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MODELLING THE RATE OF SECONDARY SUCCESSION AFTER FARMLAND ABANDONMENT IN A MEDITERRANEAN MOUNTAIN AREA

Abstract

Secondary succession after farmland abandonment has become a common process in north Mediterranean countries, especially in mountain areas. In this paper a methodology is tested which combines Markov chains and logistic multivariate regression to model secondary succession after farmland abandonment in environments where abiotic constraints play a major role, like mountain areas. In such landscapes a decay in the succession rate with time is usually found, as the best locations are progressively occupied. This is frequently addressed using non-stationary Markov chains. Here, we test if the combination of logistic multivariate regression with Markov chains, however, allows for spatially distributed transitions probabilities based on abiotic factors and therefore it is able to reproduce the preferential colonization of the most favourable locations. The model is tested in the Ijuez valley in the Spanish Pyrenees, which underwent generalised land abandoned during the 50s. Results confirm a substantial improve in the prediction success of the Markov-logistic model when compared to the standard Markov chain approach. As a result, the decay in the succession rate can be successfully modelled. The specific results for our study area are discussed further in an ecological context. The methodology proposed is applicable to any landscape where vegetation dynamics are constrained by environmental factors. However, the inclusion of land use as an explanatory factor would be necessary in human-managed landscapes.

Keywords: environmental constraints, logistic regression, Markov chains, *Pinus sylvestris*, Pyrenees, succession rate.

Introduction

North Mediterranean countries are enduring rural depopulation since last century, specially in marginal areas like mountains (Lasanta et al., 2005; Romero-Calcerrada and Perry, 2004). Immediate consequences of this process are farmland abandonment and decrease in livestock pressure (García-Ruiz et al., 1996; Lasanta et al., 2006; Pueyo and Alados, in press), which enhances natural secondary succession and leads to reforestation of previously occupied areas (Beguería, 2006a; Beguería et al., 2003; Rocchini et al., 2006; Sickel et al., 2004).

There is large interest in applied ecology and environmental planning in understanding the driving processes of secondary succession, because usually land use changes (in type or intensity) lead to land cover change. For this reason, a considerable amount of studies have been devoted to quantify the magnitude of changes in land cover and the processes originating them, like rural abandonment and global warming (Riebsame et al., 1994; Vicente-Serrano et al., 2004). At a finer scale, secondary succession is constrained by physical conditions like topography (Pan et al., 1999). This is specially true for mountain areas, where topography controls climatic gradients and soil and water distribution (del Barrio et al., 1997; Villalba et al., 1994). After a large disturbance, secondary succession is determined by the differential growth, survival and colonization ability of plant species, which can differ largely depending on the environmental conditions (Aragón and Morales, 2003; Mueller-Dombois, 2000; Myster and Pickett, 1994). As a consequence, high variability in the succession rate has been observed in highly heterogeneous areas like mountain landscapes (Prach, 1993).

There is hence great interest in the ability to model the process of secondary succession. When conveniently calibrated for a given case study, spatially-explicit simulation models can become a useful tool for decision making in landscape planning.

This is because they allow understanding the main driving factors in the process, but they also provide ecological forecasting tools for scenario testing. In this context, Markov chain models have been frequently used for modelling ecosystem dynamics, and more specifically for vegetation succession processes (Acevedo et al., 1995; Balzter, 2000; Callaway and Davis, 1993; Usher, 1979).

A Markov chain model describes the states of a system at successive times. The system is characterized by a discrete variable which can adopt several states, and hence the Markov chain describes its changes of state (transitions). In the context of vegetation dynamics, the states of the system are the different vegetation types which characterize the secondary succession sequence. A concept central to the Markov chain theory are the transition probabilities, which quantify the likelihood of a given transition. In a standard Markov chain approach, it is assumed that transition probabilities are constant across space and stationary in time. These conditions are hardly found in nature. For this reason, several authors have criticized their adequacy, and alternative models have been proposed (Hill et al., 2002; Yemshanov and Perera, 2002).

