Combining probabilistic land-use change and tree population dynamics modelling to simulate responses in mountain forests

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Abstract

Altitudinal tree lines are mainly constrained by temperature, but can also be influenced by factors such as human activity, particularly in the European Alps, where centuries of agricultural use have affected the tree-line. Over the last decades this trend has been reversed due to changing agricultural practices and land-abandonment. We aimed to combine a statistical land-abandonment model with a forest dynamics model, to take into account the combined effects of climate and human land-use on the Alpine tree-line in Switzerland.

Land-abandonment probability was expressed by a logistic regression 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. This was implemented in the TreeMig spatio-temporal forest model. Distance from forest edge and degree-day sum vary through feed-back from the dynamics part of TreeMig and climate change scenarios, while the other variables remain constant for each grid cell over time.

The new model, TreeMig-LAb, was tested on theoretical landscapes, where the variables in the land-abandonment model were varied one by one. This confirmed the strong influence of distance from forest and slope 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 a model where abandonment probability was a constant. Two scenarios were used: natural succession only (100% probability) and a probability of abandonment based on past transition proportions in that area (2.1% per decade). The former showed new forest growing in all but the highest-altitude locations. The latter was more realistic as to numbers of newly forested cells, but their location was random and the resulting landscape heterogeneous. Using the logistic regression model gave results consistent with observed patterns of land-abandonment: existing forests expanded and gaps closed, leading to an increasingly homogeneous landscape.
1. 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. Land-cover change is most commonly caused by human activity rather than natural succession (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 (Balick, 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). Subsidies may also affect the balance of costs and benefits, but a variable indicating highly subsidised (Alpine) agricultural land did not prove significant in the original model (Gellrich et al., 2007; Gellrich and Zimmermann, 2007). It therefore seems that subsidies cannot fully compensate for the costs of cultivating very steep land. 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 tree population processes (e.g. growth, competition) and is therefore well adapted to simulating the effects of changes such as climate warming or land-abandonment. By including spatial environmental drivers as well as spatial interactions, the model accounts for niche- as well as potential neutral effects on spatial species distributions. In addition, a new version of TreeMig has been specifically calibrated to simulate tree population dynamics at the Alpine tree-line ecotone (Rickebusch et al., 2007). Land-use was already present in TreeMig 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 of its parts.

The purpose of this study is to combine two different models: a statistical land-abandonment model (logistic regression) based on socio-economic factors and a forest model (TreeMig) capable of simulating tree species 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 TreeMig-LAB with two alternative approaches: natural succession on its own and a simple agriculture to forest conversion proportion.

2. Materials and methods

2.1. Statistical land-abandonment model

The statistical 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 agricultural land-abandonment, and subsequent forest regeneration, or lack thereof (absence) between the Swiss Area Statistic censuses of 1985 and 1997 (SFSO, 1992a, 2001). The definitions of “forest” and “agriculture” are the same as in the 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/copes 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. The resulting model gives 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 the “agriculture” data points from the 1985 Swiss Area Statistic census (100 m lattice) above 800 m in altitude. 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 model development and validation, 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):

\[
P(Y = 1) = \frac{\exp(\alpha + \sum(\beta_k X_k))}{1 + \exp(\alpha + \sum(\beta_k X_k))}
\]

where \( Y \) takes the value 1 if the land is abandoned and 0 otherwise, \( \alpha \) is a constant and \( X \) a vector of explanatory variables with respective coefficients \( \beta_k \). 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 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 this land-abandonment 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). Kappa (\( \kappa \)) is the proportion of specific agreement, often used to assess improvement over chance. The ROC (receiver operating characteristic) plot shows the sensitivity (fraction of true positive results) versus the opposite of the specificity (fraction of false positive results), for thresholds ranging from 0 to 1 in 0.01 steps.

