed (not shown). Further evidence is the fact that there are practically no missing rings in our tree-line data, which implies that once trees are established, they manage to grow most years, even if only very little. This corroborates findings by several authors that a large part of the regeneration pool should survive, at least as stunted growth forms (Kullman and Engelmark, 1997; Gamache and Payette, 2005). Although degree-day sum also plays a role in seedling establishment (if growth is not possible for adult trees, seedlings cannot grow either), the main factor limiting recruitment in TreeMig is minimum winter temperature. For perennial plants like trees, establishment from seed occurs less frequently and winter survival is therefore more important, so temperature during the nil or low growth period (i.e. winter in temperate regions) is crucial in controlling distribution; annual plants on the other hand are mostly affected by growing season temperature (Woodward, 1988).

Winter temperature appears as a key factor for regeneration success in several tree-line species: *Picea obovata* (Siberian spruce) at the altitudinal tree-line (Moiseev *et al.*, 2004), *Pinus sylvestris* and *Picea abies* at the boreal tree-line (Kullman, 1986; Kullman and Engelmark, 1997; Kullman, 2005), although for the latter precipitation (protective snow cover in winter and absence of drought in the growing season) is at least as important. Calibrating Norway spruce's response to drought more accurately and adding drought-dependence to the factors controlling germination would probably help reduce that species' presence in the model results to more realistic proportions, as it is still over-represented despite the improvement brought by the present work. Some studies at the boreal tree-line have shown that regeneration is also strongly influenced by wind and that correlations between regeneration and temperature match lower-frequency (decadal) trends better (Esper and Schweingruber, 2004; Gamache and Payette, 2005). For *Pinus sylvestris*, mortality remains high and climatically controlled up to 20-30 years after germination (Kullman, 1986), whereas for *Picea abies* mortality declines after the second growing season (Kullman and Engelmark, 1997). As it is not possible to include all the likely factors, particularly those which affect only few species, in a model, we decided to concentrate on improving the existing parameters. Furthermore, some factors may have several effects which counteract each other: snow cover for example protects seedlings against frost and browsing, but increases the risk of fungus infections (Hättenschwiler and Körner, 1995; Cunningham *et al.*, in revision).

The method used to determine the minimum winter was subjective and based on the assumption that the existing values were accurate for the species which had a cold limitation to establishment. Although we could not check the accuracy of absolute values in this way, the relative order of the species with respect to that parameter was re-established.

Model evaluation - case study Alps

The mean biomass values are systematically too high for the sum of all species and in some cases also for individual species. The variation in biomass per altitudinal band is greater in the NFI data than in the model output, because the inventory plots are much smaller than the simulated grid cells. In the latter, the biomass is averaged over the entire cell surface, so extreme values are less likely. However, the model results are generally within range of the National Forest Inventory data. At those altitudes for which National Forest Inventory data is available for comparison, the results per species in the newly-calibrated model generally show a slight improvement, although some strong differences remain, such as the ratio of larch to Swiss stone pine (especially around 2000-2300 m) or the absence of the latter at lower altitudes. As *L. decidua* is mostly present in early succession stages and *P. cembra* in later ones (Delarze *et al.*, 1998; Motta and Nola, 2001; Tinner and Kaltenrieder, 2005), one could imagine that the model was not allowed to run long enough for pine to establish itself. However, running TreeMig for 500 years did not really change this competitive balance, as the biomass of *Pinus cembra* remained constant, but *Larix decidua* had all but disappeared at lower altitudes while remaining very present higher up. The discrepancy between model results and NFI data may be due to the mixture of early- and late-successional stages in the field data, which is subject to disturbances such as wind-throw (stand ages vary from 1 to 359 years), whereas the model cells are more homogeneous, since they represent the average of differently aged “patches”. Including disturbance in the model would probably improve this and lead to a better ratio of *L. decidua* to *P. cembra*. However, we were not able to use this option (which exists in TreeMig) in the present study, due to the absence of data from which to parameterise the frequency and severity of disturbance episodes in our study area. Two other factors which affect larch in particular are larch bud moth (*Zeiraphera diniana*) attacks (Motta and Nola, 2001) and pasturing, as *Larix* roots seem especially sensitive to trampling by cattle (R. Niederer, pers. comm.). The latter is most likely to occur in the higher altitudinal bands, where cattle might wander in from the summer pastures above and could partly explain the depressed biomass of *Larix decidua* in the NFI data for the 2200 m band. However, the difference may also simply be due to chance, as there are only three NFI plots in that band. For *Picea abies*, although the new temperature parameters reduce its biomass slightly, the model is still far too optimistic. This is most probably linked to the drought response. In fact, it may be necessary to review this aspect for other species in the model too, as it may have been affected by the removal of the hidden drought effect in the temperature response.

For the three uppermost altitudinal bands (2300 m and above), there is no data in the first National Forest Inventory, which we used for comparison. However, this does not mean that there are no trees, but that no plots matched the NFI’s definition of “forest” (area width ≥ 50 m and tree coverage ≥ 20 %; tree height ≥ 3 m). TreeMig results extend right up to the tree species line, whereas the NFI plots are only found below the timber-line (both definitions according to Körner and Paulsen, 2004). In the third National Forest Inventory, which is currently being conducted, the presence of trees in plots which do not match the above definition is also recorded through aerial photograph analysis. Preliminary results show that trees are present up to 2400 m in the sampled points (C. Ginzler, pers. comm.), but without any indication about species. Field observations at tree-line also show the presence of *Pinus cembra* at 2355 m (trees ≥ 5 m high) and *Larix decidua* at 2452 m (shrub form) in the Engadine (J. Gehrig-Fasel, pers. comm.). Nevertheless, the overall biomass simulated by the model in the

uppermost altitudinal bands is too high for the scattered trees observed at tree-line. This can in part be explained by the fact that the model simulates the potential forest, whereas subalpine forests are to a large extent shaped by human activities, with centuries of pasturing leading to a depressed tree-line (Ellenberg, 1986; Tinner and Theurillat, 2003). For Swiss stone pine, the high altitude biomass levels in the model are consistent with these observations and with the trend shown by the NFI data at lower altitudes. However, larch constitutes the bulk of the biomass above 2200 m in the model, which is much less plausible as observations in the field indicate mostly scattered, small (shrub-like) trees of that species. The over-estimation of *Larix decidua*'s biomass in the model may result from that species' age-related sensitivity to climate. Carrer and Urbinati (2004) showed that growth in older larches (over 200 years old) was more highly correlated to variations in climatic conditions, such as summer temperature. As the larches in our dendrochronological data were mostly quite young (a few decades to 150 years), it is possible that the parameters and temperature growth response curve are too optimistic for older trees and that an age-related response curve may need to be developed, or at least two different curves, for trees younger or older than 200 years.

The discrepancy between field observations and model results may also be due to the climate data used as input. This covered three to four decades, including most of the 1990s, the warmest decade in the century. However, the forests we can observe at present are mostly a result of the climate of the last three to four centuries, which were on average colder. The model results may therefore be more a representation of forests as they might stand in a few decades if current climate trends continue.

A few other species appear, albeit in small quantities, in the model results and the NFI plots. The latter are smaller and less numerous than the cells in the TreeMig grid, so less frequent tree species could have been missed. On the other hand, the model might include species which could potentially grow in that area, but are not actually present for some reason (e.g. geographical barriers). The two main non-dominant species in the NFI data are *Pinus sylvestris* and *Pinus mugo* ssp. *uncinata*. In the new model, the former is better represented, but both models underestimate the presence of the latter. Generally speaking, however, the main secondary species which appear in the model results are also present in the National Forest Inventory data, although their relative importance may differ. Their representation in the model could perhaps be improved by a similar calibration exercise. Human influences, such as forest management practices (which are not included in the model at present), could also account for the differences between the model results and the field data for these other species.

It was not possible to draw firm conclusions on the accuracy of the biomass in the model output by comparing it to that of the NFI data, as they were two quite different types of data. We therefore have to consider this comparison as a general indication of altitudinal distribution and relative importance of the different species, rather than try to quantify the differences in absolute terms.

Conclusions

Both the old and new versions of TreeMig give a reasonable estimate of present forest composition. However, the new version has the advantage of a better theoretical basis for its growth response curve. We have also developed a methodology for deriving the species-related parameters of this curve from dendrochronological data (tree-ring width). In some cases this has led to a slight improvement in the model results, in comparison with the National Forest Inventory data, but more importantly we now have

a method which can be used to add other species to the model. This could be useful for portability to other regions, such as the boreal tree-line mentioned in this paper, or in the context of climate change and the immigration of new species.

This calibration work also brought to light the importance of regeneration as a factor controlling species distribution. Further improvement of the model would require calibrating the temperature controlling establishment for some of the other species, in particular those with no lower limit. Seedling and sapling dynamics is modelled in the same manner as that of adult trees in TreeMig, except for light requirements; once established, the influence of temperature on growth and mortality is the same for all trees. It should therefore be possible to improve the simulation of the species' distributions further by taking into account the winter temperature of several years following germination, instead of just the birth year. Although temperature is the main limiting factor for growth and establishment at tree-line, other factors, such as precipitation, wind or human activities, no doubt play a role, though their influence may be limited to certain species or regions and may be more difficult to calibrate and include in a model. They should however always be taken into consideration, at least when discussing model results.

Although the newly-calibrated version of TreeMig does not differ greatly from the original model in terms of simulation results, the theoretical framework on which it is built has been improved. We have also produced a method to derive species parameters for the model from tree-ring data. Finally, this work has also increased our knowledge of the various factors controlling tree species' distributions and opened up perspectives for further research.

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3. Combining probabilistic land-use change and forest dynamics modelling to simulate global change responses at the Alpine tree-line

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Abstract

Although tree-lines are mainly constrained by temperature, they can also be influenced by other factors, such as human activity. This is particularly true for the European Alps, where centuries of agricultural practices have affected the altitudinal tree-line. However, over the last few decades this trend has been reversed due to changing agricultural practices and land-abandonment. The aim of this study was to combine a statistical model for land-abandonment with a forest dynamics model, to take into account the combined effects of climate and human activities on the Alpine tree-line in Switzerland.

The probability of land-abandonment was expressed by a logistic regression equation as a function of degree-day sum, distance from forest edge, soil stoniness, slope, proportion of employees in the secondary and tertiary sectors, proportion of commuters and proportion of full-time farms. It was implemented in the TreeMig spatio-temporal forest model by assigning the simulation grid cells to one of three categories: “forest” (in which forest dynamics can be simulated), “agriculture” (which can turn into forest according to the output of the abandonment model) or “other” (unsuitable for forest growth). Distance from forest edge and degree-day sum may be modified through feedback from the dynamics part of TreeMig and climate change scenarios.

The new model, TreeMig-LAb, was first tested on a series of theoretical landscapes with different values for the variables in the land-abandonment model. This showed that distance from forest and slope have a strong influence on the abandonment probability. Degree-day sum has a more complex role, with opposite influences on land-abandonment and forest growth.

TreeMig-LAb was also applied to a case study area in the Upper Engadine (Swiss Alps), along with two different modelling approaches: natural succession/migration only and a constant probability of abandonment for all “agriculture” grid cells, based on past transition proportions (2.1 % per decade in that area). The former showed new forest growing in all but the highest-altitude locations. The latter was more realistic in terms of numbers of reforested cells, however their location was random and the resulting landscape heterogeneous. The new model based on the logistic regression equation gave results consistent with observed patterns of land-abandonment, namely: expansion of existing forests and closing of gaps, leading to an increasingly homogeneous landscape.

Keywords: agricultural land abandonment, climatic change, gap dynamics, logistic regression, reforestation, TreeMig, TreeMig-LAb, Switzerland

Introduction

Projections of potential impacts of climate change on forest ecosystems are often based on the assumption that climate is the only factor controlling tree species range limits (Loehle and LeBlanc, 1996). Although climatic factors, temperature in particular, affect tree growth at high altitudes and latitudes (Körner, 1998; Jobbágy and Jackson, 2000; Körner and Paulsen, 2004), other factors such as disturbance and human impact play an important part in determining forest distribution. The most notable human influence at landscape level is the allocation of land to various uses and human activity, rather than natural succession, is the most common cause of land-use change (Bockstael, 1996). To improve the forecasting of the impacts of climate and – more generally – global change on forests near tree-lines, it is necessary to link ecological modelling with land use change simulation approaches including socio-economic processes.

In the European Alps, the tree-line has long been shaped by human activities, notably pasturing (Motta and Nola, 2001). However, since the end of World War II, the rural depopulation and agricultural land abandonment trend, which started with the Industrial Revolution, has increased drastically in western Europe, especially in mountains and other regions with unfavourable cultivation conditions (Baldock, 1996; MacDonald *et al.*, 2000; DLG, 2005). Although the patterns and driving forces of land-abandonment have been investigated and modelled by economists and other researchers studying land-use decisions from the point of view of individuals, this has usually been restricted to local case studies (e.g. Kristensen *et al.*, 2004; Kobler *et al.*, 2005). Consequently, these models cannot be linked to spatially-explicit ecological models, in which land-use transition probabilities, if at all present, are often simply based on past transition proportions or on empirical models with no economic foundation (Bockstael, 1996; Irwin and Geoghegan, 2001). However, a recent study of agricultural land abandonment in the Swiss mountains (Gellrich *et al.*, 2007; Gellrich and Zimmermann, 2007) has yielded two spatially-explicit statistical model environments, suitable for implementation in an ecological model. The explanatory variables in these statistical models are of two types, geo-/biophysical and socio-economic, but they are all linked to the costs and benefits of using the land for agriculture. The balance between costs and benefits (net income) determines the farmer's decision to continue working the land or to abandon it; in the latter case, and if conditions are suitable, natural succession may lead to afforestation of grassland areas and loss of woodland clearings (Hunziker and Kienast, 1999; MacDonald *et al.*, 2000). Although some of the variables in these models may also have ecological implications, in this case they are used as proxies for factors influencing farmers' decisions rather than the outcome of succession after abandonment. For example, land which is close to the forest edge tends to have less favourable cultivation conditions because of the cost of keeping it open (heavy seed rain), shading by the neighbouring trees (less solar radiation and longer snow coverage) and competition for water and nutrients.

The spatially-explicit dynamic forest model TreeMig (*Tree Migration* - Lischke, 2005; Lischke *et al.*, 2006) includes processes for landscape dynamics (e.g. seed production and dispersal) as well as forest population processes (e.g. growth, competition) and is therefore well adapted to simulating the effects of changes such as climate warming or land-abandonment. In addition, a new version of TreeMig has been specifically calibrated to simulate forest dynamics at the Alpine tree-line ecotone (Rickebusch *et al.*,

submitted). Land-use was already present in the model to a certain extent, as grid cells could be defined as suitable for forest growth or not, independently from soil or climate characteristics. This variable, called “stockability”, had a pre-defined value which could not be modified during the course of a simulation. However, TreeMig’s modular structure means that a sub-programme could be added to act upon the value of the land-use variable without fundamentally altering any other parts of the model.

The purpose of this study is to combine two model approaches: a statistical model for land-abandonment based on socio-economic factors and a forest model capable of simulating migration and subsequent population dynamics in the newly-available areas. A sensitivity analysis of the most important variables in the resulting model, named TreeMig-LAb, is then performed using theoretical landscapes. Finally, a real landscape (case study in the Upper Engadine valley) is used to compare our new model with two more traditional approaches: natural succession on its own and a simple agriculture to forest conversion proportion.

Material and methods

Statistical model of land-abandonment

The land-abandonment model was largely derived from the work of Gellrich *et al.* (2007). In this, the target variable (Y) is derived from the occurrence (presence) of land-abandonment, and subsequent forest regeneration, or lack thereof (absence) between the Swiss Area Statistic censuses of 1985 and 1997 (SFSO, 1992a, 2001), which results in a model giving the probability of abandonment for a 12-year period. For our purpose, which was to study the abandonment of agricultural land-use in mountain areas, the model was developed using data points above 800 m in altitude from all over Switzerland. As the data set was very large (20’688 presence and 710’975 absence points), we randomly selected a subset of 10 % of each class, which was then split into two halves for training and validating, respectively. Random sampling was applied in order to reduce potential spatial dependence in the presence/absence data (Serneels and Lambin, 2001). The proportional sampling method circumvents the need to adjust the intercept for unequal sampling proportions of presence and absence points (Maddala, 2001, pp. 325-326).

The probability of abandonment is expressed by a logistic regression equation (Hosmer and Lemeshow, 2000):

$$P(Y=1) = \exp(\alpha + \sum(\beta_k \cdot X_k)) / [1 + \exp(\alpha + \sum(\beta_k \cdot X_k))] \quad (3.1)$$

where Y takes the value 1 if the costs outweigh the benefits (leading to the decision to abandon the land) and 0 otherwise, α is a constant and X a vector of explanatory variables with respective coefficients β_k . The variables used here were a subset of the most significant variables in the models developed by Gellrich and co-workers (Gellrich *et al.*, 2007; Gellrich and Zimmermann, 2007) and, aside from the degree-day sum (DDSUM), came from the same data sources (Table 3.1). DDSUM had to be adapted to make it compatible with the degree-day sum in TreeMig. It is the mean of the yearly degree-day sums for 1961-1998, calculated with Allen’s (1976) double sine-wave method (lower threshold 5.5 °C, no upper threshold); this calculation was based on mapping of daily minimum and maximum temperatures from Swiss climate stations using the DAYMET simulation model (Thornton *et al.*, 1997).

Finally, the accuracy of the new model was tested using the validation dataset. Accuracy measures were calculated with the SimTest programme (Zimmermann, 2001),

which uses various methods such as Kappa statistics (Cohen, 1960) or area under the ROC plot (AUC) (Metz, 1978; Fielding and Bell, 1997).

Table 3.1. Explanatory variables used in the statistical model for land-abandonment.

Variable	Description	Unit
DDSUM ^a	Degree-day sum (> 5.5°C)	°C·day
DISTFOR ^b	Distance from forest edge	m
SOILSTON ^c	Soil stoniness	%
SLOPE ^d	Slope angle	deg
PRSECT23 ^e	Proportion of employees in the secondary & tertiary sectors	%
PRCOMMUT ^e	Proportion of commuters	%
PRFUTIFA ^e	Proportion of full-time farms	%

Data sources: (a) see text; (b) Swiss Area Statistics (SFSO, 1992a); (c) Swiss soil suitability map (SFSO, 1992b); (d) Digital elevation model - 25 m resolution; (e) Population and agricultural censuses (Swiss Federal Statistical Office, Neuchâtel).

Implementation in TreeMig

In the original TreeMig model (Lischke, 2005; Lischke *et al.*, 2006), tree population dynamics is simulated on a grid whose cells are either “stockable” (“forest” cells, “stockability” $\in]0,1[$) or not (“stockability” = 0). In the new model version, named TreeMig-LAb (*Tree Migration with Land-Abandonment*), the non-forest grid cells were further sub-divided into two types: “agriculture” (which may become forest if abandoned) and “other” (which cannot become forest, e.g. lakes). The definitions of “forest” and “agriculture” are the same as in the statistical land-abandonment models fitted by Gellrich and co-workers (Gellrich *et al.*, 2007; Gellrich and Zimmermann, 2007) and are aggregates of several related categories from the Swiss Area Statistics (SFSO, 1992a). “Forest” includes scrubland, bushes/shrubs and groups of trees, as well as the various closed and open forest categories. “Agriculture” includes land used for growing various crops (e.g. cereals, fruit, hay), hedges/copses on agricultural land, all types of pastures and grass- or heathland. This last group is not strictly speaking an agricultural land-use category, but the transition from alpine pasture to natural grassland is gradual and livestock may also contribute to keep the latter open.

All the variables in the land-abandonment model are considered constant over time within each grid cell, except for degree-day sum and distance from forest. The former may be modified according to the climate change scenario fed into TreeMig-LAb, while the latter is constantly re-evaluated to provide feed-back from previous land-abandonment events. The total contribution of the constant variables to abandonment probability is calculated in advance for each “agriculture” cell; “other” cells are indicated by the default value of -999.0.

Land-abandonment can be started at a user-defined time, which allows for a spin-up run within currently-observed “forest” cells (map input). The spin-up serves to establish populations of reasonable age and structural distribution at the start of a simulation. After that, land-abandonment is activated and the probability of abandonment of each “agriculture” grid cell is calculated (Eq. 3.1) at 10-year intervals, using the current degree-day sum and distance from forest values. Because the original statistical model gives the probability over 12 years, the result is scaled down to 10 years by dividing it by 1.2. The actual occurrence of land-abandonment is then evaluated by drawing a random number in the [0,1] interval: if it is smaller than the 10-year abandonment

probability value, the cell is considered as abandoned and its “stockability” value is set to 1.0. This means that incoming seeds can germinate and trees grow on that cell, provided climate conditions allow it. However, this grid cell is only classified as “forest” once minimum requirements for that attribute have been fulfilled. They are: a) at least one tree in height class 1 (i.e. above 1.37 m or “breast height”; seedlings and saplings constitute height class 0) and b) a minimal biomass of 2 t per hectare. The point of these requirements is to prevent newly-abandoned cells, on which forest has not yet had time to grow, from unduly influencing the abandonment probability of neighbouring cells by reducing their distance from forest. This is particularly important at high altitudes, where tree growth may be very slow or even non-existent. In the latter case the cell, although abandoned and “stockable”, will never become “forest”. These parameters were set fairly arbitrarily, but may be modified to suit the user’s definition of forest, although this is currently only possible within the programme code.

Because the number and location of “forest” cells changes during the course of a simulation, the distance from forest variable for the remaining “agriculture” cells has to be re-calculated accordingly. This is also done in decadal time-steps, at the end of the year preceding the land-abandonment re-evaluation, e.g. if abandonment starts at year 300, distance from forest will be re-calculated in year 309, just before the next round of abandonment in year 310.

Testing on theoretical landscapes

TreeMig-LAb was tested on a series of theoretical landscapes consisting of a 40 x 60 cell grid with 250 m spatial resolution. Forest was initially present in a 40 x 5 cell band at the bottom end of the grid only. All the other cells were labelled “agriculture” and had the same values for all variables used in the statistical land-abandonment model, except DISTFOR which was the real distance from forest for each cell. One of the variables was set to a different value (Table 3.2) in each landscape, giving a total of 13 different landscapes: one with all “default” values, four with varying DDSUM values, three with varying SLOPE values and five with unique values for DISTFOR. In the latter case, the re-evaluation of DISTFOR was over-ridden to keep it constant throughout the simulation. We chose to focus on the effect of varying DDSUM, DISTFOR and SLOPE, the first two because they are modified by feed-back within the land-abandonment module or by the climate change scenario and the last because it is the “constant” variable with the most weight in the land-abandonment model. The

Table 3.2. Values taken by the variables in the land-abandonment statistical model for the simulations on theoretical landscapes. The numbers in *italics* indicate the default values, designed to maximise abandonment rate. For DISTFOR, the default is the real distance, but simulations with various distances from forests were also tested in this study. The variables are described in Table 3.1.

Variable	Unit	Values
DDSUM	°C·day	300, 600, 900, 1200, 1500
DISTFOR	m	100, 250, 500, 750, 1000
SOILSTON	%	45
SLOPE	deg	5, 20, 35, 50
PRSECT23	%	10
PRCOMMUT	%	10
PRFUTIFA	%	10

values were varied between simulations rather than within the grid (e.g. along a gradient) to avoid neighbourhood effects which would make the results difficult to interpret. The “default” values, including those of all the other variables, were set to maximise abandonment probability, so that results could be seen within a reasonably short simulation time. The only exception is DISTFOR, for which a single default value does not make sense, as it is by definition dynamic, i.e. affected by the outcome of the land-abandonment model in previous time-steps. For DDSUM, it was possible to use a single value as it is only modified in the event of climate change (not used here), not as a result of land-abandonment.

TreeMig-LAb was run on these theoretical landscapes for a total of 700 years each, with land-abandonment starting after 200 years (spin-up time to allow the forest to grow in the initial band). The years in which each cell a) was abandoned and b) became “forest” were recorded. We compared the number of grid cells which were abandoned in each century (after the initial 200-year spin-up) between the different theoretical landscapes. We also compared the rate at which the forest advanced for the different values of degree-day sum and slope. This rate was measured as the year the first cell was abandoned in each row of “agriculture” cells, in other words the time required to reach the distance represented by a particular row. Obviously this is irrelevant in the case of distance from forest, as this distance was set to an artificial value bearing no relation to the cell’s row number.