Since transition probabilities are constant across space (usually obtained from counts over the whole spatial domain), standard Markov models average the spatial effects (Usher, 1981). Thus, they are not able to represent the spatial heterogeneity of succession rates present in a real landscape, and consequently they fail in predicting vegetation dynamics in heterogeneous environments. In order to solve this problem, Yemshanov et al. (2002) defined various environmental domains in their study area and derived specific transition matrices for each of them. An improved approach consists on considering the transition probabilities as a continuous spatial variate, dependent on the spatial variation of a set of explanatory variables. These transition probabilities have been estimated using multivariate regression techniques (Augustin et al., 2001), and artificial neural networks (Gullison and Bourque, 2001).

The assumption of stationarity of transition probabilities over time, i.e. that transition probabilities remain constant during the succession process, is another important issue which complicates the application of Markov chain models to the analysis of natural systems (Childress et al., 1998; Usher, 1979). Observation often contradicts the stationarity assumption, since succession rate tends to decrease with time (Myster and Pickett, 1994; Shugart and Hett, 1973). Usher (1979) pointed out that natural succession should be usually modelled as a non-stationary Markov process, i.e., allowing the transition probabilities to change with time. If observations are available at different times, this can be approached by calculating different transition probabilities for each observation interval (Benabdellah et al., 2003; Hill et al., 2002). However, this approach fails to explain the reason why transition probabilities change in time. Besides, it does not allow predicting future states of the system, since future transition probabilities are not known. By including external abiotic factors in transition models it could be possible to explain the decay of succession rate by natural ecological processes, and thus to predict the future evolution of the succession process.

The aim of this work was to assess a methodology to predict the process of secondary succession after farmland abandonment. This methodology was tested in a small valley in the Pyrenees, the Ijuez RiverValley. We hypothesized that secondary succession rate after farmland abandonment is not spatially homogeneous, but shows important differences because of the spatial heterogeneity of the abiotic factors. Also we hypothesized that succession rate would show a decay through the process of secondary succession due to the decreasing availability of favourable locations as the process advances.

We used a simple model which simulates the process of secondary succession based on a stationary Markov chain. Transition probabilities were not spatially homogeneous, but they were estimated using multivariate logistic regression from a set of spatially distributed variables, to allow for spatial heterogeneity. We expected that such a simple model would be able to predict both the temporal and the spatial patterns of secondary succession better than the standard Markov approach.

This work will contribute to understand the process of secondary succession after farmland abandonment on environments with strong abiotic constrains, such as mountain areas. Although the specific results of our research (i.e. the vegetation transition model) are in principle valid only for the specific conditions of the study area, the theory and methods can be generalized for the analysis of secondary succession in any other area. Modelling the process of secondary succession can be a useful tool for environmental planning and forest managers, in Mediterranean mountain areas where land abandonment has been a common landscape process in the last decades, but also at a European scale, where landscape homogenization requires a scientific based landscape planning to maintain cultural and ecological values (Jongman, 2002; Lasanta et al., 2006).

Materials and methods

Study area

The study area corresponds to the Ijuez River Valley, a small tributary to the Upper Aragón River in the Central Spanish Pyrenees, covering an area of 54.6 km^2. The altitude of the valley ranges from 800 to 2200 m. a.s.l. (Fig. 1). The valley lies within the Eocene Flysch sector, lithology consisting of a succession of thin, alternating, heavy folded layers of marls and sandstones. Climate is of submediterranean type, with average temperature ranging from 3.5º to 10º and annual rainfall ranging between 1000 and 2000 mm (Ibarra and De la Riva, 1996).

The Ijuez River valley supported a high human pressure until the last decades of the 19th Century, with full occupation of the land available for cultivation and grazing. According to Ibarra and De la Riva (1996) the depopulation process was slow but steady in the first decades of the 20th century, so by 1950 the valley population was 62% of the population in 1900. In the years 1956 to 1960 the five villages in the valley and most part of the arable lands were bought by the State Forest Service for land reclamation. The population of the valley descended to 26.7% of the initial population by 1960 and 4.4% in 1970. Some reforestation works were carried out mostly between 1956 and 1965 in the abandoned lands, and the rest of the valley underwent a process of natural vegetation recovery. The forestry (natural of aforestations) is not managed for timer production or other purposes. Currently there is no significant land use in the valley except for some crops and meadows in the valley bottom (2% of the area) and cow summer grazing in the alpine pastures (7% of the area). These conditions conform an excellent scenario to study the influence of abiotic factors in secondary succession with minimum interference of land use, which is a problem often encountered.