### 2.2. 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 above (see Section 2.1).

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 feedback 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 (without land-abandonment) within currently observed “forest” cells (map input). The spin-up serves to establish tree populations of reasonable age and structural distribution at the start of a simulation. After that, land-abandonment is initiated and the probability of abandonment of each “agriculture” grid cell is calculated (Eq. (1)) at 10-year intervals, using the current degree-day sum and distance from forest values, without any stochastic factor. Because the original land-abandonment 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 are suitable. 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; seedlings and saplings constitute height class 0) and (b) a minimal biomass of 2 t/ha. Biomass in TreeMig takes into account stem and foliage weight, but not roots or seeds. 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. A very low biomass threshold was chosen because it has to include all the trees up to the tree species line (Körner and Paulsen, 2004), as models like

| Table 1 – Explanatory variables used in the statistical land-abandonment model |
|-----------------|-----------------|-----------------|
| Variable        | Description     | Unit           |
| DDSEX  (a)      | Degree-day sum  | °C day          |
| DISTFOR  (b)    | Distance from forest | m           |
| SOILSTON  (c)   | Soil stoniness  | %              |
| SLOPE  (d)      | Slope angle     | °              |
| PRSECT23  (e)   | Proportion of employees in the secondary and tertiary sectors | % |
| PRCOMMUT  (e)   | Proportion of commuters | % |
| PRFRUITA  (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).
TreeMig simulate indifferently forests, groups of trees and isolated trees.

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.

2.3. Testing on theoretical landscapes

TreeMig-LAb was tested on a series of theoretical landscapes consisting of a 40 × 60 cell grid with 250 m spatial resolution. Forest was initially present in a 40 × 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 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 2) in each landscape, giving a total of 13 different landscapes: one with all “default” values, four with varying DDDSM 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 DDDSM, DISTFOR and SLOPE, the first two because they are modified by feed-back within the land-abandonment module or by any climate change scenario fed into TreeMig and the last because it is the “constant” variable with the most weight in the land-abandonment model. The values were varied between simulations rather than within the grid (e.g. along a gradient) to avoid neighbour-hood effects which would make the results difficult to interpret. We used the maxima of each variable for Eq. (1) as “default” values to maximise abandonment probability and reduce the 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 DDDSM, it was possible to use a single value as it is only modified in the event of climate change (not applied 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 rates at which the forest advanced for the different values of degree-day sum and slope. This rate was measured as the first year a cell was abandoned in each row of “agriculture” cells. In other words, it is the time required for abandonment to occur at a given distance from the original forest edge. Rates cannot be calculated in this way when DISTFOR was being varied, as this distance was set to an artificial value bearing no relation to the actual distance on the grid.

2.4. Testing on a real landscape—Engadine case study

In order to evaluate TreeMig-LAb in a real landscape, we chose a test area of 100 × 100 cells of 250 m resolution, situated in the Upper Engadine valley, Switzerland (Fig. 1). The grid’s altitudinal range is 1370–3720 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.

This setup was used to compare the results of the simulation using the land-abandonment model and two alternatives: (a) a “natural succession only” approach, representing forest spread following complete and immediate land-abandonment, and (b) a “constant probability” approach,

<table>
<thead>
<tr>
<th>Variable</th>
<th>Unit</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>DDDSM</td>
<td>°C day</td>
<td>300*, 600, 900, 1200, 1500</td>
</tr>
<tr>
<td>DISTFOR</td>
<td>m</td>
<td>100, 250, 500, 750, 1000</td>
</tr>
<tr>
<td>SOILSTON</td>
<td>%</td>
<td>45*</td>
</tr>
<tr>
<td>SLOPE</td>
<td>°</td>
<td>5, 20, 35*, 50</td>
</tr>
<tr>
<td>PRSECT23</td>
<td>%</td>
<td>10*</td>
</tr>
<tr>
<td>PRCOMMUT</td>
<td>%</td>
<td>10*</td>
</tr>
<tr>
<td>PRFUTIFA</td>
<td>%</td>
<td>10*</td>
</tr>
</tbody>
</table>

The numbers followed by an asterisk are the default values, designed to maximise the abandonment probability in the model (Eq. (1)). 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 1.