Testing on a real landscape - Engadine case study

In order to evaluate the model in a real landscape, we chose a test area of 100 x 100

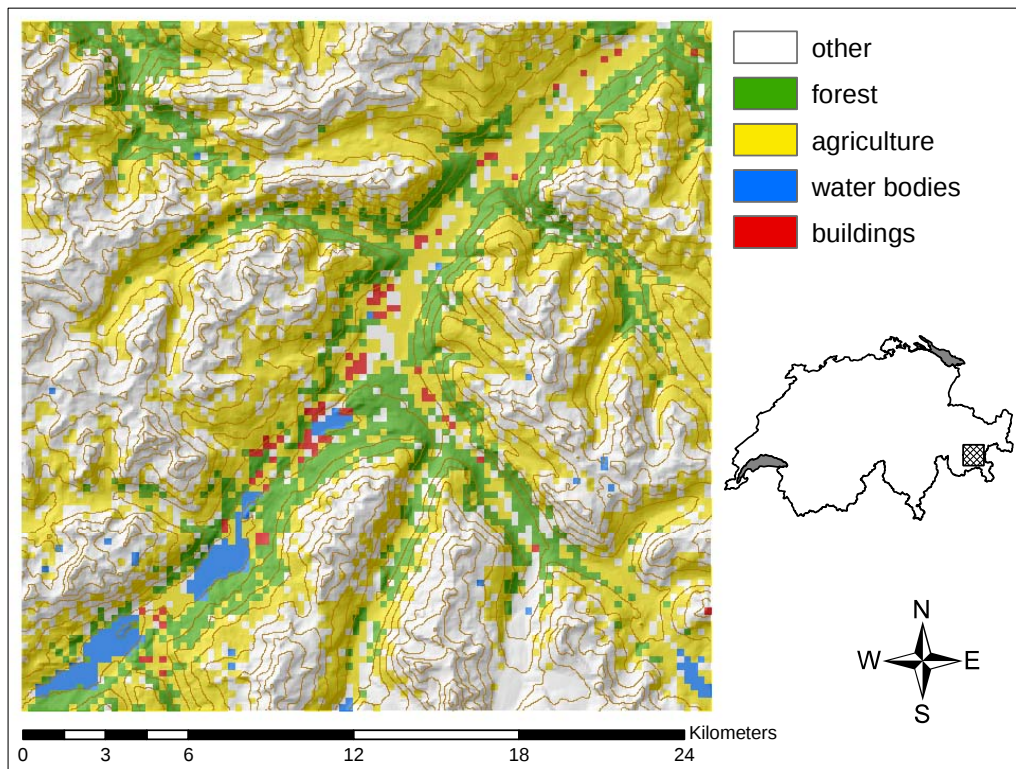


Figure 3.1. Map of the Engadine test area showing the three land-use categories: “forest”, “agriculture” and “other”. “Agriculture” includes semi- to natural grasslands, which may or may not be used for pasturing. In the “other” category, water bodies and built-up areas have been highlighted.

cells of 250 m resolution, situated in the Upper Engadine valley, Switzerland (Fig. 3.1). The grid's altitudinal range is 1370 to 3720 m, with cells classified as forest present up to 2550 m. However, half the forest cells are situated between 1850 and 2100 m. In this real-landscape simulation, TreeMig-LAb was run for a total of 500 years, with land-abandonment starting after 300 years of spin-up. The climate was set to current conditions (1961-1998), with no climate change scenario.

This setup was used to compare the results of the simulation using the new land-abandonment model with two alternatives: a) a “natural succession only” approach, representing forest spread following complete and immediate land abandonment, and b) a “constant probability” approach, where of 2.1 % of the land was abandoned every 10 years. “Natural succession only”, which includes migration, was simulated by indicating a 100 % probability of abandonment, irrespective of the cells' geo-/biophysical or socio-economic properties, i.e. all “agriculture” cells were abandoned in the first time-step after the 300-year spin-up. In the second case, the constant probability value (2.1 %) was given by the past transition proportion within the Engadine test area, scaled down from 12 to 10 years (difference between the statistical model and the time-steps in the land-abandonment module of TreeMig-LAb):

$$\text{Probability} = (P / N) / 1.2 \quad (3.2)$$

with P the number of points where abandonment occurred between 1985 and 1997 and N the total number of data points in the area.

The three approaches were compared through maps of the forest extent and biomass at two different time steps (after 100 and 200 years of land-abandonment) and by plotting the number of cells abandoned per altitudinal band in each case (for the same time-steps). Patterns in the simulation results from the statistical model and “constant probability” approaches were further compared by aggregating contiguous newly-afforested cells (at the end of the simulation) into polygons. These were then tested for differences in area and distance from the original forest edge between the two modelling approaches.

Table 3.3. Coefficients and p-values for the statistical land-abandonment model. The variables are described in Table 3.1.

Variable	Coef. estimate	P-value	
Intercept	-1.9610	0.00004	***
DDSUM	-0.0003	0.00069	***
DISTFOR	-0.0111	< 2E-16	***
SOILSTON	0.0469	5.82E-10	***
SOILSTON^2	-0.0005	1.95E-08	***
SLOPE	0.1554	< 2E-16	***
SLOPE^2	-0.0023	2.39E-14	***
PRSECT23	-0.0367	0.00098	***
PRSECT23^2	0.0002	0.00538	**
PRCOMMUT	-0.0070	0.00051	***
PRFUTIFA	-0.0193	< 2E-16	***

Results

Statistical model

The results of the logistic regression model (Table 3.3) show that the probability of land-abandonment rises if soils are stony (SOILSTON), steep (SLOPE), close to the forest edge (DISTFOR) or if they have a low heat sum (DDSUM), as this makes them harder to work and reduces the yield. SOILSTON and SLOPE have parabolic responses, so the probability of abandonment decreases again when the soil becomes too stony or the land too steep (maxima are 47 % and 34°, respectively). This can be due to the lack of agricultural activity in such unfavourable conditions or the absence of forest regeneration, which was the measure used for “presence” of abandonment. Alternative employment opportunities in other sectors and outside the community (PRSECT23, PRCOMMUT), as well as a low proportion of full-time farms (PRFUTIFA), are also factors which increase the probability of abandonment. PRSECT23 has an (inverted) parabolic response, but the curve has a minimum at 92 % and there is no visible increase in abandonment probability before it reaches the upper end of that variable’s possible range (100 %). The variables with the greatest weight in the model are SLOPE, PRFUTIFA and DISTFOR. While the pseudo- R^2 value for the model is rather low (0.15), the Kappa value of 0.606 (at optimised cut-off level) shows “good agreement” between the model predictions and the validation data, according to the scale proposed by Monserud and Leemans (1992). The ROC plot (Fig. 3.2) and its corresponding AUC of 0.911 indicate that in 91 % of cases, randomly-selected points from the “true positive” group (i.e. those where land-abandonment is present both in the model and the data) have higher scores than those from the “false positive” group (i.e. absence points classified as presence by the model).

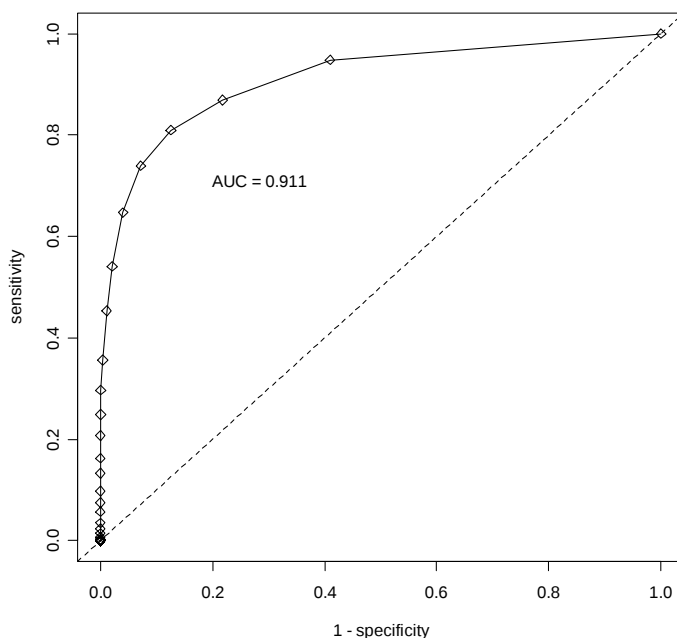


Figure 3.2. ROC (Receiver Operating Characteristic) plot for the statistical land-abandonment model’s validation data set. This shows the sensitivity (fraction of true positive results, i.e. abandoned points with a probability above the given threshold in the model) versus the opposite of the specificity (fraction of false positive results, i.e. abandoned points whose probability was below the threshold), for thresholds ranging from 0 to 1 in 0.01 steps.

Theoretical landscapes

The numbers of grid cells abandoned per century for different values of degree-day sum, distance from forest and slope (Fig. 3.3) generally reflect what would be expected from these variables' coefficients in the statistical model (Table 3.3), namely a negative trend for DDSUM and DISTFOR, and a parabolic response for SLOPE. In the case of distance from forest (Fig. 3.3b), this is only really visible in the first century after the onset of land-abandonment, as the probability is so high for a distance of 100 m that there are practically no "agriculture" cells left to be abandoned later. The decrease in probability is very sharp and a distance of 1000 m (not shown) yields so few abandoned cells that they would not be visible on the plot. There is also a decrease in the number of cells abandoned with increasing degree-day sums (Fig. 3.3a), except in the last century of the simulation; it is not as clear as for DISTFOR and the levels for 900 and 1200 degree-days are practically equal and sometimes the opposite to what is expected. There is little difference between the land-abandonment advance rates for the three lowest values of DDSUM, but this rate decreases for 1200 and especially 1500 degree-days (Fig. 3.4a). When SLOPE is varied, both the number of abandoned cells (Fig. 3.3c) and the advance rate (Fig. 3.4b) reflect the shape of the response curve, which is a parabola

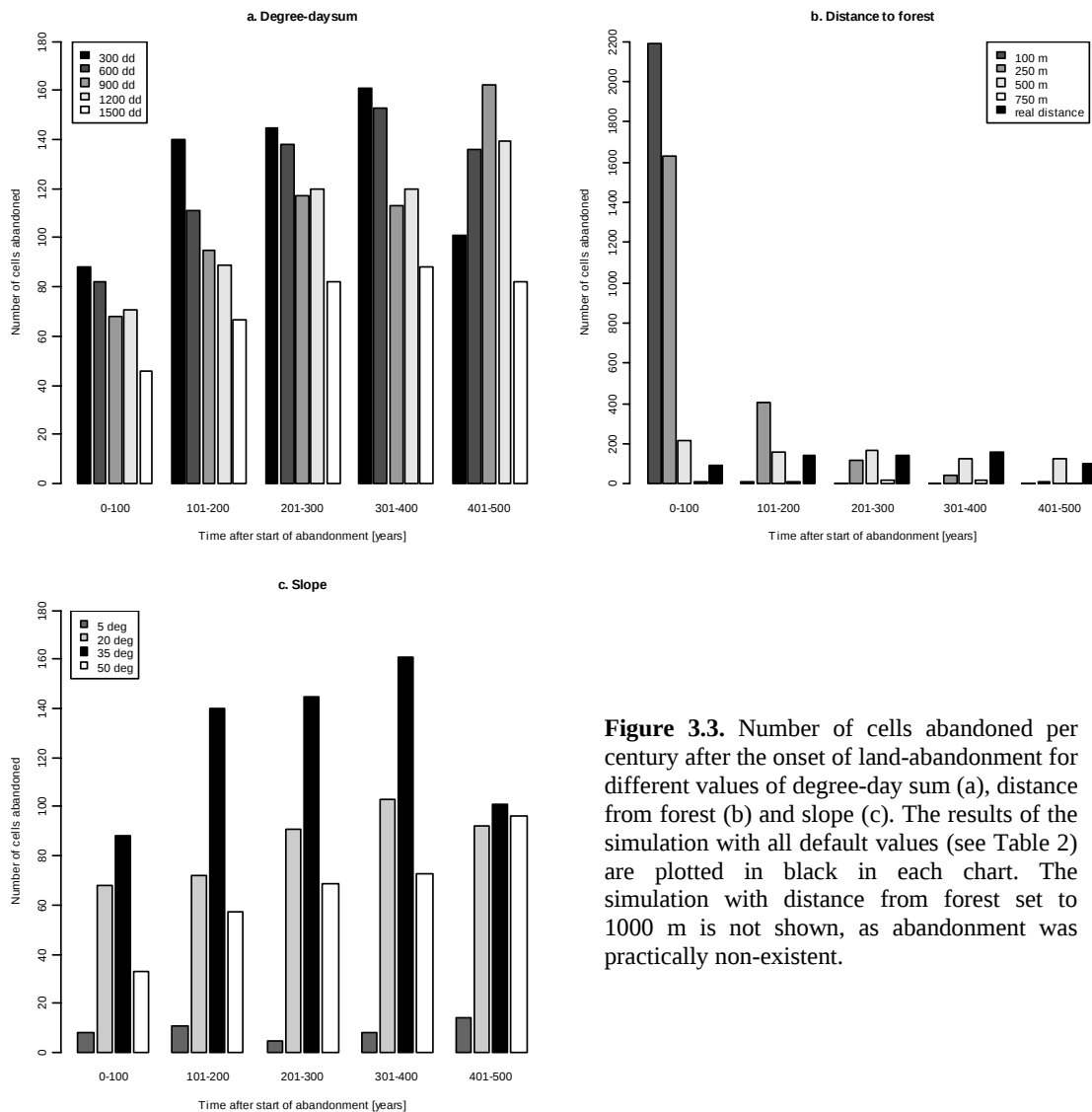


Figure 3.3. Number of cells abandoned per century after the onset of land-abandonment for different values of degree-day sum (a), distance from forest (b) and slope (c). The results of the simulation with all default values (see Table 2) are plotted in black in each chart. The simulation with distance from forest set to 1000 m is not shown, as abandonment was practically non-existent.

with a maximum for a slope value around 35 degrees.

Mapping the theoretical landscapes helps to illustrate some patterns which may appear in the land-abandonment process (Fig. 3.5). In the simulation with all default values for example, there appears to be a discrepancy between the large number of cells abandoned (161; Fig. 3.3) and the small advance (500 m; Fig. 3.4) between years 300 and 400. The map (Fig. 3.5) shows this to be a “filling-in” phase, where the patchy network of newly-abandoned land was becoming more homogenous.

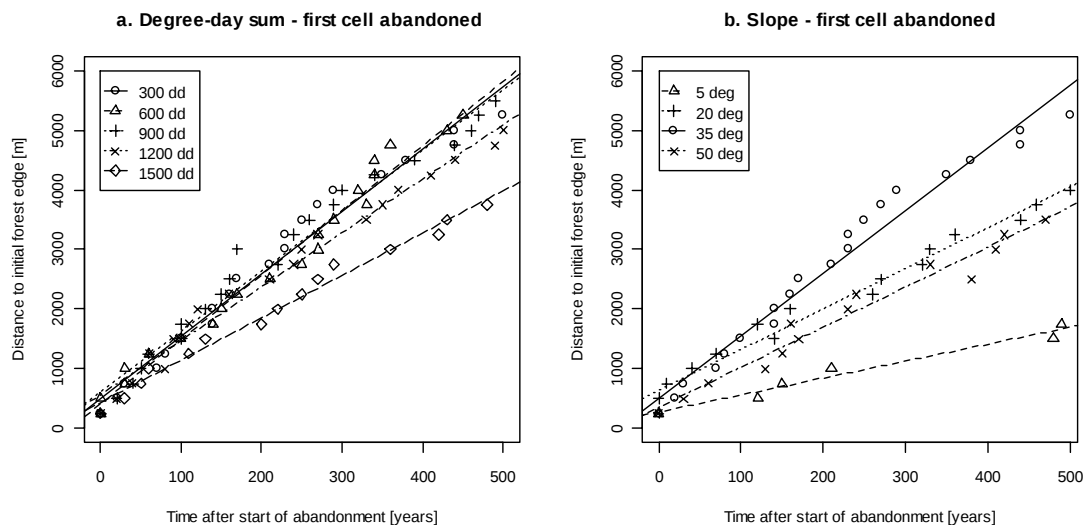


Figure 3.4. Advance rate: distance between each row and the initial forest edge versus time of first abandonment event in that row, for varying values of degree-day sum (a) and slope (b). The simulation using the default values is represented by circles, with a solid regression line (see Table 3.2 for default values).

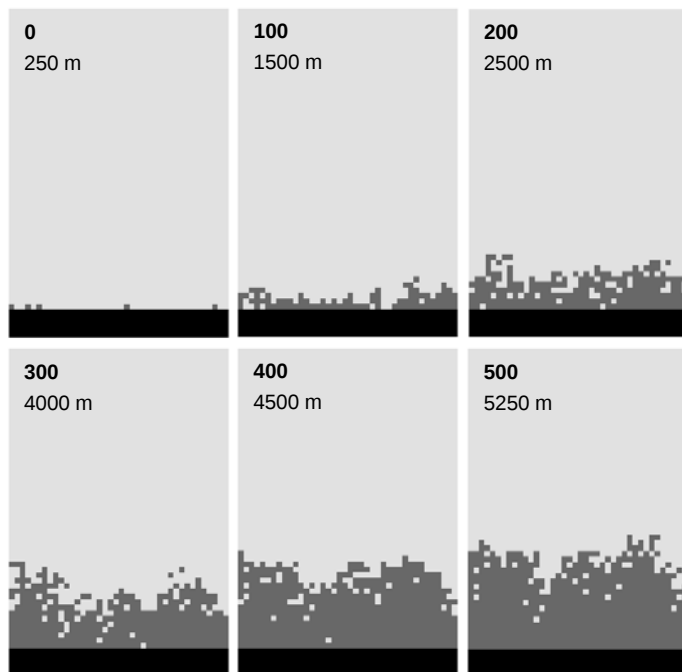


Figure 3.5. Progression of land-abandonment on the theoretical landscape with all variables set to default values (Table 3.2). The first time-step (year 0) shows land-abandonment in the first 10 years. The other time-steps each represent an additional 100-year interval (bold figures). The initial forest band is marked in black, agricultural land in pale grey and abandoned land in dark grey. The maximum distance (in metres) to the initial forest band is also indicated for each stage.

Engadine case study

The results of the simulations in a real landscape (Engadine, Switzerland), expressed as total tree biomass, show considerable differences between the three modelling approaches (Fig. 3.6). In the “natural succession only” approach (immediate and complete abandonment), most of the current grassland and agricultural land below the potential treeline turns into forest. Only high-altitude grid cells, where conditions are too unfavourable, remain unforested. The results of the “constant proportion” approach (equal probability of land-abandonment) are closer to the ones obtained using the new statistical model in terms of overall forest coverage. However, the distribution of the new forest cells in the former is random, so they are far more scattered than in the latter, where old forests tend to expand into neighbouring land. With the new model, the cells in the landscape do not have equal probabilities of being abandoned and this expansion is mainly due to the distance from the existing forest edge (DISTFOR variable).

The differences between the new model and the other two approaches can be illustrated by the number of cells abandoned (regardless of their suitability for subsequent forest growth) per altitudinal band in each case (Fig. 3.7). The natural succession approach simply reflects the number of “agriculture” grid cells available in each band. The new statistical model and “constant proportion” one yield similar total numbers of abandoned cells, but their altitudinal distribution is different: the latter is simply proportional to the number of cells available and has a similar distribution to the natural succession approach. Using the statistical model to predict abandonment produces a shift in the distribution towards lower altitudes. In the second century after the start of

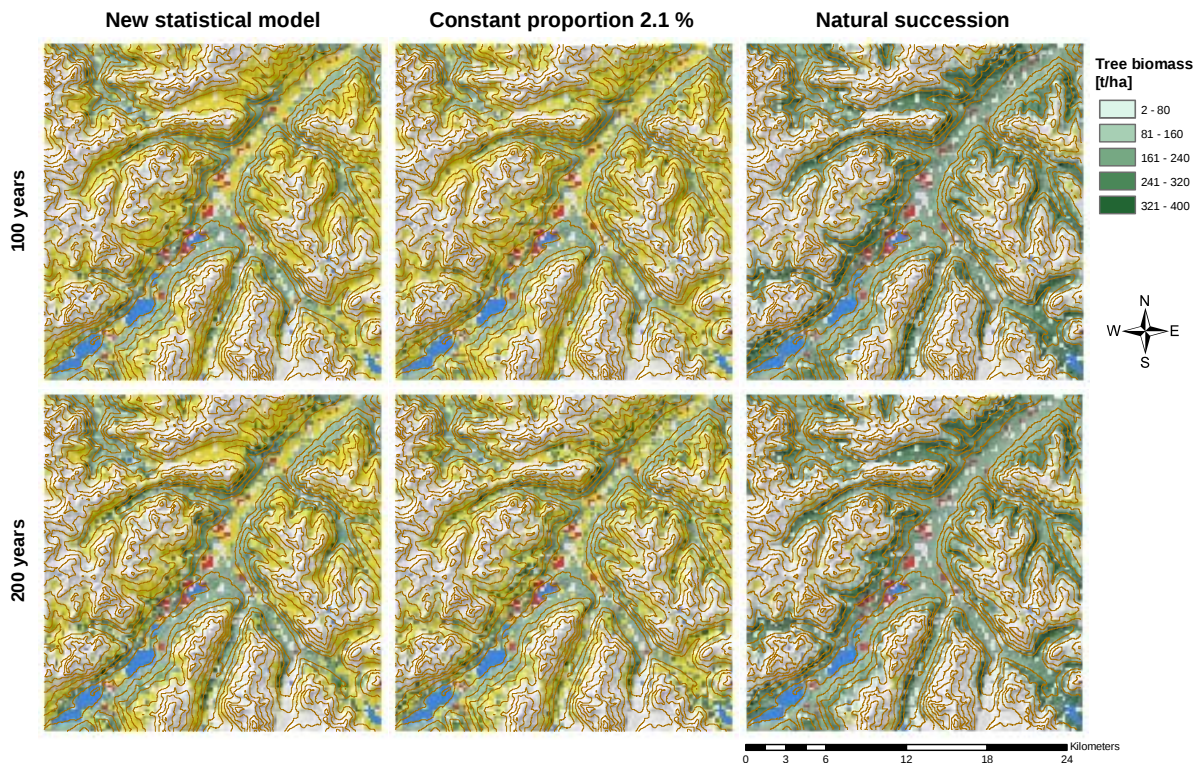


Figure 3.6. Results after 100 and 200 years of land-abandonment for three different modelling approaches: our new model, “constant proportion” (2.1 % per decade) and “natural succession only”. Forest areas are represented by different shades of green, according to biomass (with a cut-off level below 2 t/ha). Also shown are agriculture cells (yellow), water bodies (blue) and built-up areas (red).