Potential vegetation in the valley is a forest of *Quercus faginea* Lam. below 1200-1300 m, and *Pinus sylvestris* L. woodland (Scots pine) above this altitude (Montserrat, 1966). *P. sylvestris* has extended its potential area to lower altitude in detriment of *Q. faginea* forest, favoured by aforestations and faster growing rates in secondary succession (Montserrat, 1966).

Secondary succession after farmland abandonment in the study area leads to a fast invasion by weeds (*Brachypodium pinnatum* (L.) P.Beauv., *Carex flacca* Schreb., *Bromus erectus* Huds., *Medicago lupulina* L.) in the first three years, and by shrubs afterwards (*Genista scorpius* (L.) DC., *Juniperus communis* L., *Rosa sp.* and *Crataegus* *monogyna* Jacq.). Finally, *P. sylvestris* colonizes the shrublands, usually developing a monospecific forest, although it can be mixed with *Q. faginea* specially in south oriented slopes where pines grow slower (Gracia et al., 2002). As a consequence, secondary forest in the study area consists mostly on *P. sylvestris* along the whole altitude range.

Assessing land cover change

We built a GIS database based on the analysis of a sequence of aerial photos dating from 1957 (black and white images at aprox. 1:32000 scale), 1977 (black and white images at aprox. 1:18000 scale) and 2002 (digital color orthophoto with a resolution of 1 m). The older photos were orthorrectified using the 2002 image as reference and a 10 m digital terrain model (DTM) with Erdas Imagine 8.5, for a final resolution of aproximately 1 m.

Areas that were cultivated before 1957 were identified and mapped based on the 1957 aerial photos and information on the abandonment process from a previous study by Ibarra & de la Riva (1996). The succesional state of patches that were abandoned was assessed on consecutive images. The abandoned patches were determined and classified into three categories: shrubland, secondary forest and reforestation. Due to difficulties in recognizing shrubland composition in the old aerial photos, only one shrubland category was identified which includes from early to more mature stages of shrubland development. A patch was classified as forest when presenting a percentage of soil covered by trees greater than 60%. Artificial reforestation was identified very clearly, thus not leading to any uncertainty.

Since the interest of this work was the natural succession process, we identified and removed from the analysis the human-promoted transitions (i.e. conversion of natural cover into croplands, which was in any case very limited, and reforestation;

Figure 3). Thus, our analysis was restricted to abandoned farmland areas, isolating the process of natural secondary succession from human-induced changes. Usually, it is difficult to separate abiotic factors from human land use, because they are closely interrelated (Poyatos et al., 2003). However, considering the abrupt depopulation of the Ijuez valley in the decade between 1955 and 1965, we consider that these problems have been reduced to a reasonable minimum in this study.

Assessing the temporal pattern of secondary succession by a standard Markov chain

In a standard Markov chain model, stationary transition probabilities are applied recursively each time step to simulate the changes of state of the system being modelled. This requires the construction of a transition matrix, which includes the transition probability for each possible change between two states (Caswell, 2001). The transition matrices are usually inferred from empirical evidences of the state of the system at various times. From the transition matrix it is possible to predict the proportion of the different vegetation classes at any time, average transition times from one class to another and the average time to reach the final (absorbing) state. In our case we considered only the transition from abandoned fields to shrubland, and from these to incipient secondary forest (the absorbing state). We calculated three transition matrices counting the spatial units (grid cells), n_{ij}, that changed from state i to state j ($i = j =$ {abandoned field, shrubland, secondary forest}) between two consecutive land cover maps.