Fig. 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.
where of 2.1% of the land was abandoned every 10 years. Both do not take into account the geo- and bio-physical properties of each grid cell. In the first case, all “agriculture” cells were abandoned in the first time-step after the 300-year spin-up. In the second case, 2.1% of the agricultural cells were abandoned every 10 years. This percentage matches the transition proportion between the two Swiss Area Statistic censuses within the Engadine test area, scaled down from 12 to 10 years:

\[
\text{Probability} = \frac{P}{N} \tag{2}
\]

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 land-abandonment 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.

3. Results

3.1. Statistical land-abandonment model

The results of the logistic regression (Table 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 exploit 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, as both the linear and quadratic terms were significant, 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 the optimised cut-off level of 0.05) 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. 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).

The numbers of grid cells abandoned per century for different values of degree-day sum, distance from forest and slope (Fig. 3) generally reflect what would be expected from these variables’ coefficients in the logistic regression (Table 3), namely a negative trend for DDSUM and DISTFOR, and a parabolic response for SLOPE. In the case of DISTFOR (Fig. 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

![Fig. 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) vs. 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.](image)

### Table 3 – Coefficients and \(p\)-values for the statistical land-abandonment model (Eq. (1))

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient estimate</th>
<th>(z) statistic</th>
<th>(p) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>−1.9610</td>
<td>−4.122</td>
<td>0.00004***</td>
</tr>
<tr>
<td>DDSUM</td>
<td>−0.0003</td>
<td>−3.392</td>
<td>0.00069***</td>
</tr>
<tr>
<td>DISTFOR</td>
<td>−0.0111</td>
<td>−15.458</td>
<td>&lt;2E−16***</td>
</tr>
<tr>
<td>SOILSTON</td>
<td>0.0469</td>
<td>6.195</td>
<td>&lt;2E−10***</td>
</tr>
<tr>
<td>SOILSTON(^2)</td>
<td>−0.0005</td>
<td>−5.616</td>
<td>1.95E−08***</td>
</tr>
<tr>
<td>SLOPE</td>
<td>0.1554</td>
<td>9.351</td>
<td>&lt;2E−16***</td>
</tr>
<tr>
<td>SLOPE(^2)</td>
<td>−0.0023</td>
<td>−7.627</td>
<td>2.39E−14***</td>
</tr>
<tr>
<td>PRSECT23</td>
<td>−0.0367</td>
<td>−3.297</td>
<td>0.00098***</td>
</tr>
<tr>
<td>PRSECT23(^2)</td>
<td>0.0002</td>
<td>2.783</td>
<td>0.00538***</td>
</tr>
<tr>
<td>PRCOMMUT</td>
<td>−0.0070</td>
<td>−3.474</td>
<td>0.00051***</td>
</tr>
<tr>
<td>PRFUTIFA</td>
<td>−0.0193</td>
<td>−13.377</td>
<td>&lt;2E−16***</td>
</tr>
</tbody>
</table>

The variables are described in Table 1.
Fig. 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. For distance from forest (b), the default was the real distance, as measured on the grid (250 m resolution, square cells). The simulation with distance from forest set to 1000 m is not shown, as abandonment was practically non-existent.

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. 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. 4a). When SLOPE is varied, both the number of abandoned cells (Fig. 3c) and the advance rate (Fig. 4b) reflect the shape of the response curve, which is a parabola with a maximum for a slope value around 35°.

Mapping the theoretical landscapes helps to illustrate some patterns which may appear in the land-abandonment process (Fig. 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) and the small advance (500 m; Fig. 4) between years 300 and 400. The map (Fig. 5)
Fig. 4 – Advance rate: distance between each row and the initial forest edge vs. 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 2 for default values).

Fig. 5 – Progression of land-abandonment on the theoretical landscape with all variables set to default values (Table 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.
Fig. 6 – Results after 100 and 200 years of land-abandonment for three different modelling approaches: our land-abandonment 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).

shows this to be a “filling-in” phase, where the patchy network of newly abandoned land was becoming more homogenous.