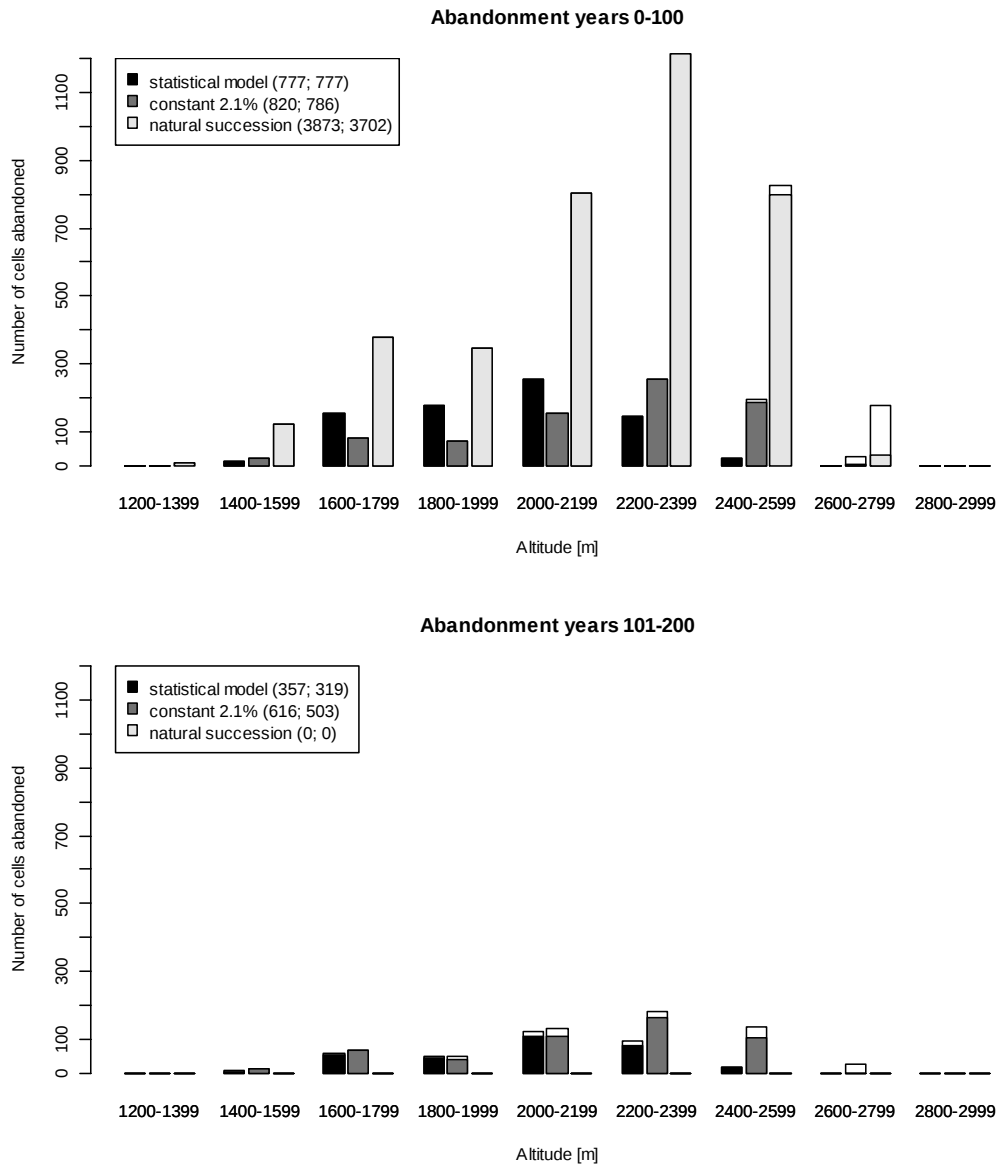


Figure 3.7. Number of abandoned and reforested cells, per 200-metre altitudinal band, in the first and second century after the onset of land-abandonment. The different shades of grey indicate the new “forest” cells (i.e. at least one tree in height class 1 and a minimum biomass of 2 t/ha) in the different modelling approaches, while white areas show abandoned cells without regeneration. None of the few cells above 2800 m are reforested. The non-forested cells below 2400 m (bottom figure) were all abandoned shortly before the end of the simulation, so trees did not have time to grow. The numbers in brackets in the legend indicate the respective sum totals of abandoned and reforested cells in each case.

land-abandonment, there are no cells left to be colonised by natural succession (Fig. 3.7). In both other cases the number of newly-abandoned cells drops, but more drastically in the case of the new statistical model. Below 2600 m, most of the abandoned cells eventually reach the models’ requirements for “forest” (2 t/ha biomass and at least 1 tree in height class 1), although this may take decades to over a century. Above that altitude, very few cells qualify as “forest”.

The differences in patterns of land-abandonment between the statistical and “constant proportion” models are shown by the area and distance from original forest edge of the newly-regenerated forest patches (aggregates of contiguous cells) (Fig. 3.8). One-sided

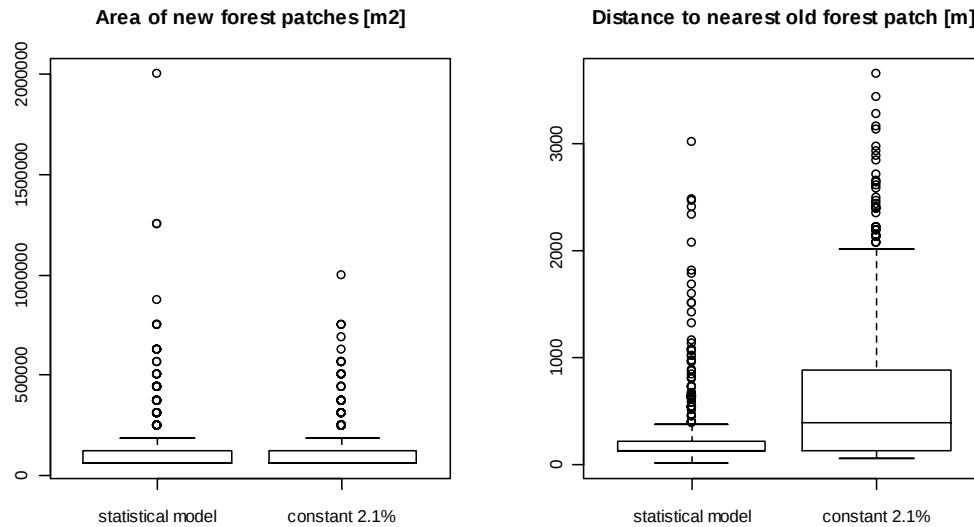


Figure 3.8. Area and distance from the edge of the nearest original forest patch for the new forest patches in the statistical model and constant proportion approaches. The average patch area is 140'657 m² for the new statistical model and 112'833 m² for the “constant proportion” approach. The average distance from forest is 265.8, respectively 630.3 m.

t-tests show that the average area of the patches from the statistical model approach is greater ($t = 3.255$ ***) and their average distance from the old forest smaller ($t = -12.36$ ***) .

Discussion

Statistical model

The statistical model for land-abandonment we developed for inclusion into TreeMig-LAb is very similar to that of Gellich *et al.* (2007), to whom we refer for further explanations as to the significance of the explanatory variables. The evaluation exercise shows that the new statistical model predicts significantly higher probabilities of abandonment for land where this had effectively occurred. However, the probabilities are low in both the absence and presence groups, as is shown by the low value of the optimised threshold for Kappa statistics. This can be explained by a number of factors, some of which are difficult to measure. First of all, the decision to continue to farm the land may not be motivated by economic factors alone, but force of habit, family circumstances or emotional attachment may also play a part. Secondly, the intrinsic quality of a parcel may weigh differently on the decision to abandon depending on the economic value of the rest of the farmer's land, as he is more likely to stop using the worst land he owns. There is no farm-level data (e.g. income, degree of mechanisation) in our model, as all the socio-economic variables were measured on the municipality level. Additionally, land-abandonment and subsequent forest regeneration show considerable random variation which is difficult to capture in a statistical model. Finally, it is important to bear in mind that the validation data only covers a 12-year period and land which was not abandoned despite a high predicted probability may well be abandoned during the next time-step.

The Kappa value is unreliable if one class dominates, as is the case here: there are far fewer points with abandonment than without. The “good agreement” it shows between

the model predictions and the validation data must therefore be taken as an indication only. However, the ROC plot and AUC value are good and give more confidence in the model, although the low pseudo- R^2 value shows that it probably only captures part of the reasons behind land-abandonment.

Theoretical landscapes

The results obtained by running the new statistical model in the TreeMig model environment under controlled conditions (theoretical landscapes) confirm the strong influence of distance from forest and slope on the probability of abandonment. Degree-day sum on the other hand does not show such a clear relationship between the response curve in the statistical model and the forest model output (number of abandoned cells, advance rate) for different levels of DDSUM. This can partly be explained by that variable's slightly lower significance in the statistical model. However, the main reason lies in the complex role of DDSUM in TreeMig-LAb: low values favour land-abandonment but hinder growth (Körner, 1998; Körner and Paulsen, 2004). Slower growth means that it takes longer for an abandoned grid cell to become "forest" and influence the abandonment probability of neighbouring cells. The positive direct effect of low degree-day sums on abandonment is therefore at least partly counterbalanced by a negative indirect effect. One could also expect interaction effects with distance from forest, which affects seed availability and therefore recruitment in the newly-abandoned plots. In that case however, the effects would be cumulative, as a smaller distance means a greater likelihood of abandonment and a faster establishment of forest, so the pattern would still follow the response curve. It must also be noted that distances from forest which allow abandonment to happen are well within the seed-dispersal ranges of the species in the model. At distances exceeding 1000 m, the abandonment probability drops to near zero.

The sudden drop in abandonment observed in the last century of the simulation (particularly when it was initially strong, as with the default setting) has two possible causes, which are not mutually exclusive. Firstly, the number of agriculture ("abandonable") cells left becomes smaller with time. Secondly, the "filling-in" process observed in the previous century has reduced the length of the forest edge, therefore there are fewer cells with a very small distance from forest, i.e. a high abandonment probability.

Engadine case study

All three modelling approaches show "forest" cells above the currently-observed tree-line (as defined by Körner and Paulsen, 2004), which is approximately 2300-2400 m in Engadine. Because the threshold set in the model is very low, "forest" must in this case be seen as representing all types of woody vegetation up to the tree species line (as defined by the same authors), as well as what is more commonly viewed as "forest". It is also possible that this threshold was slightly too low, as in some cases it was reached briefly but the "forest" did not persist, so it may require some fine-tuning. However, it did serve the purpose of differentiating between cells where tree growth was possible to some extent and those where conditions were too harsh.

The "natural succession" approach reflects the potential forest distribution in the absence of all human influence, apart from the built-up areas which we did not remove, but does not seem to be a realistic scenario of future human impact. Agriculture can be expected to continue diminishing and concentrating in the most favourable parts of the

landscape, following current trends, but it is unlikely to disappear altogether and immediately.

The “constant proportion” and statistical model approaches both yield similar proportions of forest and agricultural land. However, the former sees the new forest cells randomly distributed throughout the landscape, whereas in the latter they are mostly constrained to the proximity of forest patches (expansion of the forest front and filling-in of gaps) and often form clumps of several forest cells. This pattern is, of course, partly due to the spatial distribution of values for the variables in the statistical model. However, the clumping observed is also due to the positive feed-back process between the different parts of the forest model, which modifies DISTFOR. This reflects the fact that abandonment affects remaining agriculture by making adjacent plots harder to manage (MacDonald *et al.*, 2000) and therefore an individual’s land-use decision is affected by the decisions of those around him (Irwin and Geoghegan, 2001). It has been shown that feed-back processes, such as sheltering by upwind trees, are important in pattern formation at tree-line (Alftine and Malanson, 2004) and our results show that this is also the case with processes pertaining to human activities. The patterns resulting from simulations with TreeMig-LAb, namely homogenisation of forest areas (and the landscape in general) and reduction in length of forest edges, are consistent with current observations in Engadine and generally in the Swiss Alps (Schöne and Schweingruber, 2001; Graf Pannatier, 2005). These consequences of land-abandonment result in loss of biodiversity in the long term (though there may be an increase in the medium term), loss of cultural landscapes and reduction of landscape attractiveness for tourism (MacDonald *et al.*, 2000; Graf Pannatier, 2005; Höchtl *et al.*, 2005).

TreeMig-LAb does not require much more computing time than TreeMig, partly because most of the variables in the land-abandonment part can be pre-processed, except for distance from forest, which is important for feed-back from the forest dynamics part of the model, and degree-day sum, which is essential in case a climate change scenario is used. However, the fact that the abandonment sub-model is implemented to operate in decadal, rather than annual, time steps is the most important factor which contributes to speeding up the simulation process. This means it would be possible to develop the land-abandonment module further and include scenarios for one or more variables in the statistical model without too much additional computation time. Using the same method as for the climate change scenarios, the contribution to the model of all variables except DDSUM and DISTFOR could be calculated in advance for various key time-points and the values for each decade interpolated between the time-points on either side. This would improve the socio-economic aspect of the model, as the “business as usual” scenario, currently the only option available, is not realistic for simulations over several centuries. However, a more detailed socio-economic analysis would be necessary to produce likely scenarios.

Because running the same socio-economic scenario for more than a few decades is unrealistic, the results from the case study, especially those after 200 years, should not be taken as predictions for the future. It was nevertheless useful to run the simulations for that length of time to visualise the patterns emerging from the different modelling approaches. The TreeMig-LAb results show patterns consistent with current observations of land-abandonment, so we can be confident that simulations, over the next few decades, with this model will give a more realistic image of possible forest expansion than would be obtained without the addition of the land-abandonment module.

Conclusions

The addition of a land-abandonment module to TreeMig, resulting in the new model TreeMig-LAb, has enabled us to add a human dimension, which cannot be ignored in densely-populated countries like Switzerland, to dynamic landscape simulations of forests. It gives more realistic results than a purely natural succession-driven approach or even a simple stochastic process (constant proportion). Although the statistical model is still based on landscape units (which make it compatible with the forest model) rather than individual decision-makers, it is nevertheless based on economic theory, thus answering some of the criticisms about attempts to mix ecology and economics in landscape models (Bockstael, 1996; Irwin and Geoghegan, 2001). The resulting model can now be used to investigate the combined effects of human activity and climate change in the coming decades.

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4. Climate change effects and interactions with human land use at the Alpine and northern European tree-lines

To be submitted to Global Change Biology

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Abstract

Both altitudinal and latitudinal tree-lines are sensitive ecotones which are expected to react strongly to climate change. In Europe, human activity has also been shaping tree-lines for centuries, though these impacts have undergone changes in recent decades. Using the spatially-explicit forest dynamics model TreeMig-LAb, which has been calibrated for the Alpine and northern European tree-lines and includes a module for land-abandonment in the Alps, we studied the impacts of four climate change scenarios in two case study areas, in the Swiss Alps and Finnish Lapland. The first scenario was a base-line “no change” scenario, while the other three contained different levels of temperature change (+1.3, +3.5 and +5.6 °C) for the 21st century, based on estimations by the IPCC and HadCM3.

Our results showed an upwards shift of the distributions of the main tree-line species by approximately 200 m with the most moderate climate change scenario (+1.3 °C). In both cases where the change was more abrupt, this resulted in drastic decreases in biomass for some species and even led to the disappearance of *Pinus cembra* in the Alpine case study area. In the boreal case study area, species distributions shifted both in altitude and latitude, though the extent of the latter was not measurable, as migration extended to zones outside the simulated area. Human impacts on the Fennoscandian tree-line were also a source of uncertainty, as they are not currently implemented in the model. However, we concluded that under current estimates of climate change for this century both the Alpine and Fennoscandian tree-lines will suffer radical disruptions, which may take centuries to stabilise and may lead to the loss of some tree species.

Keywords: land-abandonment, TreeMig-LAb, Switzerland, Finland

Introduction

The latitudinal and altitudinal tree-lines share many features, but differ through a few important characteristics. Both are essentially cold-limited ecotones (Körner, 1998; Jobbágy and Jackson, 2000; Körner and Paulsen, 2004), though the boreal (latitudinal) tree-line may also be affected by other environmental factors such as wind exposure (Esper and Schweingruber, 2004; Gamache and Payette, 2005). These two types of tree-lines within a given ecoregion may also have some tree species in common. For instance, *Picea abies* (Norway spruce) can be found at both altitudinal (Alps) and latitudinal (Fennoscandia) tree-lines in the European Palaeartic region. However, the main difference between these two ecotones lies in the distances which they cover. Air temperature decreases by approximately 0.6 °C per 100 m altitude difference (e.g. Lacoste and Salanon, 1969; Theurillat and Guisan, 2001), but on a latitudinal gradient

the same temperature difference is equivalent to a polewards distance of around 55 km. Vegetation belts are therefore far more spread out in boreal zones, which increases the migration distance for species in the event of climate change. On the other hand, although distance may not be a problem, migration in response to climate change at the altitudinal tree-line will be impossible if that change is very large, especially on lower mountains which have no areas available for colonisation above the current tree-line (Theurillat and Guisan, 2001). At the boreal tree-line, day lengths vary greatly throughout the year, which results in a short but intense growing season. Additionally, sun angles are low so the amount of radiation received is smaller. Nevertheless, the altitudinal and latitudinal tree-line ecotones do share one other common characteristic: they are both sensitive systems which are likely to be strongly affected by climate change, resulting in migration upwards or polewards (Dullinger *et al.*, 2004), and are classified amongst the systems at risk (IPCC, 2001b).

Forests, whether at tree-line or otherwise, are not only affected by climate, but more generally by global change, including human activities. On a global scale, anthropogenic forcing due to greenhouse gas emissions adds to natural forcing (volcanic and solar) to produce climate change (IPCC, 2001a). Various models have been used to estimate future climate change, such as HadCM3 (Gordon *et al.*, 2000; Pope *et al.*, 2000), which gives an average increase of +3.5 °C between 2000 and 2100 AD for the northern hemisphere. The estimates produced by the Intergovernmental Panel on Climate Change (IPCC, 2001a) take into account the SRES emission scenarios (IPCC, 2000), which reflect the effect of different policies on greenhouse gas emissions and climate, and include results from several climate models. The SRES scenarios are grouped into 4 main families, labelled A1, A2, B1 and B2, where A or B denotes economic versus environmental concerns and 1 or 2 indicates global versus regional development patterns. The estimates for temperature change vary between +1.4 and +5.8 °C for the 1990 to 2100 AD period, depending on the emission scenarios and climate models used.

Locally, human activities can have a strong impact on the shape, position and species composition of tree-line forests. In the Alps for example, activities like pasturing or forestry have been taking place for centuries, often resulting in a depressed tree-line (Motta and Nola, 2001; Theurillat and Guisan, 2001; Holtmeier and Broll, 2005). However, this has changed drastically in recent decades, with a strong trend towards rural depopulation and abandonment of land where cultivation conditions are unfavourable (Baldock, 1996; MacDonald *et al.*, 2000; DLG, 2005). Boreal tree-line forests in Fennoscandia are also influenced by humans, through forestry or grazing of semi-domesticated reindeer (Suominen and Olofsson, 2000; Cairns and Moen, 2004), though as this region is far less densely-populated than the Alps, the main influences remain climate and natural disturbances, such as fires, insects or wind throw.

Dynamic forest models are a useful tool for studying the effects of climate change on forest composition and structure (Loehle and LeBlanc, 1996). Many models have been developed for that purpose (e.g. Prentice *et al.*, 1993; Bugmann, 1994, 1996) and were applied to local scales. However, one of the main consequences of climate change is its effect on the spatial distribution of species, the simulation of which requires spatially-explicit models (e.g. He *et al.*, 1999; Dullinger *et al.*, 2004). The spatially-explicit dynamic forest model TreeMig (Lischke, 2005; Lischke *et al.*, 2006) is particularly well suited to simulating tree migration under changing climate, because its process rates depend explicitly on climate and it includes a specific seed production and dispersal module. It has been adapted for simulations of Alpine and Fennoscandian tree-line

forests through calibration of the existing species parameters, particularly those pertaining to cold limitations, and the addition of *Betula pubescens* to the boreal species' list (Rickebusch *et al.*, submitted-a). A variant named TreeMig-LAb (Chapter 3 and Rickebusch *et al.*, submitted-b) also includes a module for simulating land-abandonment in the Swiss Alps, following the statistical model developed by Gellrich and co-workers (Gellrich *et al.*, 2007; Gellrich and Zimmermann, 2007). The land-abandonment module receives positive feedback from the reforestation process, as abandonment probability is higher along forest edges. Simulations under current climate show that land use significantly slows down the reforestation of higher altitudes, compared to simulations where all non-forested land is available for forest colonisation (Rickebusch *et al.*, submitted-b). It is therefore not obvious what the outcome might be when climate change interacts with land-use change.

The goal of this study was to compare, by means of the TreeMig-LAb model, the effects of various climate change scenarios on the location and species composition of two European tree-line ecotones, one altitudinal and latitudinal (Fennoscandia) and the other altitudinal (Alps). For the latter, interactions with human impacts in the form of land-abandonment were included.

Materials and methods

Forest dynamics were simulated with the TreeMig-LAb model (Chapter 3 and Rickebusch *et al.*, submitted-b) in two case study areas, using four climate change scenarios, three with different levels of temperature increase over the next century and one without change. The case studies were located in the Engadine valley (Swiss Alps) for the altitudinal tree-line and in the Lake Inari region (Finnish Lapland) for the latitudinal tree-line. The basic simulation set-up was: 300 years of spin-up time to initiate the “present time” forest, 100 years of climate change and 300 years of stabilisation with the new climate (Fig. 4.1). This is similar to the set-up described by Prentice *et al.* (1993).

Climate change scenarios

The input climate data for the model came from maps of temperature and precipitation for 1961-1998 (Switzerland) and 1973-2003 AD (Fennoscandia). These maps were generated from climate station records of daily meteorological measurements and digital elevation models, using the DAYMET climate surface mapping environment (Thornton *et al.*, 1997; Thornton and Running, 1999; Thornton *et al.*, 2000). They were then processed for input into TreeMig-LAb as described in Chapter 2 (Rickebusch *et al.*, submitted-a).

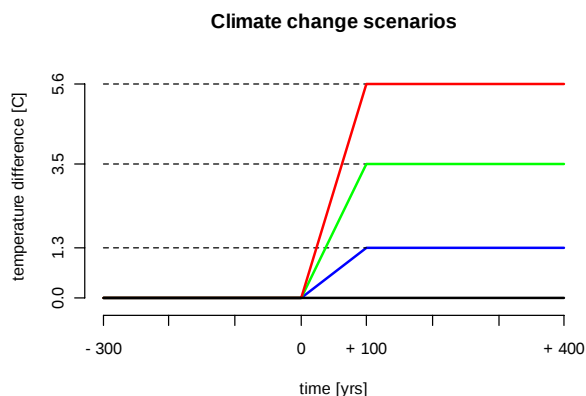


Figure 4.1. Four climate change scenarios used in the simulations: no change (black), + 1.3 °C in 100 years (blue), + 3.5 °C (green) and + 5.6 °C (red). The simulations were run over a total of 700 years, divided into 300 years of spin-up, 100 years of climate change and 300 years of stabilisation with the new climate.

Four scenarios of surface air temperature change over 100 years were derived from the minimum and maximum IPCC (IPCC, 2001a) estimates and an intermediate value provided by the HadCM3 model (Gordon *et al.*, 2000; Pope *et al.*, 2000), the first scenario being “no change” (Table 4.1, Fig. 4.1). The IPCC values, which originally covered the 1990 to 2100 period, had to be adapted because our base-line climate data included the 1990s and we wanted to set the “present time” at 2000 AD. This was done by subtracting the minimum and maximum predicted temperature changes by the year 2000, respectively +0.1 and +0.2 °C, from the original IPCC extrema. The minimum IPCC value for 2000-2100 is therefore +1.3 °C (emission scenario B1) and the maximum +5.6 °C (emission scenario A1FI).

Table 4.1. Climate change scenarios. The temperature difference values are for the 2000 (“present time”) to 2100 AD period and were adapted when the original source had a different time frame.

Scenario	ΔT [°C]	Source
1	+0.0	-
2	+1.3	Adapted IPCC minimum value (+1.4 °C for 1990-2100 AD)
3	+3.5	HadCm3, northern hemisphere
4	+5.6	Adapted IPCC maximum value (+5.8 °C for 1990-2100 AD)

The temperature change was interpolated linearly between the beginning and end time points and evenly distributed throughout the year. Precipitation was assumed to remain at current levels. This is a simplification, as temperature changes can be expected to vary seasonally and precipitation regimes may also be affected. However, similar set-ups have been used by other authors (e.g. He *et al.*, 2002) and make sense when climate change scenarios are based on global trends, as is the case here.

Alpine case study - model setup

The case study area for the altitudinal tree-line was situated in the Upper Engadine valley of the Swiss Alps (Fig. 4.2). It consists in a grid of 100 x 100 cells of 250 m resolution. Altitudes range from 1370 to 3720 m, with cells currently occupied by “forest” present up to 2550 m. This may seem high, but “forest” must be understood here to include all woody vegetation, such as shrubs and stunted growth forms of tree species. The “forest” therefore extends to the tree species line, as defined by Körner and Paulsen (2004). The valley bottom contains several small lakes, built-up areas (e.g. St Moritz) and cultivated land. Above the tree-line, the land labelled as “agriculture” consists of mountain pastures and (semi-)natural grasslands, which may also be used for pasturing. The mountain-tops are unsuitable for vegetation growth, as they are covered in bare rock, snow and ice, which is reflected in the model by a null “stockability” value. The main tree-line species in that region are: *Picea abies* (Norway spruce), *Larix decidua* (European larch) and *Pinus cembra* (Swiss stone pine).

The “bucket size” (difference between the field water holding capacity and the permanent wilting point) data used to process the climate data was derived from the Swiss soil suitability map (SFSO, 1992). The different land-use categories were aggregated from the Swiss Area Statistics (SFSO, 2001). All 30 tree species in the original TreeMig model (Lischke *et al.*, 2006) were included, with the new parameters defined in Chapter 2 (Rickebusch *et al.*, submitted-a) for the three tree-line species.

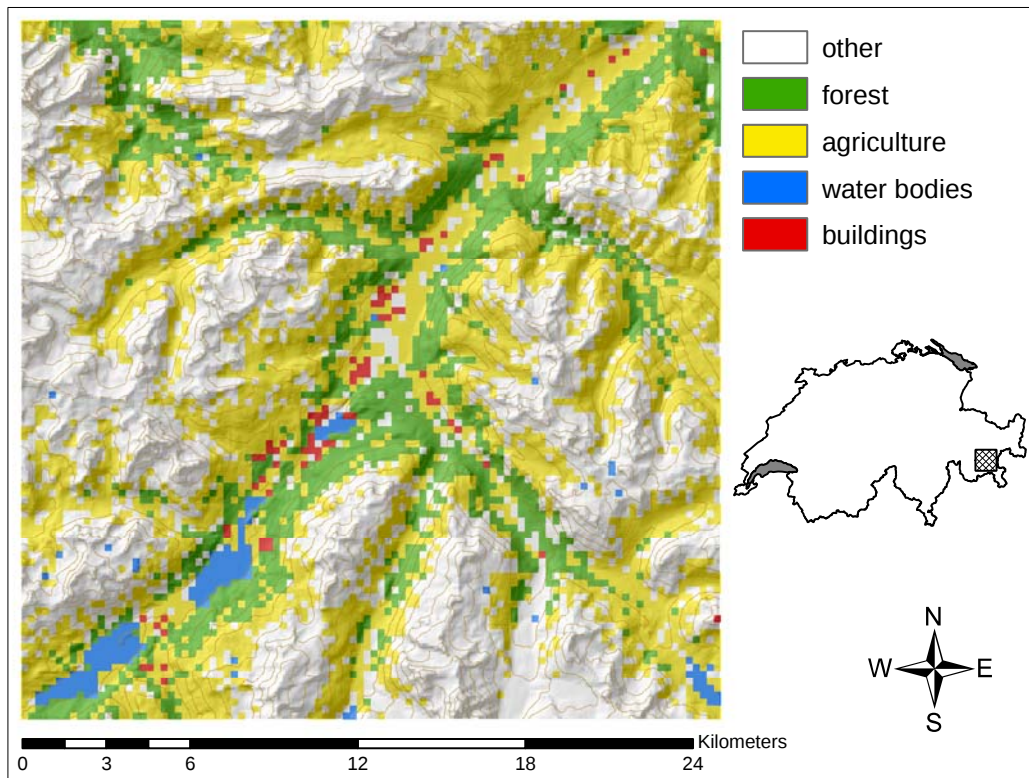


Figure 4.2. Map of the Engadine (Switzerland) case study area showing the three land-use categories used in TreeMig: “forest”, “agriculture” and “other”. “Agriculture” includes semi- to natural grasslands, which may or may not be used for pasturing. In the “other” category, water bodies and built-up areas have been highlighted.

In addition to the climate change scenarios described above, the simulations in the Engadine included the joint effects of land-abandonment. Trees were only allowed to colonise new cells if these were former “agricultural” land which had been abandoned. Land-abandonment followed the model for the Swiss Alps implemented in TreeMig-LAb and a continuation of the current trend (“business as usual”) was assumed. Details of the land-abandonment model can be found in Chapter 3.

Boreal case study - model setup

The case study area for the latitudinal tree-line was situated in the Lake Inari region of Finnish Lapland (Fig. 4.3). It consists in a grid of 82 x 172 cells of 600 m resolution. Altitudes range from 110 to 710 m, with cells currently occupied by “forest” present up to 480 m. The definition of forest is similar to the one used for the Engadine area. The northern end of the study area is partly occupied by the southern reaches of Lake Inari. The main built-up area is the village of Ivalo. The hill-tops are occupied by grasslands, which could potentially be colonised by trees in the event of climate change. The “other” areas (“non-stockable” in the model) at the southern end of the simulation area are mostly peat bogs. The main tree-line species are: *Picea abies* (Norway spruce), *Pinus sylvestris* (Scots pine) and *Betula pubescens* (Downy birch).

The bucket size was derived from the Soil map of Northern Finland 1:400 000 raster provided by the Geological Survey of Finland. The different land-use categories were aggregated from the CORINE Land Cover database, at 100 m grid cell resolution, supplied by Eurostat-GISCO. The tree species list was modified slightly compared to

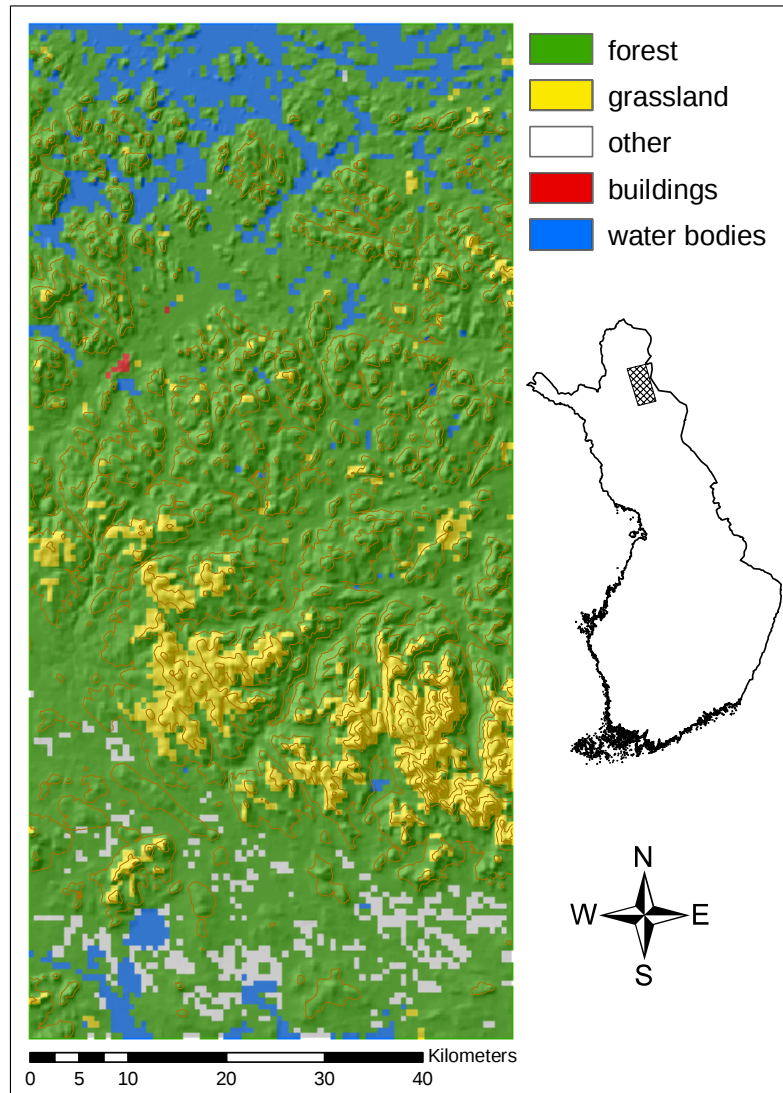


Figure 4.3. Map of the Inari (Finland) case study area showing the three land-use categories used in TreeMig: “forest”, “grassland” and “other”. “Grassland” has been used instead of “agriculture” to indicate areas which could potentially become forest, as there is no agricultural land in that region. In the “other” category, water bodies and built-up areas have been highlighted.

the Alpine simulation. *Larix decidua*, *Pinus cembra* and *Pinus montana* were removed, as they do not occur naturally that area. *Betula pubescens* was added, with the parameters described in Appendix II.

Land-abandonment is not an issue in this area and the module in TreeMig-LAb would not have been suitable anyway, as it was developed for the Swiss Alps. It was therefore switched off for this set of simulations. Instead, trees were allowed to migrate into the grasslands from the onset of climate change (present time), to simulate natural succession driven by new climate conditions.

Results

Alpine case study

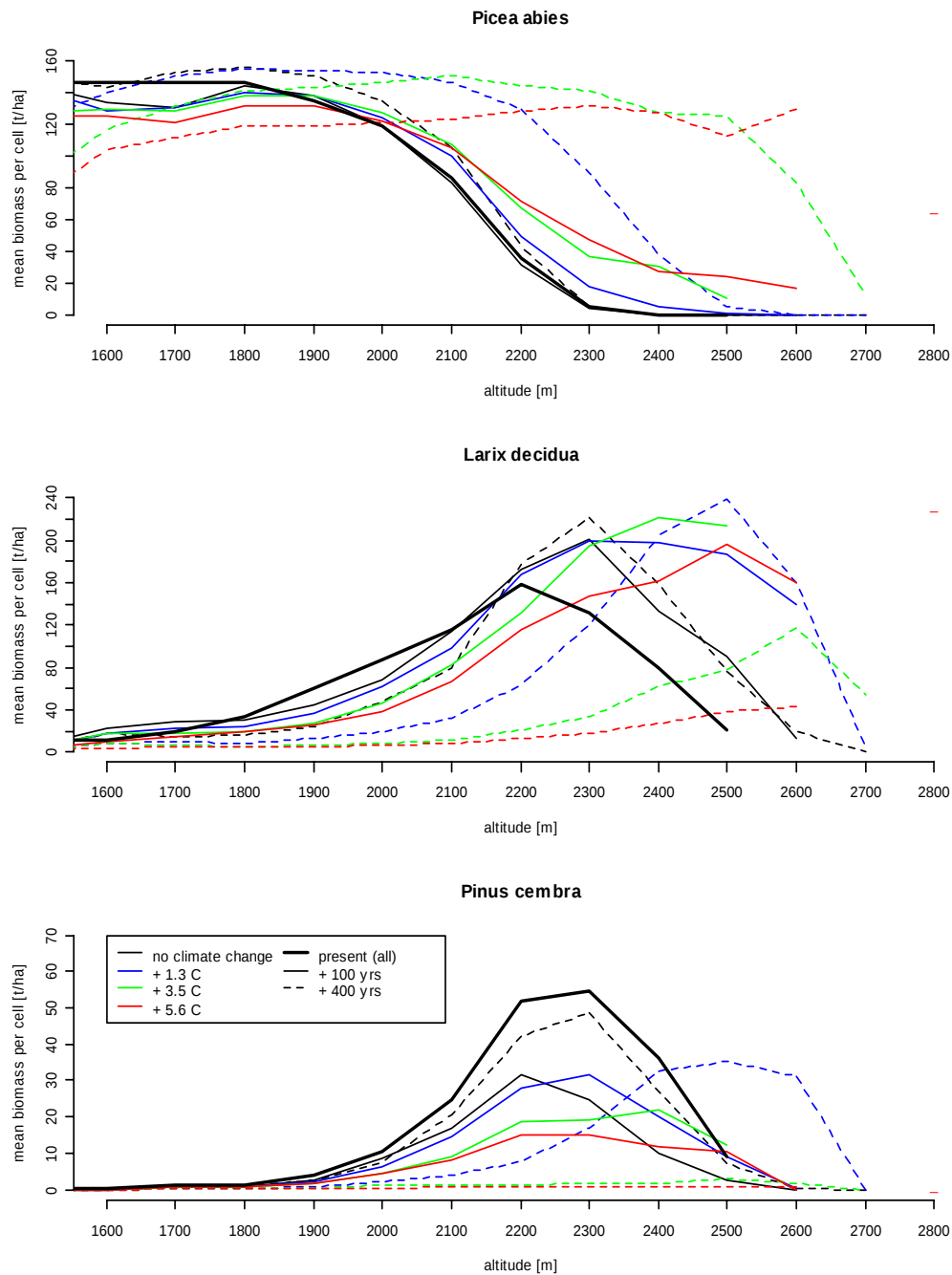


Figure 4.4. Engadine (Switzerland) case study: mean biomass per grid cell in each 100-m altitudinal band for the three main tree-line species. The present-time values (bold) are the means for all four scenarios, which have similar values. The biomasses after 100 (end of climate change; solid) and 400 years (end of simulation; dashed) are shown, with different colours for the climate change scenarios (see Fig. 4.1). The red dash represents a single cell in the 2800-m band at the end of the simulation with the + 5.6 °C scenario (no cells at 2700 m). Only bands above 1600 m are shown, although the forests in the study area do extend to lower altitudes, as the focus here is on tree-line.

The biomass per grid cell and altitudinal band (100 m) for the three Alpine tree-line species shows a tree-line rise of up to 100 m after 100 years (end of climate change) and 200-300 m after 400 years (Fig. 4.4). Under current climate conditions (“no change”), the altitudinal distribution and biomass of *Picea abies* do not vary much with time, while *Larix decidua* and *Pinus cembra* show a slight upwards shift and variations in biomass in response to the sudden availability of newly-abandoned land.

Spruce distribution reacts slowly to climate change. The biomass values after 100 years are similar to the present ones, save for a slight increase in the highest bands. However, after 400 years the distribution has settled 200 m higher with the moderate scenario (+1.3 °C) and 400 m higher with the intermediate one (+3.5 °C). In the most extreme case, *P. abies* is present in large quantities up to the highest altitude, though the single grid cell in the 2800 m band shows a slightly lower value. The absence of data at 2700 m for the +5.6 °C scenario is due to stochasticity in the land-abandonment module: no cells happened to be abandoned in that band during the course of that simulation. At lower altitudes, the biomass per cell decreases. This decrease is larger but more gradual with more extreme climate change scenarios.

Larch reacts quickly to climate change and the biomass distribution after 100 years shows an upwards shift and an increase in biomass above 2200 m for all three levels of climate change. After 400 years, that species’ distribution has settled 200 m higher up, similarly to what is observed for *P. abies*. With 3.5 and 5.6 °C increases in temperature, *Larix* declines everywhere except at the very highest altitude.

The average biomass per cell of Swiss stone pine decreases to about half the initial quantity within the first 100 years in all four cases. After 400 years however, the distribution is again similar to the current one when no climate change is involved. As for the other two species, a moderate increase in temperature results in a 200-m upwards shift of the species’ distribution. However, in both cases where the temperature change is more severe, *Pinus cembra* disappears from the study area.

Boreal case study

When no climate change occurs but trees are allowed to migrate into the hill-top grasslands (Fig. 4.5), *Betula pubescens* moves upwards with an increase in biomass, *Pinus sylvestris* follows but in relatively low quantities and *Picea abies* sees its biomass increase without any marked upwards movement. These changes occur after 400 years and only Birch shows any strong difference after 100 years.

Spruce biomass does not change much for the first 100 years whatever the climate change scenario. However, after the stabilisation period there is an increase in biomass and an upwards shift of 50-100 m for the two lowest temperature change scenarios. This is accompanied by a sharp decrease in biomass in the lowest altitudinal band, in comparison with the outcome of the “no change” scenario. When the most severe climate change scenario is applied, *P. abies* biomass decreases drastically.

The biomass and altitudinal distribution of Scots pine does not vary much between the different scenarios after 100 years: all show a slight increase in biomass and an upwards shift of the distribution. After 400 years, the +1.3 °C scenario shows an upwards shift of around 200 m. With higher levels of temperature change, the upwards shift of *P. sylvestris* is stronger, but biomasses are lower than with the more moderate scenario, except in the lowermost altitudinal band.

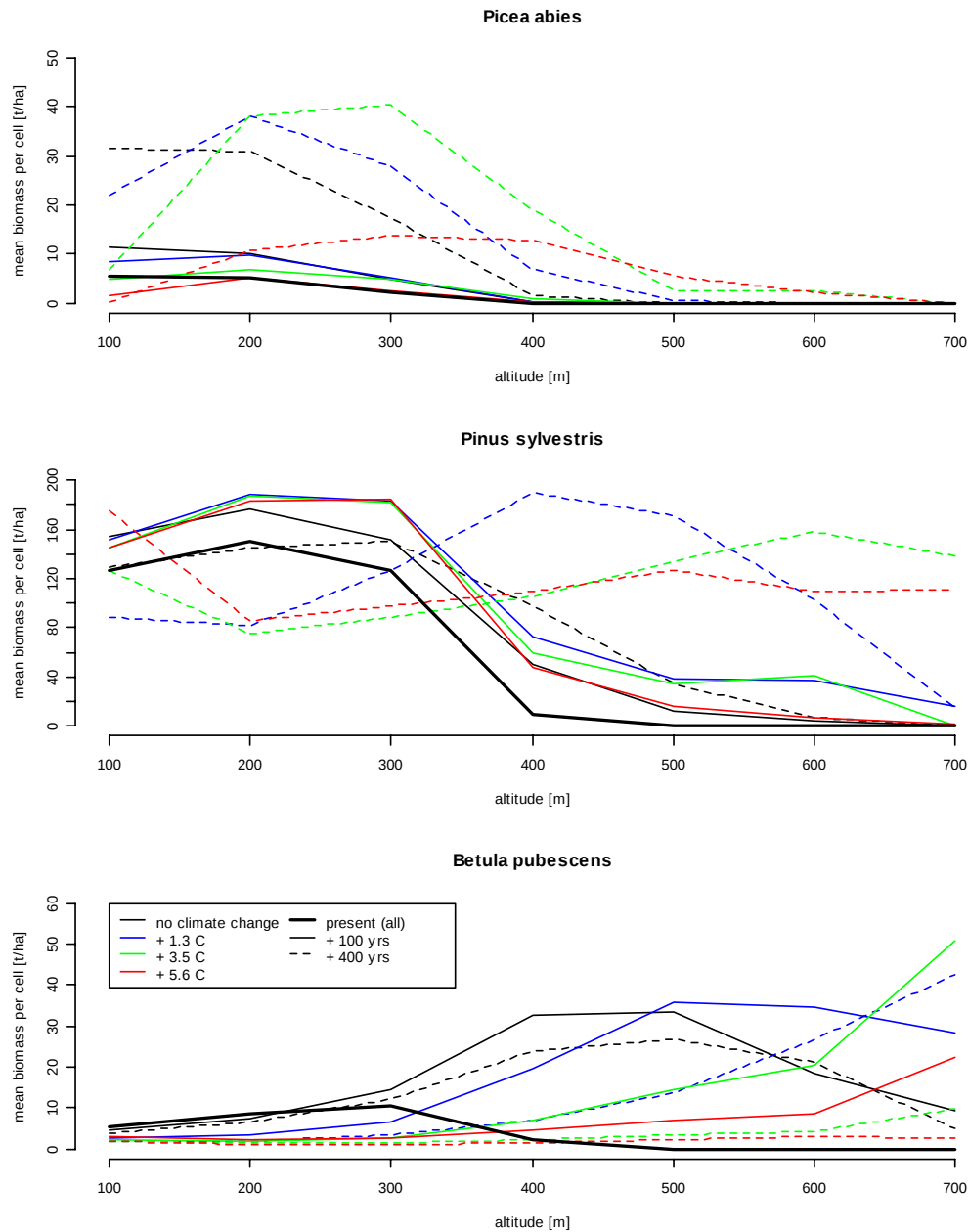


Figure 4.5. Inari (Finland) case study: mean biomass per grid cell in each 100-m altitudinal band for the three main tree-line species. The present-time values (bold) are the means for all four scenarios, which have similar values. The biomasses after 100 (end of climate change; solid) and 400 years (end of simulation; dashed) are shown, with different colours for the climate change scenarios (see Fig. 4.1).

Downy birch shows different reactions to the degree of temperature change already after 100 years. For moderate climate change, there is an initial shift of 100 m, which continues to increase during the stabilisation period, so that the species is mostly present on the hill-tops. With the 3.5 and 5.6 °C temperature increase scenarios, there is a strong and rapid upwards migration during the first 100 years, followed by a decrease in biomass to very low levels, though the species remains present at both ends of the altitudinal range.

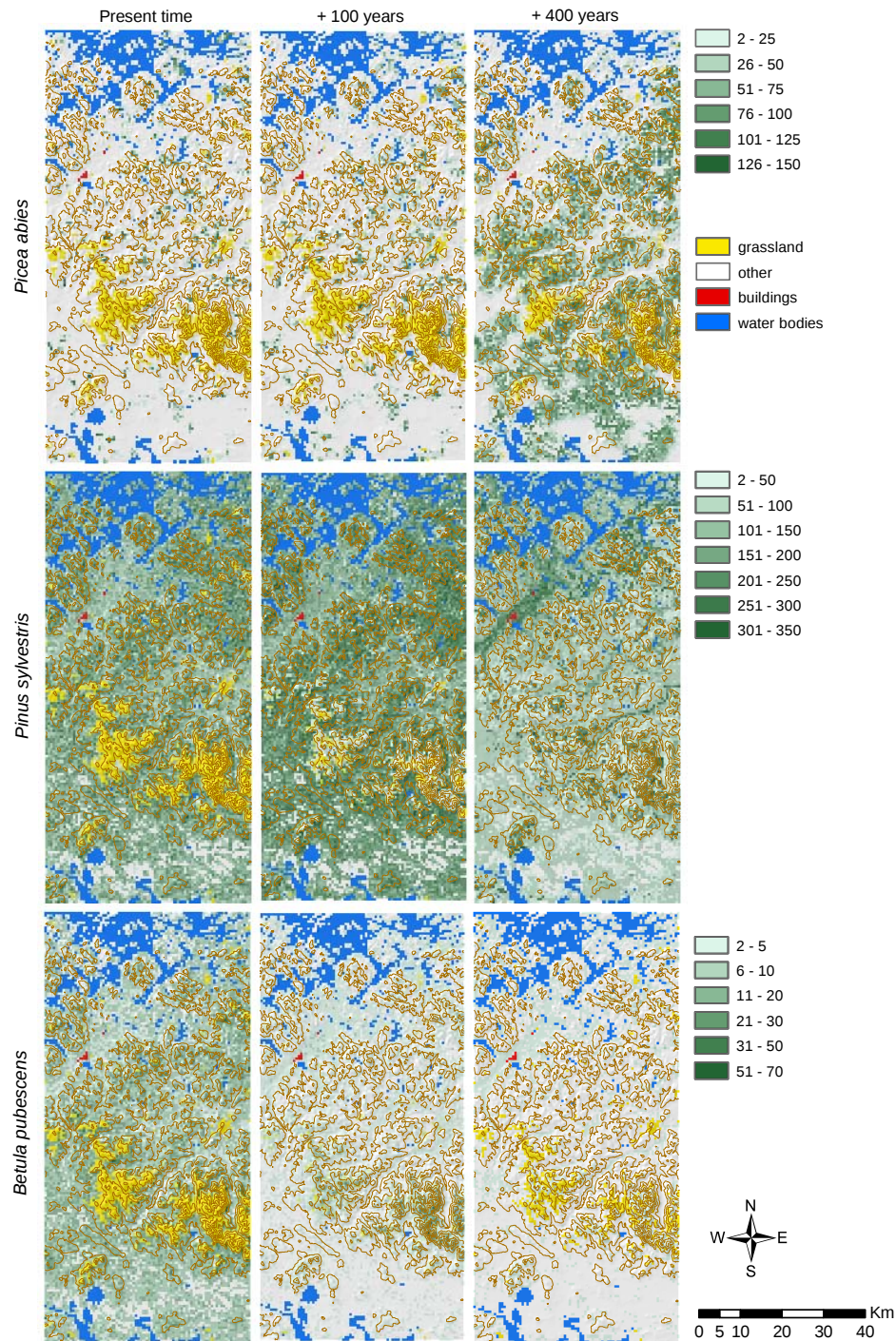


Figure 4.6. Inari (Finland) case study: biomass of three tree-line species at present time and after 100 and 400 years, under the intermediate climate change scenario (+ 3.5 °C in 100 years). The “grasslands” represent the current land-use category and their presence after 100 or 400 years only shows that they are not colonised by the species in question. For example, the hill-tops appear as grasslands in the 400-year Spruce map, but are in fact mostly occupied by Pine, with a little Birch.