3.3. Engadine case study

The results of the simulations in a real landscape (Engadine, Switzerland), expressed as total tree biomass, show considerable differences between the land-abandonment model and the two alternatives used (Fig. 6). In the “natural succession only” approach (immediate and complete abandonment), most of the current grassland and agricultural land below the potential tree species line (2400–2600 m) turns into forest. Only high-altitude grid cells (>2600 m), 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 land-abandonment 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 land-abandonment 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 TreeMig-LAb 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. 7). The natural succession approach simply reflects the number of “agriculture” grid cells available in each band. The land-abandonment 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 land-abandonment model to predict abandonment produces a shift in the distribution towards lower altitudes. In the second century after the start of land-abandonment, there are no cells left to be colonised by natural succession (Fig. 7). In both other cases the number of newly abandoned cells drops, but more drastically in the case of the land-abandonment model. Below 2600 m, most of the abandoned cells eventually reach the models’ requirements for “forest” (2 t/ha biomass and at least one tree in height class 1, i.e. >1.37 m), 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 land-abandonment model and the “constant proportion” one are shown by the area and distance from original forest edge of the newly regenerated forest patches (aggregates of contiguous cells) (Fig. 8). One-sided t-tests show that the average area of the patches from the land-
abandonment model is greater ($t = 3.255^{***}$) and their average distance from the old forest smaller ($t = -12.36^{***}$).

4. **Discussion**

4.1. **Statistical land-abandonment model**

The statistical land-abandonment model we developed to extend TreeMig into TreeMig-LAb is very similar to that of Gellrich et al. (2007), to whom we refer for further explanations as to the significance of the explanatory variables. The evaluation exercise shows that the land-abandonment 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
Fig. 8 – Area and distance from the edge of the nearest original forest patch for the new forest patches in the land-abandonment model and constant proportion approaches. The average patch area is 140,657 m² for the land-abandonment model and 112,833 m² for the “constant proportion” approach. The average distance from forest is 265.8, respectively 630.3 m.

of mechanisation) in our model, as all the socio-economic variables were measured on the municipality level. Additionally, land-abandonment and subsequent forest regeneration in the calibration data show considerable unexplained 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.

4.2. Theoretical landscapes

The results obtained by running TreeMig-LAb 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 land-abandonment model and the TreeMig-LAb output (number of abandoned cells, advance rate) for different levels of DDSUM. 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 TreeMig-LAb. 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.

4.3. 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 TreeMig-LAb 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, as is the case in a “natural succession only” model.

The “constant proportion” and land-abandonment models 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 land-abandonment model, as there is for instance some correlation between SLOPE and DISTFOR. These two variables were nevertheless kept through the step-wise variable selection process, as DISTFOR explains an additional part of the variation linked to shade, seed rain, duration of snow coverage, shortage of water due to roots, etc. (Gellrich et al., 2007). However, the clumping observed is also due to the positive feed-back process between the different parts of TreeMig-LAb, 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 Schwegler, 2001; Graf Pannatier, 2005). These consequences of land-abandonment result in loss of biodiversity in the long term (though there may be an initial increase), 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 TreeMig-LAb, and degree-day sum, which is essential in case a climate change scenario is used. However, the fact that the abandonment part of TreeMig-LAb 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 land-abandonment model without too much additional computation time. Using the same method (linear interpolation between values at key time points) as for the climate change scenarios which already part of TreeMig, the contribution to the land-abandonment 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 TreeMig-LAb, 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.

Finally, the variables and parameters in the model developed here are only valid for land-abandonment in Switzerland, because policies and other socio-economic factors vary from one country to another. However, the structure implemented in the TreeMig-LAb code may easily be used to support land-abandonment models for other situations.

5. 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 land-abandonment model is still based on landscape units (which make it compatible with TreeMig) rather than individual decision-makers, it is nevertheless based on economic assumptions, thus answering some of the criticisms about attempts to mix ecology and economics in landscape models (Bockstael, 1996; Irwin and Geoghegan, 2001). TreeMig-LAb can now be used to investigate the combined effects of human activity and climate change in the coming decades in Switzerland.

Climate change will affect crop yields, so an upwards shift of the different agricultural land uses (crop growing, pasturing) is possible. However, forest yields will also increase, accelerating the closing of open land. Some factors, such as slope, will remain an obstacle to agriculture and limit the upwards shift due to climate change.

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