Because of the combined effects of altitude and latitude at the boreal tree-line, it is helpful to visualise the spatial distribution of these three species (Fig. 4.6). We chose here the intermediate climate change scenario (+3.5 °C). The time steps are the same as

in the plots showing the altitudinal biomass distribution. *P. abies*, which currently has a very patchy distribution, increases in biomass and migrates to higher ground. This response takes time and there is no visible alteration immediately after the climate change period (100 years). However, within the 300 years following the end of the climate change period, that species spreads considerably in space and occupies new areas. For *Pinus sylvestris*, the initial upwards shift and general increase in biomass is also visible on the 100-year map. However, after 400 years it is apparent that the species only maintains high biomass levels on the summit of hills and at the northern end of the study area. Finally, *B. pubescens* rapidly migrates upwards and polewards, but after 400 years it is only found in small quantities in the northernmost reaches of the map and on the highest mountain tops. The yellow coloration on the map indicates that the species is no longer present in all former grasslands, as was the case after 100 years. Instead, it has been replaced by *Pinus sylvestris*, as shown by the map for that species.

Discussion

Alpine case study

The lagged response of spruce to climate change can be explained by the continued presence of and Swiss stone pine at higher altitudes. Instantaneous die-back following climate change is unlikely (Loehle and LeBlanc, 1996) and existing trees may be expected to survive for most of their natural life-span. After stabilisation (400 years), the distribution of *P. abies* is primarily constrained by a lack of land which can be colonised when the most extreme climate change scenario is applied. The decrease in biomass observed at lower altitudes is due to displacement by lowland species, such as *Fagus sylvatica* and *Populus tremula*, which are also migrating upwards.

Because larch is a pioneer species with a rapid growth rate in its early years (Motta and Nola, 2001; Dullinger *et al.*, 2005; Tinner and Kaltenrieder, 2005), it reacts quickly to changes in climate and land use by colonising new cells. *Larix* is constrained in its response to climate change by competition with the advancing spruce and the lack of available land into which to retreat above the current tree-line with both the +3.5 and +5.6 scenarios, especially the latter which causes a severe decrease in that species' biomass. These effects of temperature could be increased if these temperature changes resulted in more frequent or severe larch bud moth (*Zeiraphera diniana*) attacks.

The decrease in biomass of Swiss stone pine after 100 years of climate and land-use change, whatever the scenario, may seem surprising. Natural succession cycles could partly explain this and the fact that biomass springs back after 400 years in the absence of climate change. However, this mainly seems to be an artefact of the way the results are represented: because the probability of abandonment and the number of cells open to abandonment are very high at the centre of pine's distribution (2100-2400 m), there are suddenly many new "forest" cells in those bands. As these are first colonised by *Larix*, the average for *Pinus* goes down because its biomass remains constant in older, late-successional cells. After 400 years, the ratio of new to old cells decreases and the average biomass per altitudinal band returns to its previous level. Similarly, this same artefact may explain the apparent increase in biomass of larch at those same altitudes. When climate change is too severe (3.5 or 5.6 °C increase in temperature), *P. cembra* disappears from the study area, contrary to *L. decidua* which survives, albeit in smaller quantities. The latter clearly benefits from being a pioneer species and therefore able to colonise newly-opened land, whereas *P. cembra* is out-competed by *P. abies*. However, this could only be deferring the inevitable and larch may also eventually disappear if

insufficient open land remains or if other, more competitive pioneer species migrate from lower altitudes. In reality, we would not expect *P. cembra* to disappear completely. Suitable habitats may still remain outside our study area. It is also able to survive for a long time on rocky outcrops, sites which are not suitable for *P. abies*, even within the study area. However, such rapid climate change events may severely reduce the biomass and the distribution of a late-successional species like *P. cembra*, which has a comparatively slow growth rate and low shade tolerance.

In the Swiss Alps, the upwards shift of the altitudinal tree-line in the event of climate change is primarily limited by human activities. Despite a certain amount of land-abandonment, the continuation of agriculture mitigates the effect of climate on tree-line position, which shifts by approximately 200 m in our simulations whatever the degree of climate change. This concurs with the values given by Theurillat and Guisan (2001), namely a 100-200 m tree-line altitudinal shift for a 1-2 °C temperature increase, which corresponds to our most moderate scenario. In the absence of limitations through human activity, the expected vertical shift would be 640 m for a 4.5 °C temperature increase (half-way between our two highest scenarios) in 100 years (Grace *et al.*, 2002). The current rate of land-abandonment (which averages approximately 2.1 % of agricultural land per decade in the Engadine) means that land is not made available for tree establishment fast enough to allow species to migrate far above the current tree-line in response to climate change. In the event of a medium to severe increase in temperature, high-altitude tree species are therefore out-competed by lower-altitude species migrating upwards (e.g. *P. abies*) and they eventually decline (*Larix decidua*) or even disappear (*P. cembra*) within a given area, if not from the entire landscape. However, the loss of these tree species due to human pressure has to be put into perspective with a possibly greater loss of biodiversity through homogenisation of the landscape as a consequence of land-abandonment (Schöne and Schweingruber, 2001; Graf Pannatier, 2005).

The continuation of agricultural practices and the current land-abandonment rates also affect the speed of tree response to climate change, resulting in considerable lags in the readjustment to simulated temperature increases. Finally, it should be mentioned that despite the fact that degree-day sum is a component of the land-abandonment module and affects the probability of abandonment, using the same model for 400 years is unrealistic if climate conditions are changing that much. After the first 100 years, land-abandonment (or lack thereof) should therefore only be viewed as a general representation of some form of human pressure.

Boreal case study

There are at least two possible explanations for the slight upwards migration and increase in biomass observed when species are allowed to migrate into grasslands but the climate does not change. One possibility is that reindeer grazing pressure is currently keeping the grasslands open and that the removal of the “stockability” constraint (which could be interpreted as removing the reindeer) allows the trees to re-invade the land. However, if that were the case this effect should only be apparent for *B. pubescens*, which is grazed by reindeer in summer (Väre *et al.*, 1996; Suominen and Olofsson, 2000), not for the conifers which are rather unpalatable and not directly affected. The other possibility is that this shift is a response to the climate change which has already occurred towards the end of the 20th century. The climate data used as input covered the last 30 years of the 20th century, including the 1990s which were warmer than average, but the land-use map probably uses earlier survey data, so that the initial

“forest” area may in fact reflect the climate of the mid-20th century. This type of response is not observed in “no change” simulation for the Alps because: a) the input climate data goes back further (1961) and covers nearly 40 years instead of 30, so the warm 1990s do not affect the long-term means and standard deviations (model input) as much and b) the continued land-use pressure from the land-abandonment module would mask it anyway.

Similarly to what is observed in the Alps, *P. abies* shows a lagged response to climate change, because its expansion is limited by small initial numbers, slow growth (at least in bright conditions) and the presence of other species, Scots pine in particular. During the stabilisation phase, spruce’s biomass increases and its distribution shifts upwards by 50 to 100 m with moderate to medium temperature change. The decrease in biomass at the lowest altitudes and when climate change is severe is probably an effect of *Picea*’s sensitivity to drought stress, which increases both in frequency and intensity if temperatures rise while precipitations remain constant. The mean biomass of spruce is overall low in this study area and reflects the species’ patchy distribution, which is limited to soils which can meet its water-supply demands. These are higher than those of *Pinus sylvestris*, which has a deeper rooting system (Kullman and Engelman, 1997).

As expected, Scots pine shows an upwards and polewards shift in its distribution as a result of climate change. This is partly limited by the availability of land at higher altitudes when the temperature change is high, but does not lead to a drastic decrease in biomass. The higher biomasses observed in the lowest (100 m) altitudinal band could be an effect of drought, to which *P. sylvestris* is quite tolerant, in contrast with the more dominant *P. abies*. However, the geographical location of these low-altitude cells, which are mostly situated in the northern part of the study area, around the shores of Lake Inari, suggests that this is mostly due to the northwards migration of Scots pine following climate change.

The fast response of *Betula pubescens* to climate change, resulting in an upwards shift into the hill-top grasslands is consistent with its status as pioneer species (Nieuwenhuis and Barrett, 2002). It also has small seeds, which can disperse further than those of other species (Grace *et al.*, 2002). After stabilisation at the new temperature level, birch biomass diminishes drastically if the climate change is intermediate (+3.5 °C) to severe (+5.6 °C). Small quantities are nevertheless maintained at lower altitudes because of the latitudinal distribution of the low-lying areas. These relicts of the species’ presence at the northern end of the study area indicate that it would probably migrate further northwards, outside the spatial extent of our simulation grid. However, two factors which are not currently included in TreeMig-Lab could hinder the migration of Downy birch into grasslands: reindeer (*Rangifer tarandus*) browsing and larch bud moth (*Epirrita autumnata*) attacks (Holtmeier and Broll, 2005). The latter could in fact lower the tree-line in the event of climate warming, which could result in increased insect outbreaks (Virtanen *et al.*, 1998). If the lower altitudes were occupied by other species, this could possibly lead to a near-disappearance of *B. pubescens* within the area considered. However, this species would be expected to migrate northwards as well, so it could persist outside the study area.

The predicted changes in species distributions at the boreal tree-line are consistent with the continuation of current trends, such as the 75 m altitudinal rise of birch’s tree-limit over the past century observed by Kullman (2003). In the Swedish Scandes, the same author records the presence of saplings of all three boreal tree-line species 500 to 700 m

above their current limit, which suggests the potential for encroachment into the tundra (Kullman, 2004).

General discussion

Our results rely on the fact that the climate change estimates we used for the next century are reliable, though there is some debate about the IPCC forecasts, which some authors find too low (e.g. Scheffer *et al.*, 2006) and others too high (e.g. Khandekar *et al.*, 2005). However, the assumption that climate change will stop after 100 years and remain stable at the new level, may well be too optimistic. For this to happen, greenhouse gas emissions would have to be cut immediately, as the impact of current emissions on the climate is likely to continue over the next decades. A climate-induced increase in forest extent and density could also lead to feed-back effects on the climate, which have not currently been considered in our climate-change scenarios: the resulting increase in carbon sequestration would have a negative effect on climate forcing and mitigate the impact of climate change. However, due to differences in albedo, boreal forests heat the atmosphere up more than tundra or meadow systems do and this positive forcing could outweigh the gain from a rise in carbon sequestration (Betts, 2000).

Human impacts could change at both tree-line ecotones as a result of climate change. As has already been mentioned, the “business as usual” scenario of the land-abandonment module can only be expected to hold true for a few decades at most. A severe increase in temperature, as found in the +5.6 °C scenario, could lead to a northwards shift of agriculture in Fennoscandia. This would put further pressure onto forests at the current tree-line, which would already be struggling to respond to climate change.

Some species are better parameterised than others in the model and biomasses may be over- or under-estimated (Rickebusch *et al.*, submitted-a), which has a bearing on the results shown here. The overall trends are probably correct, but the increase in biomass of *P. abies* and *L. decidua* may be exaggerated, as these species tend to be over-represented in the model. Similarly, the decrease of *P. cembra* may be less severe than in the simulations. In both case study areas, the predicted (near-)disappearances are only valid locally, as species may survive at higher altitudes in the surrounding areas. This is particularly true for the boreal study area, which did not extend far enough to the north to cover the extent of polewards migration likely to occur in the case of severe climate change.

Conclusions

The Alpine tree-line simulations take into account land-abandonment, which is an important human factor for that ecotone. The results show reasonable estimates of the impact of combined climate and land-use changes on the three main tree-line species. A lag in the readjustment of the equilibrium between climate and vegetation in response to climate change appeared at both tree-lines and for all levels of climate change. This lag is mostly an effect of competition dynamics, reinforced at the Alpine tree-line by the fact that land-abandonment progresses more slowly than climate change and tree species migration when the entire landscape is considered, although abandonment of single parcels or grid cells is immediate.

Although the results from the Fennoscandian boreal tree-line are consistent with observed trends, some strong uncertainties remain. Integrating factors specific to that ecotone, such as increased grazing pressure from reindeer or climate-induced changes in

insect outbreaks, are considered to be necessary future improvements for scenario studies. On the chosen scale of 80 km and 400 years, the latitudinal effects detected are only small and overridden by the altitudinal effects. Simulations over a longer north-south transect would bring more information on latitudinal migration rates. However, the size of the simulation area was constrained by memory capacity and the need to have a sufficiently wide strip to allow spatial interactions between the cells.

The simulations in both case study areas show a risk of strong decrease and even disappearance, at least locally, of tree-line species, such as *P. cembra* or *B. pubescens*, in the event of climate change according to the IPCC and HadCM3 estimates in our study areas. Only with the most conservative temperature change values are all species maintained, albeit with shifted distributions and some changes in the relative representation of species. Even then, the disruption is such that it takes decades, if not centuries for the species' distributions reach a new equilibrium.

Acknowledgements

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5. Effect of reindeer browsing on Scots pine growth in Northern Finland

Article in preparation.

Diploma project for the post-graduate diploma in applied statistics at the ETH, Zürich

Abstract

The effect of reindeer (*Rangifer tarandus*) browsing on Scots pine (*Pinus sylvestris*) growth was investigated using tree-ring data from 44 trees within (14 young trees) and without (15 young and 15 old trees) a area in Muonio, Finland, which was fenced-off in 1961. The reindeer do not browse the trees themselves but the lichen covering the forest floor, the removal of which in turn modifies the influence of climate and other variables on tree growth.

The potential effect of the fence was investigated first alone, then in conjunction with four climate variables (degree-day sum, minimum winter temperature, precipitation and average autumn temperature of the previous year). This was done by means of linear mixed-effects models (LME). The first model, without climate variables, included fence effect, age group (young or old) and spline functions of the tree diameter at breast height (DBH) and calendar year (the latter as a proxy for climate), with a random term for the effect of individual trees and an AR1 model for the temporal autocorrelation within each tree. As the climate data was only available for the 1973 to 2002 time period, the effects of DBH, age group and tree identity were removed from the original data and the de-trended ring-width values for those years used in the second part of the analysis. The second model was also an LME, but with fence effect and the climate variables as fixed effects, the random and correlation effects being the same as in the first model. Various versions were tested, using different combinations of the four climate variables, the fence effect and interactions between them.

A significant positive effect of the fence on tree growth was found in all models, though it was not always very strong. Although the climate variables mostly seemed to influence tree growth, an interaction effect between fence presence and climate was only found with degree-day sum. So, although the trees apparently benefit from the fence and the lichen cover, it was not possible to point to one single factor underlying this effect. The lichen cover most probably interacts with several factors (climatic or other) influencing tree growth, amongst which degree-day sum.

Introduction

In Finnish Lapland, reindeer (*Rangifer tarandus*) have been part of the natural ecosystem since the last Ice Age. Large-scale nomadic reindeer herding began in the 17th century, which led to semi-domestication. During the 20th century, herding practices changed and reindeer now remain within the same region all year round, rather than migrating between summer and winter pastures. The number of reindeer has been increasing steadily since the end of the Second World War and reached a peak in the early 1990s (Väre *et al.*, 1996; Suominen and Olofsson, 2000).

Reindeer have very different diets in summer and winter. In summer they feed on herbs and deciduous tree leaves, whereas in winter their food consists of arboreal and ground lichen, such as *Cladina spp.* (Suominen and Olofsson, 2000). Removal of the lichen

layer through browsing affects the forest ecosystem in many ways, for instance through changes in competition, water retention or protection of the soil against frost (Väre *et al.*, 1996; Kumpula *et al.*, 2000; den Herder *et al.*, 2003). Scots pine (*Pinus sylvestris*) growth and regeneration could be affected by increased exposure to adverse climate conditions, such as frost or drought, changes in mycorrhiza development or regeneration niche (den Herder *et al.*, 2003).

Part of a forest situated in the Municipality of Muonio (Fig. 5.1) was fenced-off in 1961. The difference in lichen cover between the two sides of the fence is now clearly visible (Fig. 5.2). However, lichen grows slowly and it would have taken approximately 15 years (i.e. until the mid-1970s) for the cover to regenerate to its present level (R. Jalkanen, pers. comm.) A model by Kumpula *et al.* (2000) showed that Finnish lichen ranges would have to remain ungrazed for an average of 18 years to recover to maximum production levels. A field study of lichen recovery rate in a Finnish mountain birch forest site fenced-off in 1968 showed a regeneration time of roughly 15 years (Kärenlampi and Kytöviita, 1988).

This study aims first of all to test for differences in tree growth between the browsed and non-browsed areas and then to investigate possible links between lichen cover and the influence of various climate factors.



Figure 5.1. Location of the fenced-off area in the Municipality of Muonio (Finnish Lapland). The thin black dotted line shows the boreal tree-line. [Adapted from M. Tuovinen and R. Jalkanen]

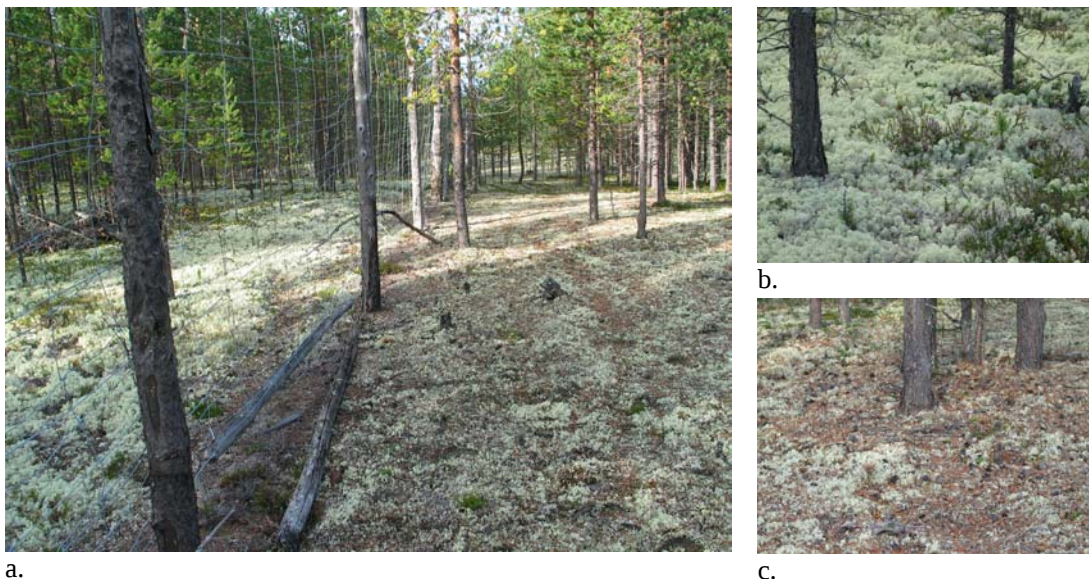


Figure 5.2. Fence (a) and details of the ground lichen cover: unbrowsed (b) and depleted by browsing (c). The pictures were taken in 2003, i.e. 42 years after the fence was erected.

Data

Site characteristics

The Muonio site is situated close to the boreal tree-line (68°08'N, 23°22'E, see Fig. 5.1), at an altitude of 255 m. Site conditions are dry, due to a combination of low precipitation and sandy soil. The forest consists mainly of *Pinus sylvestris*, fairly open and with little undergrowth (*Cladina* sp., *Ericaceae*).

Dendrochronological data

In 2004, 29 young Scots pines were sampled in Muonio, 14 in the fenced-off area and 15 in the browsed area. The pith (central part of tree stem) age for these trees ranged from 44 to 66 years old at the time of sampling. Additionally, 15 older trees of the same species, with pith ages ranging from 205 to 267 years old, were sampled in the browsed area.

Average tree-ring width, equal to half the yearly diameter increment, was used as the measure for growth. The data was raw, i.e. not previously corrected for age or size. The tree-ring data was used to calculate the “birth” year (first year in series) and the diameter at breast height (DBH, Eq. 5.1) of each tree (Table 5.1).

$$DBH_y = 2 \cdot \sum_{i=1}^{y-1} rw_i \quad (5.1)$$

A one-sided t-test of the birth years of the fenced-off trees vs. the young trees in the browsed area shows that the former are significantly younger (higher birth year) than the latter ($t = 4.8869$, $df = 26.917$, $p\text{-value} = 2.079e-05$). This results in a slight difference in girth between the two groups, as the younger trees had a smaller DBH at time of sampling ($t = -2.9892$, $df = 25.685$, $p\text{-value} = 0.003044$).

Table 5.1. Descriptive statistics of the trees in the three groups: young trees in fenced-off area, young trees in browsed area and old trees in browsed area. The variables given are “birth” year, ring-width (values for all years) and diameter at breast height (DBH) at time of sampling.

Group	Variable	Unit	Min	Max	Median	Mean	St Dev
Young, fenced	birth	years	1947	1960	1952	1952	3.7
	ring-width	mm	0.29	2.36	0.97	1.03	0.369
	DBH	cm	9.23	13.42	10.36	10.51	0.986
Young, browsed	birth	years	1938	1951	1947	1946	3.8
	ring-width	mm	0.26	2.84	0.87	1.01	0.330
	DBH	cm	9.81	14.12	11.69	11.80	1.336
Old, browsed	birth	years	1737	1799	1767	1766	18.3
	ring-width	mm	0.05	2.85	0.70	0.75	0.330
	DBH	cm	28.65	40.30	36.56	35.83	3.717

To account for the slow regeneration of the reindeer lichen cover, the binary variable “browsing” (trees in browsed B vs. fenced-off F area) was transformed into a “fence effect”, scaled between 0 and 1 over 15 years from 1961, which reflects the state of the lichen cover (Eq. 5.2).

$$\begin{cases} \text{brow} = \text{B or } \text{year} \leq 1961 & \text{fen} = 0 \\ \text{brow} = \text{F and } \text{year} \in [1962, 1976] & \text{fen} = (\text{year} - 1961)/15 \\ \text{brow} = \text{F and } \text{year} > 1976 & \text{fen} = 1 \end{cases} \quad (5.2)$$

Climate data

The climate data at the site was extracted from DAYMET maps, which were calculated using data from 100 climate stations located throughout Finnish and Swedish Lapland. These maps give daily precipitation, minimum and maximum temperature values from 1973 to 2002. Different climate variables, supposed to affect tree growth, were calculated from the daily values (Table 5.2).

Table 5.2. Climate variables derived from the daily precipitation, minimum and maximum temperature values extracted from the DAYMET maps, with summary statistics for 1973-2002.

Variable	Unit	Calculation method	Min	Max	Median	Mean	St Dev
DD_sum	°C·d	Yearly degree-day sum above 5.5°C, using Allen's (1976) double sine-wave	530.8	939.2	686.7	707.6	98.95
MinWiT	°C	Minimum of monthly average temperature for December (year-1), January & February	-24.90	-9.34	-17.31	-17.24	3.444
Prec	mm	Yearly sum of precipitation	315	623	476	463	75.4
AveAuT_p	°C	Mean of monthly average temperature for September, October & November of previous year	-5.13	2.37	-1.70	-1.69	1.616

Although the climate data does not cover the entire time-span of the dendrochronological data, it nevertheless includes all the years in which the lichen cover is supposed to have sufficiently regenerated to make a difference to tree growth (from approximately 1976 onwards).

Statistical methods and results

Model without climate data

The effect of fencing on tree growth was modelled using a Linear Mixed-Effects model and taking into account some of the other factors known to influence tree growth:

$$\text{lme}(rw \sim \text{ns}(dbh, df=...) + \text{ns}(\text{year}, df=...) + \text{fen} + \text{age_gr}, \\ \text{random} = \sim 1 | \text{tree_id}, \text{correlation} = \text{corAR1}(), \text{data} = \dots)$$

where ring-width rw is a function of diameter at breast height dbh , calendar year $year$, fence effect fen (see Eq. 5.2) and age group age_gr (young or old trees). dbh and $year$ were included as spline functions, which take into account the effect of those variables over all the trees (global trends). Although $year$ in itself does not influence tree growth, it is used here as a proxy for climate and other factors which vary over time. As the number of degrees of freedom used in the spline function is relatively low, it is a substitute for multi-decadal trends rather than yearly variations. The random effect models the differences between individual trees. The autocorrelation between the ring-width values of successive years within the same tree is modelled as an AR(1) process (first order autoregressive model).

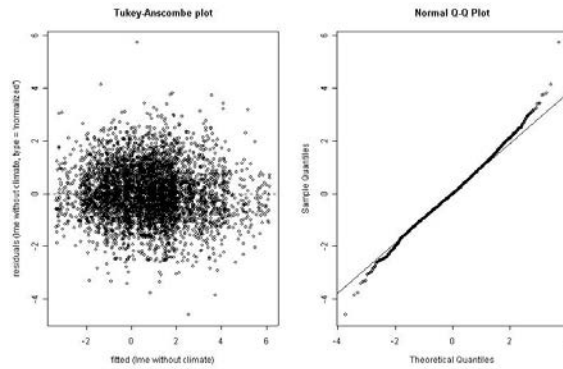


Figure 5.3. Residual analysis of the linear mixed-effect model (LME) without climate variables. Neither the Tukey-Anscombe plot nor the QQ plot show very strong unwanted structures, although there are a few slightly outlying values.

Various forms of this model were compared using ANOVAs. The different models included more or less variables (fixed effects), varying numbers of degrees of freedom in the spline functions, different spline functions (natural cubic spline *ns* or polynomial spline *bs*). The response variable *rw* also had to be transformed, in order to minimise unwanted structures in the Tukey-Anscombe and QQ plots (residual analysis). The best results were obtained with the following model:

```
lme(sqrt(rw) ~ bs(dbh, df=8) + ns(year, df=8) + fen + age_gr,
    random = ~ 1|tree_id , correlation = corAR1(), data = ...)
```

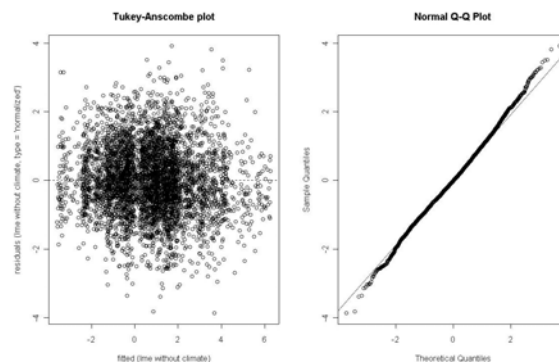
This model shows a significant positive effect of fencing (value = 0.272217; df = 5100; p-value = 0.0341) on tree ring-width. It also shows a highly significant negative effect of belonging to the “young” (~50 years old) rather than the “old” (~250 years old) age group (value = -18.663684; df = 42; p-value < 0.0001). The residual analysis was carried out on the normalized residuals, i.e. the standardized residuals pre-multiplied by the inverse square-root factor of the estimated error correlation matrix. It shows that the distribution is slightly long-tailed, particularly towards the upper end (Fig. 5.3). This is mainly due to two outliers, one at each end, but other than that the plots do not show any strong unwanted structures. The two furthestmost “outliers” belong to trees 48 (low value for 1790) and 55 (high value for 1761).

Applying the same model to a subset of data from which trees 48 and 55 have been removed gives similar results, though the effect of fencing becomes (just) non-significant (value = 0.250274; df = 4638; p-value = 0.0554). The results of the residual analysis on the other hand are improved (Fig. 5.4).

Models including climate data

In order to accurately model the effect of climate on growth, this model also had to include the effects of tree size, differences between individual trees and age group. However, these can only be modelled by using the full dataset for each tree and the

Figure 5.4. Residual analysis of the linear mixed-effect model (LME) without climate variables and without the values from trees 48 and 55. Neither the Tukey-Anscombe plot nor the QQ plot show unwanted structures.



climate data was only available for 1973-2002. It was therefore necessary to start by removing these effects, as they appear in the model without climate data, to create a new, de-trended ring-width variable (*drw*). As only some of the terms in the previous model were used for this, the individual effects had to be predicted, which is not possible with LME models. A similar linear model (LM) was therefore used for de-trending purposes, with *tree_id* as a fixed rather than a random effect:

```
lm(sqrt(rw) ~ bs(dbh, 8) + ns(year, 8) + fen + age_gr +
  tree_id, data = ...)
```

The effect of each term was calculated using `predict(<lm-model>, type = "terms")`. The effects of *bs(dbh, 8)*, *age_gr* and *tree_id* were subtracted from the square root of the raw ring-width values, to give the de-trended (square root) ring-width (Eq. 5.3).

$$drw = rw^{1/2} - pred.bs(dbh, 8) - pred.age_gr - pred.tree_id \quad (5.3)$$

The four climate variables *DD_sum*, *MinWiT*, *Prec* and *AveAuT_p* (Table 5.2) were added to the dataset. As the climate data only starts in 1973 (and even 1974 for *AveAuT_p*), all calculations including climate data were carried out on a subset of the original, namely all values from 1974 to 2002 (29 years).

The model used was again an LME model, with *drw* as the target variable and the climate variables, plus the fence effect and its interaction with climate, as explanatory variables:

```
lme(drw ~ fen + DD_sum + MinWiT + Prec + AveAuT_p + fen:DD_sum
  + fen:MinWiT + fen:Prec + fen:AveAuT_p, random =
  ~ 1|tree_id, correlation = corAR1(), data = ...)
```

The least significant terms were removed successively in a stepwise manner, to finally give the following model, where all the climate variables and the fence effect have been retained, but only one interaction term, the one between fence effect and degree-day sum:

```
lme(drw ~ fen + DD_sum + MinWiT + Prec + AveAuT_p + fen:DD_sum,
  random = ~ 1|tree_id, correlation = corAR1(), data = ...)
```

The model output (Table 5.3) shows positive effects for all terms except minimum winter temperature and the interaction between fencing and degree-day sum. The negative effect of minimum winter temperature is rather unexpected, but the negative interaction effect could be due to a difference in the effect of degree-day sum on the trees in each group.

Table 5.3. Results for the different terms retained in the model with all four climate variables and their interactions with the fence effect.

	Value	Std Error	DF	t-value	p-value
(Intercept)	0.5843609	0.02967	1226	19.7	0.0000
fen	0.1297334	0.03816	1226	3.4	0.0007
DD_sum	0.0000664	0.00003	1226	2.5	0.0110
MinWiT	-0.0049089	0.00062	1226	-7.9	0.0000
Prec	0.0000618	0.00003	1226	2.2	0.0300
AveAuT_p	0.0087758	0.00161	1226	5.4	0.0000
fen:DD_sum	-0.0001542	0.00005	1226	-3.3	0.0009

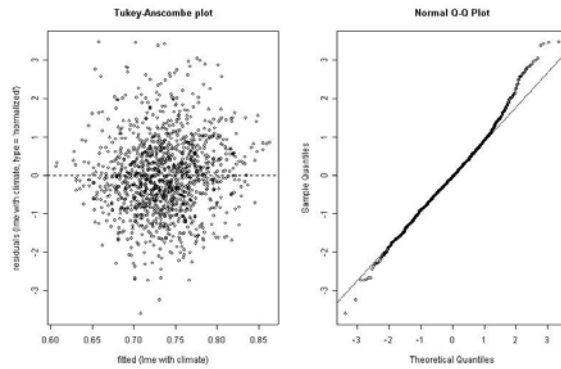


Figure 5.5. Residual analysis of the linear mixed-effect model (LME) with four climate variables. The Tukey-Anscombe plot has a tendency to be funnel-shaped and the QQ plot shows that the distribution differs somewhat from normality. This is partly due to a few mild outliers, particularly at the lower end.

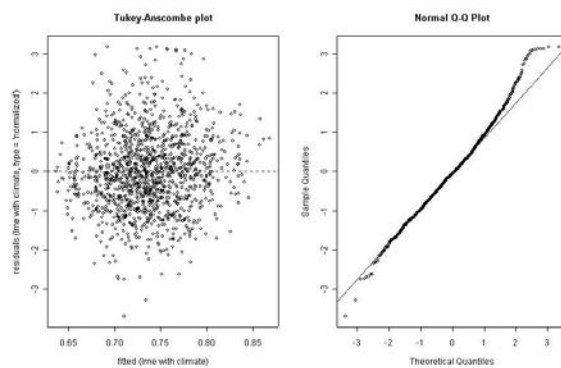


Figure 5.6. Residual analysis of the linear mixed-effect model (LME) with three climate variables. The Tukey-Anscombe plot is similar to that of the previous model at the lower end, with the same outliers, but the upper end does not have clear outliers any more. The QQ plot again shows the same type of structure as with the previous model (Fig. 5.5).

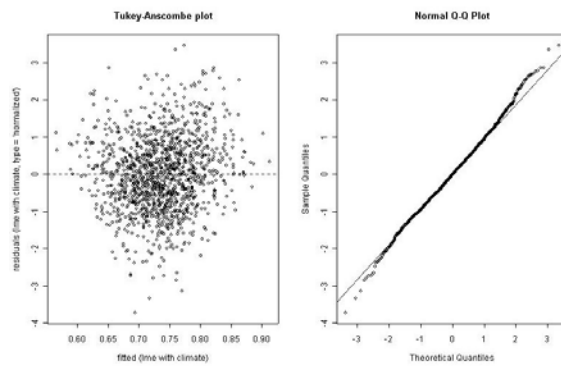


Figure 5.7. Residual analysis of the linear mixed-effect model (LME) with all climate variables, the fence variable and all second order interactions. The Tukey-Anscombe plot is similar to that of the other two models at the lower end, with the same outliers. The QQ plot again shows that the distribution is more in keeping with model assumptions.

The residual analysis (Fig. 5.5) shows some discrepancy with the model assumptions, though it is not excessive. The funnel shape in the Tukey-Anscombe plot is partly due to a few outliers, in particular the two data points with the lowest residuals. These are both values measured in 1981. At the other end, three of the four most extreme values were measured in 1993.

As the ecological or physiological relevance of minimum winter temperature is difficult to assess and its effect in the previous model is somewhat surprising, there is a possibility that it is not a meaningful variable to include in this model. A new model without *MinWiT* (or its interaction term) was therefore constructed. After the non-significant terms have been removed, the final model is:

```
lme(drw ~ fen + DD_sum + AveAuT_p + fen:DD_sum, random =
  ~ 1|tree_id, correlation = corAR1(), data = ...)
```

The remaining terms (Table 5.4) are the same as in the model with all four variables, except for precipitation, which has been removed. It was already the closest to the threshold p-value of 0.05 in the previous model.

Table 5.4. Results for the different terms retained in the model with only three climate variables (MinWiT excluded) and their interactions with the fence effect.

	Value	Std Error	DF	t-value	p-value
(Intercept)	0.7020996	0.02214	1228	31.7	0.0000
fen	0.1380541	0.03907	1228	3.5	0.0004
DD_sum	0.0000555	0.00003	1228	2.1	0.0381
AveAuT_p	0.0064880	0.00149	1228	4.3	0.0000
fen:DD_sum	-0.0001663	0.00005	1228	-3.5	0.0006

The residual analysis (Fig. 5.6) also shows fairly similar patterns, with strongly negative residuals for some of the trees in 1981. At the upper end on the other hand, there are now no clearly outstanding values. The distribution is still slightly long-tailed, though not excessively so.

Removing minimum winter temperature from the model caused precipitation to lose its significance. This could point to interaction effects between those two variables. All the climate variables would be likely to interact anyway, even if they were independent, because of the complexity of climate systems. One final model was therefore constructed with all four climate variables, plus the fence variable and all the second order interactions between them. The interaction terms can be difficult to interpret, but this will nevertheless give an insight into their extent and significance:

```
lme(drw ~ (fen + DD_sum + MinWiT + Prec + AveAuT_p)^2, random =
    ~ 1|tree_id, correlation = corAR1(), data = ...)
```

The significant terms retained in the model are shown in Table 5.5. The parameters for the random effects are $\sigma = 0.09115$ and for the AR(1) process $\phi = 0.6018$. The main effect of the average autumn temperature of the previous year has been removed, as have most of the interactions between *fen* and the climate variables, with only *fen:DD_sum* remaining. On the other hand, almost all the interaction terms between the climate variables are significant, with the exception of *DD_sum:AveAuT_p*.

Table 5.5. Results for the different terms retained in the model with four climate variables plus the fence variable and their second order interactions. Residuals: $\sigma = 0.09115$; AR(1) correlation structure: $\phi = 0.6018$.

	Value	Std Error	DF	t-value	p-value
(Intercept)	2.1366754	0.14618	1222	14.6	0.0000
fen	0.1314705	0.03534	1222	3.7	0.0002
DD_sum	-0.0019031	0.00019	1222	-10.0	0.0000
MinWiT	0.0657227	0.00552	1222	11.9	0.0000
Prec	-0.0012070	0.00031	1222	-3.9	0.0001
fen:DD_sum	-0.0001539	0.00004	1222	-3.7	0.0003
DD_sum:MinWiT	-0.0000948	0.00001	1222	-11.8	0.0000
DD_sum:Prec	0.0000008	0.00000	1222	2.1	0.0366
MinWiT:Prec	-0.0000319	0.00001	1222	-4.3	0.0000
MinWiT:AveAuT_p	-0.0035874	0.00032	1222	-11.0	0.0000
Prec:AveAuT_p	-0.0000919	0.00001	1222	-8.5	0.0000

The Tukey-Anscombe plot shows a similar pattern to the previous models, with the same outliers with very low values for 1981. The QQ plot on the other hand points to a distribution which is much closer to normal (Fig. 5.7).

Discussion

Model without climate data

This model is essentially incomplete, as it does not include climate variables, which are known to influence growth. It must therefore be viewed as a necessary step to remove the size trend, rather than as a model from which conclusions can be drawn and will only be briefly discussed.

The results of this first model show that being in the fenced-off area has a positive effect on tree growth, when some other factors, such as tree size or age group, have been accounted for. This effect is however not strongly significant.

The decision to remove the two trees with the outlying values and apply the model to the resulting subset might have been justified by the possibility of measurement error, for instance. However, the ring-width value for the point with the lowest residual (0.77 mm) is in fact close to the average for its group and the value for the other extreme is not out of the ordinary, although it is the highest overall value (2.85 mm). This rather contradicts the idea of measurement or other types of error. This second model should therefore be considered with even more caution, despite giving better results in the residual analysis.

Models including climate data

The first model, with all four climate variables, fence effect and interactions between fence and climate, still shows a significant positive effect of fencing on growth, despite the presence of the climate variables in the model. The only significant interaction is that of the fence with degree-day sum. This leads to the conclusion that, although the climate variables used in the model all affect growth to a certain extent, only the effect of degree-day sum is influenced by the lichen cover. It is however obviously not the only factor behind the fence effect, as this remains significant as well, but the other factors may be either different climate variables or of a different nature altogether. For instance, the fence effect which remains may represent changes in soil chemistry or in the development of mycorrhiza due to the presence or absence of ground lichen.

Minimum winter temperature was not expected to affect growth particularly, as it concerns the time of year when trees are dormant, so it was debatable whether it should be included in the model to start with. It was therefore removed from the second model. This leads to the further loss of the main effect of precipitation, which was the weakest effect in the first model. The other effects, including that of the fence and the fence/degree-day sum interaction, remain and are quite similar to the first model.

The results of the final model, with all climate data and interactions between each variable, are rather more difficult to interpret. In this case the main effect of average autumn temperature has been removed, while all the others, including the fence main effect, remain. The only interaction term between climate and fence effect to remain is again the one with degree-day sum. Most of the interaction terms between the different climate variables were retained and nearly all of them are strongly significant, which illustrates the complexity of the influence of climate on tree growth.

General conclusions

Although the various models are not always very good, particularly with regard to model assumptions about the distribution of residuals, it does seem that Scots pine growth benefits from the presence of the fence, which protects ground lichen from browsing. This effect is however not very strong and other factors, such as tree age, climate, etc. have a much greater influence. The underlying causes for this fence effect could not be established with certainty. They are most probably multiple and not necessarily all linked to climate, although degree-day sum seems to be one of them.

The models in this study could no doubt have been improved with additional data, from this site or a different one, as the number of trees, particularly in the fenced area, was limited. Apart from degree-day sum, the climate variables included in the models did not show significant interaction effects with the presence of the fence and different variables might have given better results. However, the underlying causes for the influence of lichen cover on tree growth might be better investigated by linking this approach to long-term measurements in a newly-fenced site, including lichen layer thickness and soil temperature, nutrients or other relevant factors.

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6. Synthesis and conclusions

Model development

The work required to develop the TreeMig-LAb model resulted in the following new developments in the field of forest population dynamics modelling:

- Model calibration with tree-ring data: first of all, this confirmed that the asymptotic temperature response function developed by Bugmann and Solomon (2000) to replace the traditional parabolic curve was indeed closer to reality. More importantly, a method for deriving species parameters from tree-rings, following the suggestion by Loehle and LeBlanc (1996), was developed. Growth curves derived in this way should be closer to the physiological response than theoretical curves fitted between the extremes of the realised niche. This new method can be reproduced to fine-tune species parameters and add new species. However, it does require a considerable amount of tree-ring data, which may not be available for some species.
- Importance of regeneration in determining tree-line position: the calibration work with the tree-ring data, although it improved the growth curve, was not sufficient to obtain realistic distributions of tree-line species under current conditions. The subsequent search for other causes lead to the conclusion that the temperature limitation for seedling establishment was more important than that on growth for controlling the position of the tree-line. Although this by no means solves the debate of growth versus recruitment as the limiting factor at the tree-line, this confirmed observations in the field by several authors (Kullman and Engelmark, 1997; Moiseev *et al.*, 2004; Kullman, 2005).
- Implementation of land-use management change in a forest dynamics model: the combination of the two models resulted in a more flexible forest model, where the suitability of grid cells for forest growth was not pre-determined. Indeed, the outcome for one cell was a combination of initial conditions and feed-back from the changes to the other cells on the grid. This new model represents a small but significant step into improving the integration of social sciences into landscape modelling (Perry and Enright, 2006). However, this type of approach requires a spatial statistical model of the socio-economic factors, which was why the reindeer browsing model developed in this study could not be used directly for implementation in the forest model. The down side of statistical models such as the one used here is that there is no direct link between the unit of observation (grid cell) and the decision-maker (Irwin and Geoghegan, 2001), so it does not simulate socio-economic aspects mechanistically, like an agent-based model would.

Effects of global change on tree-lines

Under current climate warming previsions, the simulations with the new forest dynamics model TreeMig-LAb showed dramatic changes in both the altitudinal and latitudinal tree-lines. There was a general upwards and polewards expansion of the forest. However, at the altitudinal tree-line this expansion was limited by the pressure of human activities, as the rate of land-use change stemming from the land-abandonment model did not result in sufficient new land to meet the needs of migrating species. Although anthropogenic tree-lines are changing (Holtmeier & Broll, 2005), under

current rates of change they will therefore continue to be shaped primarily by human land use.

Only the most conservative forecast of climate change allowed all the species to adapt through a shift in the respective distributions and in all other cases some extinctions or near-extinctions were observed in the study areas. However, this does not preclude persistence in neighbouring areas. Most species showed lagged responses to climate change, whatever the rate of change or type of tree-line. This confirms what can be inferred from comparing past migration rates, derived from palynological records, with projected isotherm migrations, which are one order of magnitude faster (Grace *et al.*, 2002). The only species which reacted rapidly were pioneer species already present at the highest or most northerly reaches of the tree-line, such as *Larix decidua* or *Betula pubescens*. These lagged responses are linked to the fact that regeneration was found to be the key to tree-line species distribution. Pioneer tree-line species may colonise new, open land rapidly, while species from lower altitudes or latitudes have to wait for existing trees to disappear before they can establish new seedlings and migrate upwards or polewards. Climate change will affect how much existing trees grow and may possibly reduce their life expectancy, but it is unlikely to kill them outright. As trees are a long-lived life form, it may therefore take decades to centuries for changes to occur, as was also found by He *et al.* (1999), whose simulations showed lags of 200-300 years before boreal tree species disappeared from our study area.

From the point of view of stake-holders and decision-makers, these results raise a few questions which have to be addressed when planning future forest and land-use management. Firstly, some species are likely to become extinct, at least locally, due to climate change, so conservation measures will be necessary if this is to be avoided. Secondly, because of the lagged response to climate, these effects are not likely to be immediately apparent. However, this time will probably be necessary to plan and put into practice these measures, as planning in forestry always has to be done with future generations in mind.

Future research perspectives

The work presented here, despite answering some questions, has inevitably raised at least as many new ones and opened up perspectives for future study of tree-lines and development of forest dynamics models.

As mentioned in the introduction, feed-back effects of forests on the climate in response to change can be expected (Betts, 2000; Sjögersten and Wookey, 2002; Beniston, 2003; Callaghan *et al.*, 2004; Gray, 2005). The climate scenarios in the model do not currently allow that, as they are set in advance. One way of taking feed-back into account would be to integrate possible effects into these pre-processed scenarios. The other solution would be to re-calculate the climate input periodically, on the basis of the biomass or forest area in the model. This would be more realistic, but also more challenging as it could be limited by computing time and memory.

One improvement already mentioned in chapter 3, which could be implemented relatively easily, is the addition of scenarios for land-use change, for instance those by Rounsevell *et al.* (2005, 2006). These scenarios also have the advantage of having been developed for Europe generally (15 European Union members, Norway and Switzerland), as opposed to the current land-abandonment part of TreeMig-LAb, which is only valid for Switzerland. However, this would require down-scaling the land-use scenarios. For some regions, implementing other types of human impacts, such as

increased reindeer browsing pressure, would also be necessary to improve the model predictions.

Finally, TreeMig-LAb currently assumes that newly-abandoned agricultural land is bare and that trees can establish freely if the climatic conditions are suitable. This is of course not the case and taking into account the presence of existing vegetation, such as herbs or shrubs, could alter the dynamics of advancing tree-line. Integrating grass or shrub species dynamics with as much detail as for trees may take up too much computing time, aside from problems relating to differences in scale. However, adding aggregates such as plant functional types would be feasible. This could be done for instance by adding two “generic” species in TreeMig-LAb, a grass and a shrub, or by linking this model to one which simulates plant functional through the LAMOS modelling shell (Lavorel *et al.*, 2000).

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List of abbreviations

age_gr	Tree Age Group
ANOVA	Analysis Of Variance
AR1	First order Auto-Regressive model
AUC	Area Under Curve
AveAuT_p	Average Autumn Temperature of the previous year
brow	Browsing presence/absence
DBH	Diameter at Breast Height (usually set at 1.37 m above ground)
DDSUM, DD_sum	Degree-Day Sum (> 5.5°C)
DGVM	Dynamic Global Vegetation Model
DISTFOR	Distance from Forest edge
drw	Detrended Ring-Width
fen	Fence effect
HadCM3	Hadley centre Climate Model 3
IPCC	Intergovernmental Panel on Climate Change
kDDMin(s)	Minimum Degree-Day sum allowing growth (for species s)
kG(s)	Growth factor (for species s)
kWiT(s)	minimum Winter Temperature allowing seedling establishment (for species s)
LM	Linear Model
LME	Linear Mixed-Effect model
MinWiT	Minimum Winter Temperature
NBM	Niche-Based Model
NFI	(Swiss) National Forest Inventory
PRCOMMUT	Proportion of Commuters
Prec	Precipitation
PRFUTIFA	Proportion of Full-Time Farms
PRSECT23	Proportion of employees in the secondary & tertiary Sectors
QQ plot	Quantile-Quantile plot
ROC	Receiving Operator Characteristic
SLOPE	Slope angle
SOILSTON	Soil Stoniness
SRES	(IPCC) Special Report on Emissions Scenarios

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

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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.

Keywords: landscape patterns, dynamic forest-landscape model, spatially explicit, spatially linked, pattern formation, tree migration, distribution-based approach

Introduction

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 gradients or treelines (altitude, latitude, climate change), 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 (inter)act 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; Bolliger *et al.*, 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 can not 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 landscapes 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.

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 subcontinent.

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.

The TreeMig model

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 bioclimate, 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. I.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 $Sb_{s,x,y,t}$ 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} (I.3–I.5) and spatial interactions, i.e. seed inflow I (I.6). (For a detailed model description and the parameter values see the online appendix.)

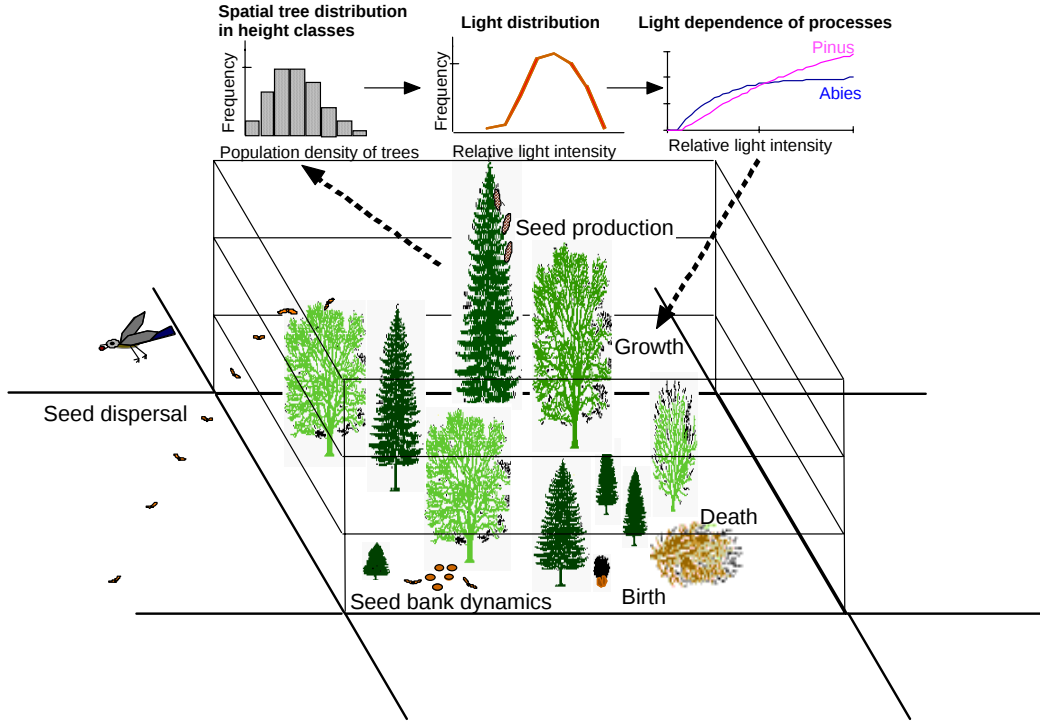


Figure I.1. Concept of the TreeMig model. It is implemented on a rectangular grid. In each grid cell, trees in different height classes germinate, grow, die and produce seeds. In each height class, a theoretical distribution of tree densities across the entire stand is calculated, based on the average 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.

$$N_{s,i,x,y,t+1} = N_{s,i,x,y,t} + L_{s,i,x,y,t} \quad (\text{I.1})$$

$$Sb_{s,x,y,t+1} = Sb_{s,x,y,t} + L_{Sb,s,x,y} + I_{s,x,y,t} \quad (\text{I.2})$$

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 .

$$\begin{aligned} L_{s,i,x,y,t} = & IG_{s,i,x,y,t}(N_{s,i-1,x,y,t}, N_{j \geq i-1,x,y,t}) \\ & - OG_{s,i,x,y,t}(N_{s,i,x,y,t}, N_{j \geq i,x,y,t}) \\ & - D_{s,i,x,y,t}(N_{s,i,x,y,t}, N_{j \geq i,x,y,t}), \quad i = 1..15 \end{aligned} \quad (\text{I.3})$$

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

$N_{j \geq i, x, y, t}$ 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 model ForClim-E model (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.

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) (I.5). The number of seeds S produced per year by each tree depends on its height, species and mast seeding period. The seed inflow I into a cell (I.2, I.6) builds up the local seed bank Sb (I.2), which is decreased by the local change L_{Sb} (I.4), given by loss of germinability, predation D_{Sb} and germination B .

$$L_{Sb,s,x,y,t} = -D_{Sb,s,x,y,t} - B_{s,x,y,t}(Sb_{s,x,y,t}, N_{j \geq 0,x,y,t}) \quad (I.4)$$

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 (B) 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 $L_{s,0,x,y,t}$:

$$\begin{aligned} L_{s,0,x,y,t} = & B_{s,x,y,t}(Sb_{s,x,y,t}, N_{j \geq 0,x,y,t}) \\ & - OG_{s,0,x,y,t}(N_{s,0,x,y,t}, N_{j \geq 0,x,y,t}) \\ & - D_{s,0,x,y,t}(N_{s,0,x,y,t}, N_{j \geq 0,x,y,t}) \end{aligned} \quad (I.5)$$

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

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 x 1 km). The forests in the different cells interact through seed dispersal.

$$\begin{aligned} I_{s,x,y,t} &= \sum_{lat,lon,i} S_{i,lat,lon,t} \cdot k_s(z) \\ k_s(z) &= (1 - \kappa_s) \cdot \frac{1}{\alpha_{s,1}^2} e^{\frac{-z}{\alpha_{s,1}}} + \kappa_s \cdot \frac{1}{\alpha_{s,2}^2} e^{\frac{-z}{\alpha_{s,2}}} \end{aligned} \quad (I.6)$$

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 (ξ, ϖ) 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 α_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 κ_s , $\alpha_{s,1}$ and $\alpha_{s,2}$ were roughly assigned (Table 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.

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 vs. 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.

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 x 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 °C, minimum winter temperature of -2.7 °C and absence of drought stress). The simulation was run with the 30 most important Central European species (for a list see Table 1a and 1b in 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. I.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 to 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

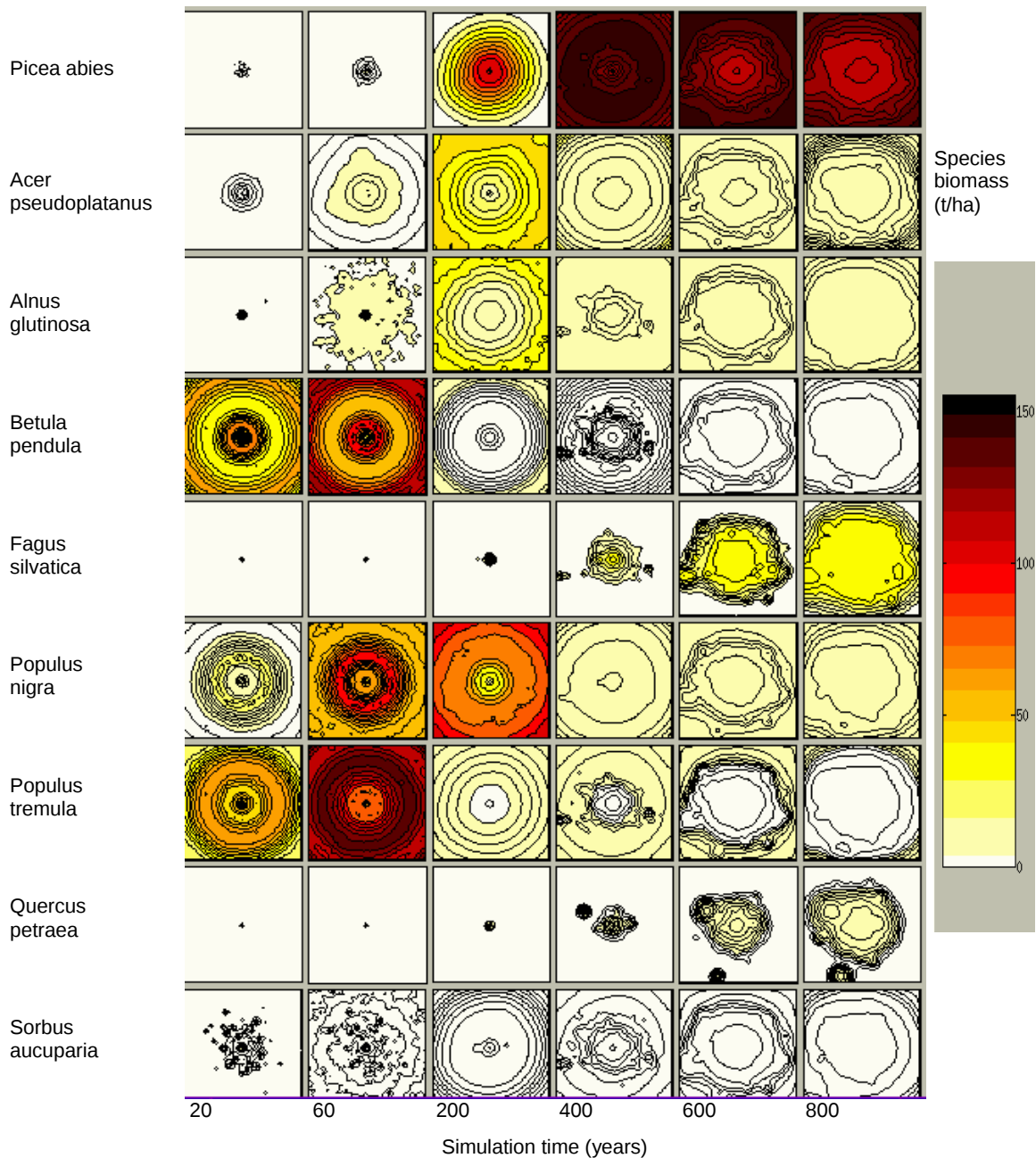


Figure I.2. Biomass of selected species (out of 30) in a simulation with constant environmental conditions (temperate humid climate) at selected time points. Each square corresponds to the biomass of one species in 50 x 50 cells of 100 m x 100 m each. The simulation was initialized with all species in the centre cell and empty cells everywhere else. For an animation of the spatio-temporal dynamics see “LocalPatternFormation.avi” in the electronic appendix.

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 homogeneously 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 homogeneously 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.

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. I.3) spans a large range of environmental conditions, with altitudes stretching from 400 to 4600 m, yearly mean temperatures between -10 and 11 °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 southeast. The simulation was carried out on an area of 50 km x 110 km (Fig. I.3) with 1 km x 1 km grid cells and ran from the end of the last Ice Age, ~14'000 before present (BP), to present.

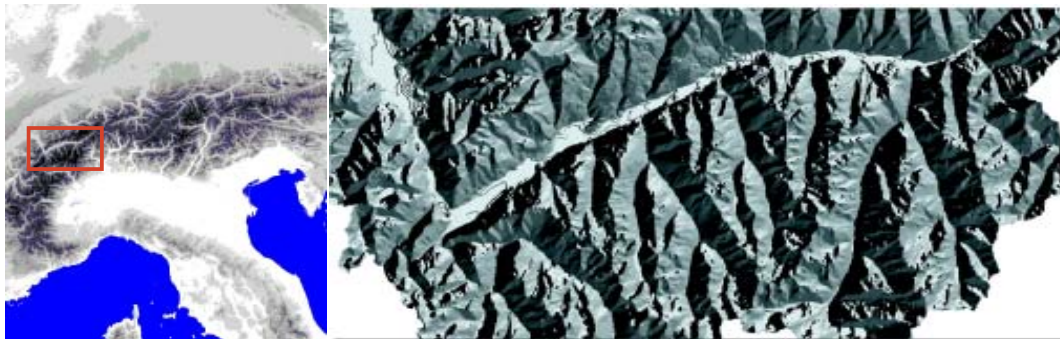


Figure I.3. Study area for case study 2 in the Valais, Switzerland.

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.

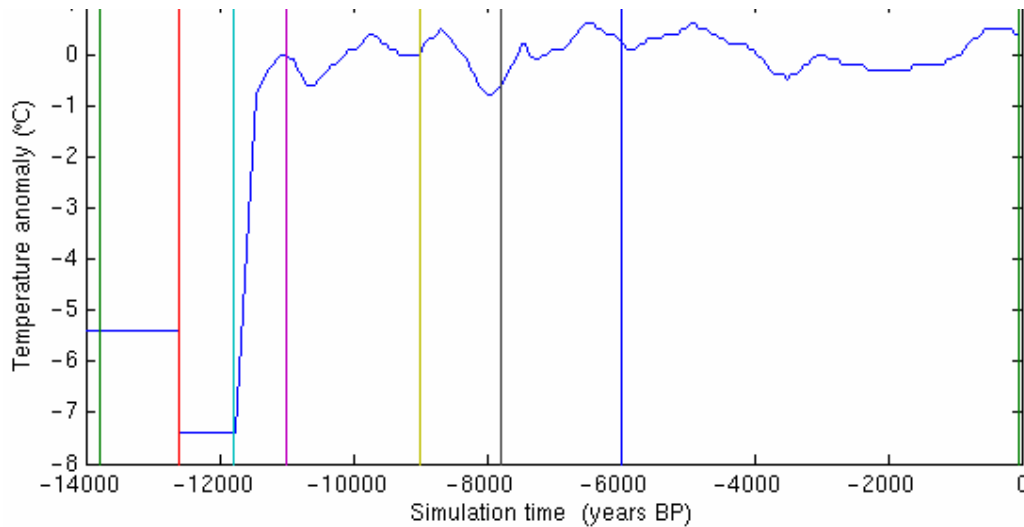


Figure I.4. Assumed temperature anomaly, along with the times corresponding to the maps shown in Figs. 5 and 6 (vertical lines).

The temperature anomaly (Fig. I.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 BP–12'500 BP), cold conditions were assumed, followed by even lower temperatures during the Younger Dryas (12'500 to 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 14000 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).

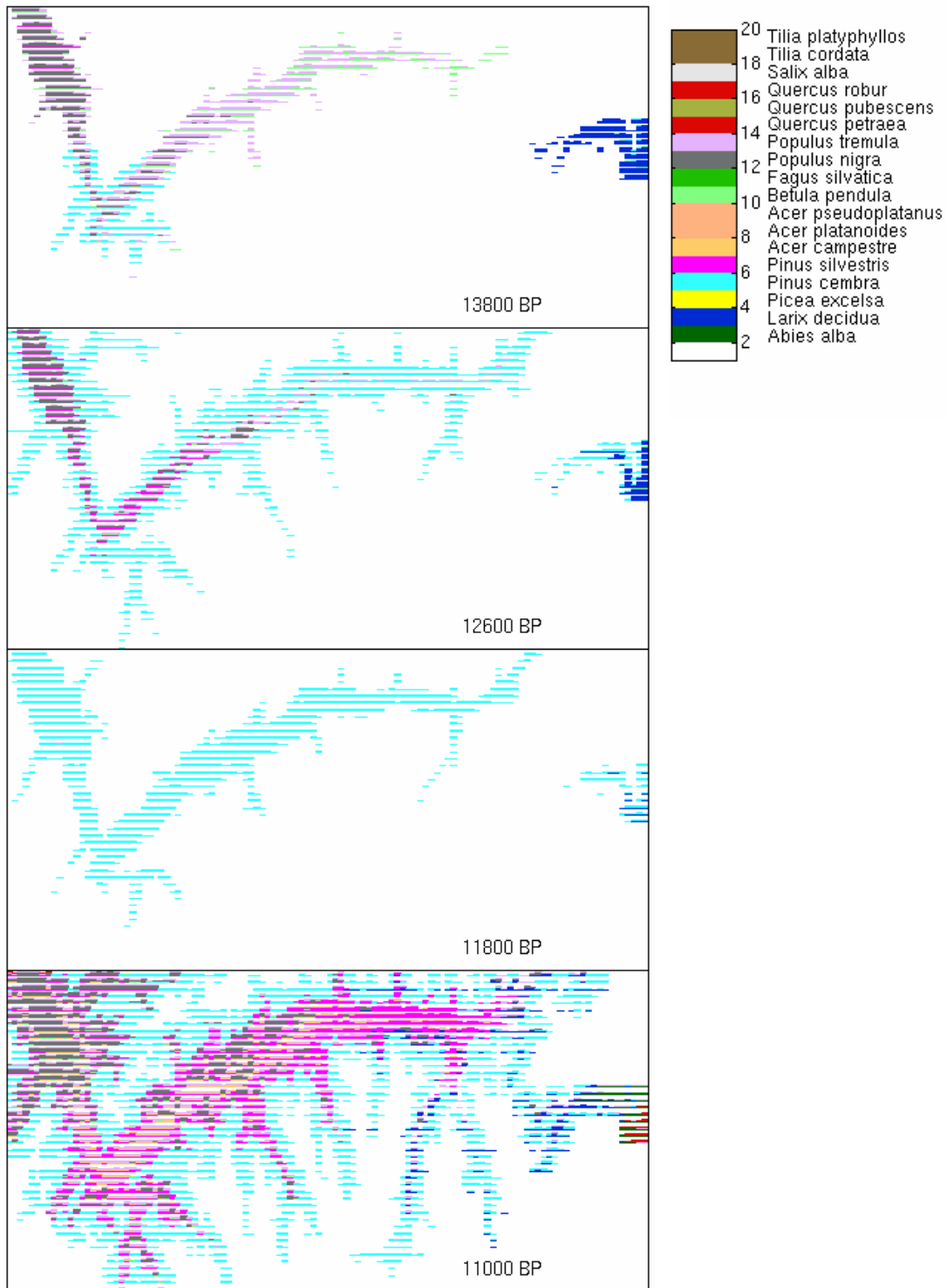


Figure I.5. TreeMig simulation (13800 BP to 11000 BP) of tree species spread on a 1 km x 1 km grid, over a 100 km x 50 km area in the region of the Valais, Switzerland. In each cell, the species biomasses (t/ha) are drawn as stacked columns. A completely filled cell corresponds to 435 t/ha total biomass. For an animation of the spatio-temporal pattern, see “HoloceneTreeMigration.avi” in the electronic appendix.

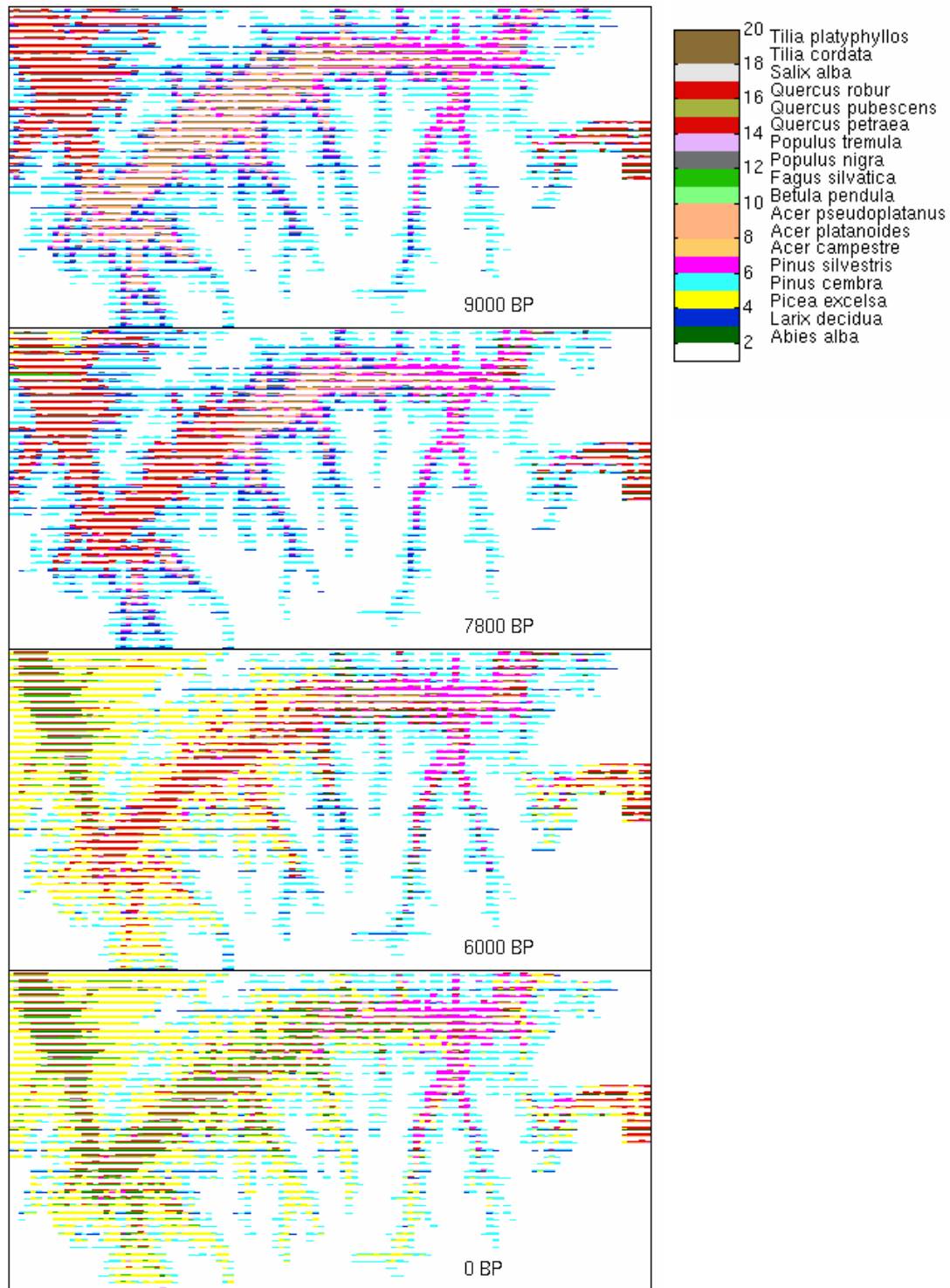


Figure I.6. TreeMig simulation of tree species spread for years 9000 BP to today. For explanations, see fig. 5.

The results (Figs. I.5 and I.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 succession, 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. I.5). During the initial colonization (14'000 to 12'600 BP), fast migrating species such as birch (*Betula pendula*) and aspen (*Populus tremula*) spread rapidly at low altitudes, poplar (*Populus 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 to 11'700 BP), only Swiss stone pine remains within the Valais. With the rapid warming between 11'700 and 11'000 BP (corresponding to $\sim 0.8 - 1$ °C/century), poplar spreads again and pine colonizes the dry valley bottom. Larch has managed to cross the Simplon pass and spreads westward along the subalpine belt. The timberline, with Swiss stone pine, has shifted upwards tremendously. By 7'800 BP, maple has spread throughout the valley, while oak follows at a slower pace (9'000 BP, 7'800 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 (*Picea abies*) and beech (*Fagus silvatica*) enter the valley from the northwest. By 6'000 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, 5) and initiate transient phases of strong spatio-temporal endogenous pattern formation (aspects 1, 3, 4). At this coarse scale (grain = 1 km x 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 BP to 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 Simplon 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.

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.

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.

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 to 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), land-use and climate change at the Alpine and boreal tree-lines 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 900MHz CPU with 1GB RAM, what amounted to 48 h for the Holocene study, which encompasses 6'050 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 1km 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 833m². 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 (ForClim, Bugmann, 1994). However, the new parameters for reproduction and seed dispersal were compiled from the literature, and some of them contained large uncertainties. Others were fitted by eye or derived using best estimates. Therefore the shape of the dispersal kernel in particular, but also the estimated parameter values have to be considered as preliminary and will be tested in a sensitivity analysis.

Despite these uncertainties, the species compositions simulated in both case studies for current conditions largely correspond to empirical evidence, such as forest inventory data. The simulations, however, differ from observations in that they show high biomasses of *Picea abies* and low biomasses of *Abies alba* (not shown in case study 1) and *Fagus silvatica*.

This implies that in a next step the model should be tested thoroughly by a validation against local and spatio-temporal data and by a comprehensive sensitivity analysis of its spatial behaviour.

Acknowledgements

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Appendix I.A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [10.1016/j.ecolmodel.2005.11.046](https://doi.org/10.1016/j.ecolmodel.2005.11.046). Two parts of this online appendix have been reproduced here: the description of the main TreeMig modules, which was the main contribution to that paper out of this thesis, and the list of species parameters, which are necessary to understand Appendix II.

Modules

The TreeMig model describes local stand dynamics in each cell of a spatial grid by the demographic processes seed-bank dynamics, birth, growth, death and seed production (fecundity). The spatial interactions between the cells are realized by species-specific seed dispersal (wind/ballistic, small rodents, and birds). With this design it goes far beyond traditional stand simulators such as gap models which ignore seed production and seed dispersal.

TreeMig consists of 62 subroutines that can be summarized into four thematic modules (Fig. I.A.1). Here, the most important modules are described: (1) SpatialSimu; (2) Dynamics; (3) Interact, (4) Lfcalc. The simulations start by opening various parameter and input files that define technical details and specify the life-history traits of the individual tree species and the abiotic environment within which the simulation will be performed. Subsequently, the SpatialSimu module is called within which the local tree dynamics is assessed (Fig. I.A.2). SpatialSimu calls two submodules, Dynamics (Fig. I.A.3) and Interact (Fig. I.A.5). The Dynamics module (Fig. I.A.3) assesses seeds, juvenile and adult tree dynamics for each stand height class. The dynamics are driven by the light density distribution as calculated in the submodule Lfcalc (Fig. I.A.4). The Interact module (Fig. I.A.5) regulates seed dispersal in geographical space. Seeds are dispersed using a linear combination of two exponential equations to account for short- and long-distance dispersal. The TreeMig simulations are closed by writing the results in an output file.

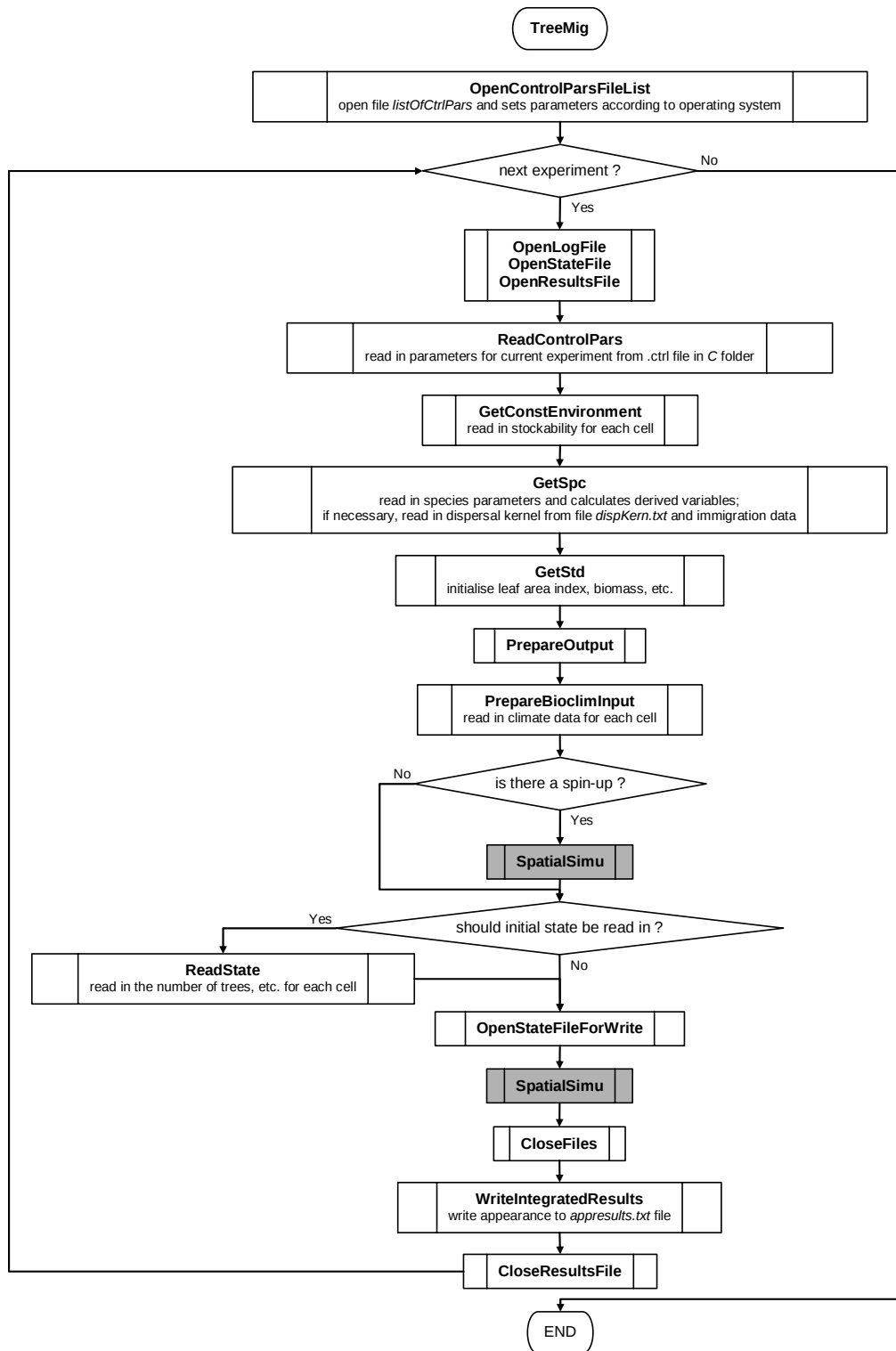


Figure I.A.1. General detailed TreeMig flowchart.

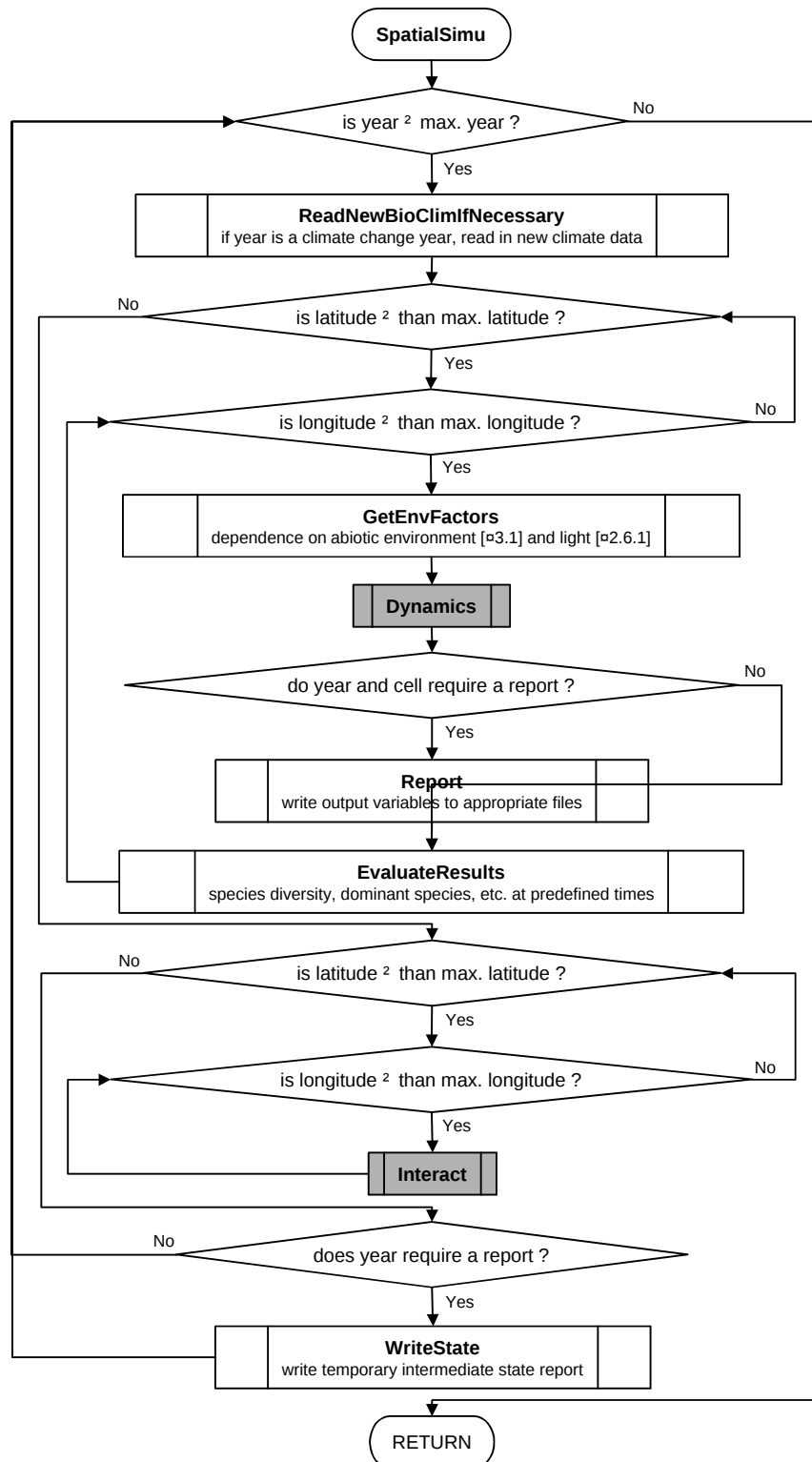


Figure I.A.2. The TreeMig *SpatialSimu* module.



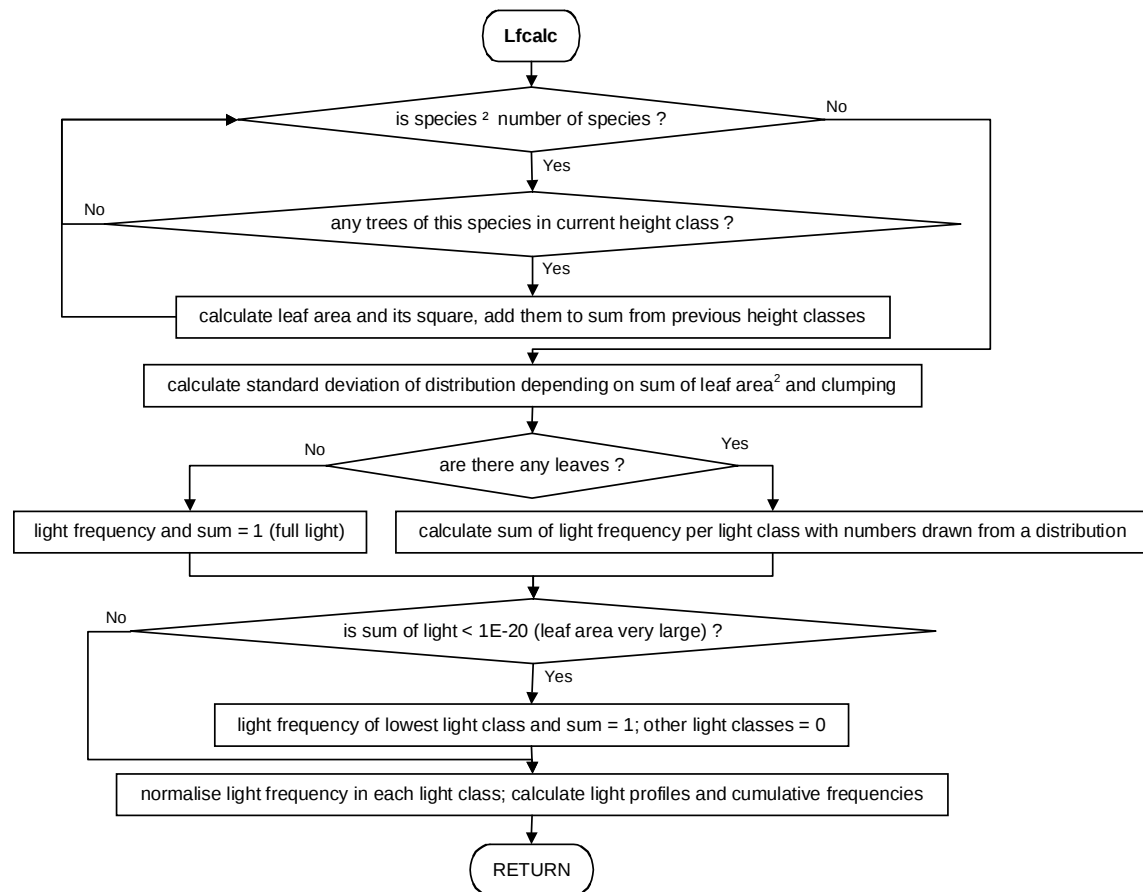


Figure I.A.4. The TreeMig *Lfcalc* module.

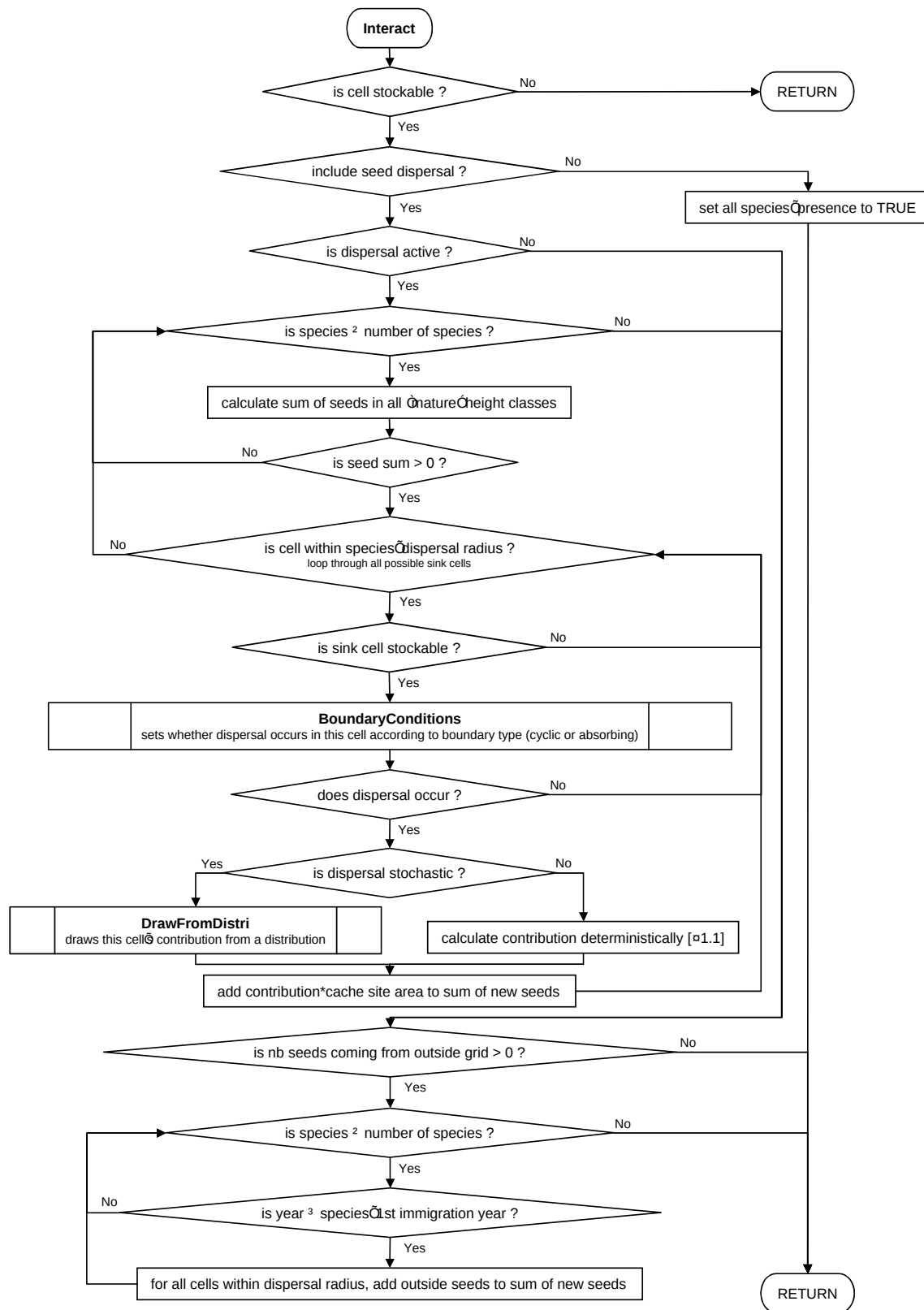


Figure I.A.5. The TreeMig *Interact* module.

*Species parameters***Table I.A.1a.** Species parameters of TreeMig, adult trees.

Name	Abbr	sType/ B	sType/ N	DMax	HMax	AMax	G	DDMin	DDMax	WiT	DrT	NTol	brow	ligha
Abies alba	Aa	C	5	215	60	700	117	641	4491	-6	0.3	2	3	1
Larix decidua	Ld	D	2	185	52	850	170	323	2325	-11	0.3	1	2	9
Picea excelsa	Pe	C	5	210	58	930	171	385	2325	-999	0.2	2	2	5
Pinus cembra	Pc	C	5	180	26	1050	115	323	1124	-11	0.4	1	3	5
Pinus montana	Pm	C	5	50	23	300	138	436	1925	-999	0.5	1	2	9
Pinus silvestris	Ps	C	4	155	45	760	119	610	2777	-999	0.5	1	2	9
Taxus baccata	Tb	C	5	355	22	2110	47	1011	4491	-5	0.4	2	3	3
Acer campestre	Ac	D	2	80	23	170	156	1062	4491	-999	0.4	2	1	5
Acer platanoides	Ap	D	3	170	32	380	142	1042	4768	-17	0.3	2	1	4
Acer pseudoplatanus	As	D	3	215	37	550	125	898	4491	-999	0.3	2	1	4
Alnus glutinosa	Ag	D	2	130	31	240	250	898	5230	-16	0.1	2	2	5
Alnus incana	Ai	D	2	160	22	150	266	610	4204	-999	0.1	2	2	7
Alnus viridis	Av	D	2	20	4	100	265	272	1237	-999	0.2	2	2	7
Betula pendula	Bp	D	1	115	29	220	278	610	4655	-999	0.2	1	1	9
Carpinus betulus	Cb	D	3	110	27	220	177	898	4655	-9	0.3	2	3	3
Castanea sativa	Cs	D	3	355	33	1510	142	1237	4778	-999	0.4	1	2	5
Corylus avellana	Ca	D	3	70	10	70	95	898	4655	-16	0.4	2	3	6
Fagus silvatica	Fs	D	3	225	45	430	191	723	4655	-4	0.3	1	3	1
Fraxinus excelsior	Fe	D	2	190	42	350	177	980	4491	-17	0.2	3	2	6
Populus nigra	Pn	D	2	190	36	280	285	662	5405	-999	0.1	3	3	5
Populus tremula	Pt	D	2	125	30	140	310	610	4655	-999	0.3	1	3	7
Quercus petraea	Qp	D	3	285	45	860	195	785	4655	-5	0.3	1	2	7
Quercus pubescens	Qu	D	3	90	25	500	148	1011	4655	-999	0.4	2	2	7
Quercus robur	Qr	D	3	320	52	1060	195	1042	4655	-17	0.4	1	2	9
Salix alba	Sa	D	1	100	27	170	278	1062	5405	-999	0.1	3	1	5
Sorbus aria	So	D	2	55	22	180	82	898	5343	-999	0.4	2	2	7
Sorbus aucuparia	Sr	D	1	65	19	110	167	498	4204	-999	0.4	1	2	7
Tilia cordata	Tc	D	3	230	30	940	114	1339	4491	-19	0.4	2	2	5
Tilia platyphyllos	Tp	D	3	405	39	960	110	1339	4491	-999	0.3	2	2	3
Ulmus scabra	Us	D	3	195	43	480	153	1062	5230	-16	0.3	3	1	3

Table I.A.1b. Species parameters of TreeMig, reproduction , dispersal, saplings.

Name	lighs	Min mat	seed Germ	Seed Loss	SeedMax Age	period	maxseed	disp Fac	alfa1	alfa2
Abies alba	3	7	0.46	0.8	1	4.3	50000	1	100	0
Larix decidua	8	4.4	0.39	0.8	6	5.7	133000	1	100	0
Picea excelsa	5	10.1	0.76	0.8	6.6	5.4	96500	1	100	0
Pinus cembra	6	2.4	0.64	0.8	3	8	1000	0.99	25	200
Pinus montana	8	1.6	0.54	0.8	5.3	4	11000	1	100	0
Pinus silvestris	7	2.6	0.91	0.8	7	2.8	22000	1	100	0
Taxus baccata	4	0.6	0.6	0.8	4.5	1	23000	0.99	25	200
Acer campestre	5	4.1	0.8	0.8	2.8	3.5	193000	1	100	0
Acer platanoides	2	3.1	0.55	0.8	2.8	3.4	510000	1	100	0
Acer pseudoplatanus	2	2.6	0.6	0.8	2.1	4	551500	1	100	0
Alnus glutinosa	5	4.5	0.4	0.8	4	2.3	218500	0.99	25	200
Alnus incana	6	2.6	0.33	0.8	5.5	2	400000	0.99	25	200
Alnus viridis	7	2.3	0.15	0.8	5	2	47000	0.99	25	200
Betula pendula	7	4.5	0.19	0.8	4.8	2	1177500 0	1	200	0
Carpinus betulus	4	3.4	0.67	0.8	6.3	2	154000	1	100	0
Castanea sativa	5	2.2	0.58	0.8	0.5	1	4000	0.99	25	200
Corylus avellana	6	0.7	0.3	0.8	1.5	1.5	6000	0.99	25	200
Fagus silvatica	3	14.7	0.71	0.8	3.3	8	29000	0.99	25	200
Fraxinus excelsior	4	5	0.6	0.8	3.7	3.2	42000	1	100	0
Populus nigra	5	2.7	0.2	0.8	0.6	1	1890000	1	200	0
Populus tremula	6	4.8	0.4	0.8	3.8	1	1680000	1	200	0
Quercus petraea	6	10.2	0.69	0.8	2.6	5.5	47000	0.99	25	200
Quercus pubescens	7	8.7	0.7	0.8	1	5	18000	0.99	25	200
Quercus robur	7	11.6	0.75	0.8	1.8	4.9	27500	0.99	25	200
Salix alba	5	15.6	0.2	0.8	2	2	1512000	1	200	0
Sorbus aria	6	2.6	0.6	0.8	4.3	1	80500	0.99	25	200
Sorbus aucuparia	6	3.6	0.7	0.8	8	1	375000	0.99	25	200
Tilia cordata	5	2.2	0.45	0.8	2.9	2	720000	1	100	0
Tilia platyphyllos	4	1.6	0.48	0.8	2.5	3	380500	1	100	0
Ulmus scabra	4	6.4	0.35	0.8	7.7	2.1	372000	1	100	0

Table I.A.2. Explanation of species parameters in Table I.A.1.

Variable	Symbol	Definition	Unit
Name		Species name	
Abbrv		2-letter abbreviation of species name	
sType/B		Species type: coniferous [C] or deciduous [D]	
sType/N		Species type: shading capability low [1] to high [5]	
DMax	$d_{\max}$	Max. diameter at breast height (DBH)	cm
HMax	$h_{\max}$	Max. height	m
AMax	$T_{\max}$	Max. age	year
G	$\gamma_{\max}$	Max. growth rate	cm/year
DDMin		Max. yearly degree-day sum above 5.5 °C	degree-day
DDMax		Min. yearly degree-day sum above 5.5 °C	degree-day
WiT		Min. mean temperature of winter months (Dec, Jan, Feb)	°C
DrT		Drought tolerance: prop. of evapotranspiration deficit tolerated	
NTol		Low nitrogen concentration tolerance: tolerant [1] to intolerant [3]	
brow		Susceptibility to browsing: high [3] to low [1]	
lighs		Sapling light parameter: shade-intolerant [1] to shade-tolerant [9]	
ligha		Adult light parameter: shade-intolerant [1] to shade-tolerant [9]	
minmat	$l_{s,\min}$	Min. height for maturity	m
seedGerm	β	Seed germination rate	
seedLoss	μ_s	Seed loss rate	
seedMaxAge	T_{germ}	Max. seed age	year
period	p	Mast seeding period	year
maxseed	$S_{\max}$	Max. number of seeds	
dispFac	κ	Fraction of long-distance dispersal	
alfa1	α_1	Short-distance dispersal	m
alfa2	α_2	Long-distance dispersal	m

Appendix II Parameters for *Betula pubescens*

The parameters are defined in Lischke *et al.* (2006, see also Appendix I - Table I.A.2), which also lists the values for all the other species in the model. The values of some parameters are given by the calibration described in this paper. Others were derived from literature (Edlin and Nimmo, 1983; Polunin, 1984; Marcet and Gohl, 1985; Leibundgut, 1991; Aeschimann and Burdet, 1994; Godet, 1999; Amann, 2004) and expert knowledge (R. Jalkanen, personal communication). Following the method described by Bugmann (1994), these parameters are equal to the average between the mean and maximum of all values found in the literature (including expert knowledge). The number of literature sources is given in brackets. The remaining parameters were given the same values as for the closely-related species *Betula pendula*.

Parameter	Value	Source
Name	Betula_pubescens	
Abbrv	Bu	
sType/B	D	
sType/N	1	id. <i>B. pendula</i>
kDMax	60	literature (3)
kHMax	27	literature (8)
kAMax	115	literature (4)
kG	180	calibration
kDDMin	325	calibration
kWiT	-13	calibration
kDrT	0.4	id. <i>B. pendula</i>
kNTol	1	id. <i>B. pendula</i>
kbrow	1	id. <i>B. pendula</i>
klighs	6	id. <i>B. pendula</i>
kligha	8	id. <i>B. pendula</i>
minmat	2	literature (1)
seedGerm	0.19	id. <i>B. pendula</i>
seedLoss	0.8	id. <i>B. pendula</i>
seedMaxAge	4.8	id. <i>B. pendula</i>
period	2	literature (2)
maxseed	11775000	id. <i>B. pendula</i>
dispFac	1	id. <i>B. pendula</i>
alfa1	200	id. <i>B. pendula</i>
alfa2	0	id. <i>B. pendula</i>

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