We tested for non-stationarity of transition probabilities using the Anderson–Goodman test (Anderson and Goodman, 1957),

$$-2\ln(\lambda) = 2\sum_i \sum_j \sum_t n_{ij}(t)\ln(p_{ij}(t)/p_{ij}) \qquad (1)$$

where $n_{ij}(t)$ and $p_{ij}(t)$ are the frequency and transition probabilities at time t, and p_{ij} is the average transition probability from i to j. $-2\ln(\lambda)$ follows a χ^2 distribution with $m(m-1)(t-1)$ degrees of freedom, m being the number of possible states. The null hypothesis tested is that $p_{ij}(t)$ is constant and equal to p_{ij}.

Assessing the spatial pattern of secondary succession by multivariate logistic regression

The use of averaged transition probabilities as calculated in the transition matrix has the drawback of masking the spatial heterogeneity in secondary succession rate that usually exists in real landscapes. For this reason, we used multivariate logistic regression to estimate transition probabilities from spatially distributed variables, in a similar way that was proposed by Augustin et al. (2001). We performed logistic regressions for the transitions between every two consecutive maps. We used forward and backward stepwise procedures to choose only the variables that were relevant to the models. We looked at the variables entering the models and their importance for transition probabilities through their Wald statistics (Hair et al., 1998). Overall fitting of the models was evaluated by the receiver operating characteristic (ROC) curve and computing the area under the curve, AUC (Beguería, 2006b; Swets, 1988). Then, we derived forest transition probability maps for each time period from the regression models, as well as a transition time map.

The explanatory variables were derived from a DTM with 10 m resolution. The variables were the elevation (km), the slope gradient (m m^{-1}), the topographic index, and the potential radiation (kJ). Elevation strongly determines temperature and rainfall in mountain areas (Barry, 1922), and thus it is broadly used as a proxy for climatic gradients (Arroyo and Marañón, 1990; Fernandez et al., 2004). In the study area the temperature gradient with altitude can be determinant, because secondary succession by *P. sylvestris* is observed in its natural range and also at lower elevation. Slope gradient and the topographic index account for water and nutrient availability in the soil. Slope gradient represents the potential energy available at a point, and controls hydrological and erosion processes in the soil (Florinsky et al., 2002). The topographic index $\ln(A_S/\beta)$ (non-dimensional) is calculated from the relative accumulated drainage area, A_S, (i.e. the total upslope area draining to a certain pixel divided by the area of the pixel) and the slope gradient, β (Beven and Kirkby, 1979). The topographic index has been extensively used to express the accumulation of water and soil in the landscape (Gómez-Plaza et al., 2001). Annual potential radiation influences soil temperature and evaporation and hence soil water content, and thus it may also be a decisive factor for determining the succession rate. Potential radiation was estimated using the Potrad 5.1 model, written in the PCRaster dynamic modelling language.

As a result of this stage, the logistic models were translated into maps showing the spatial distribution of the transition probabilities from shrubland to forest for the three observation intervals.

Stochastic simulation of the secondary succession process

In order to assess the capability of the above transition models to adequately represent the time development of the succession process, we performed a stochastic simulation using the transition probability map obtained from the first observation interval. The transition probabilities were applied recursively to the cells corresponding to the abandoned fields, which were initially set to shrubland. The simulation period was set to 1950-2002, corresponding to the observation time, and it was subdivided into a number of equal timesteps. At each time step a random field was generated, and the state of each cell was either changed to forest if the random value at the cell was equal or lower than the transition probability, or left as shrubland in the opposite case. Cells changed to forest were not changed in subsequent time steps. For comparison purposes, an alternative simulation was made using the average transition probabilities obtained from the transition matrices, which represents a standard Markov chain approach. The ability of the Markov-logistic stochastic simulation to predict the observed spatial distribution of vegetation in 2002 was assessed. The statistic employed was the success rate, computed as the percentage of pixels that were well predicted in 2002 (Fielding and Bell, 1997). We also compared the proportion of forest predicted by both models at the three moments with real observations. This allowed us to determine which model best predicted the decay in secondary succession rate. Due to the stochastic nature of the modelling approach, a different final configuration is obtained each time a new simulation is run. In order to obtain reliable validation statistics we used a Monte Carlo technique, consisting on performing a high number (1000) of simulation runs and using the most frequent final state (shrub or forest) for each pixel to compute the statistic (Manly, 1997).

Results

The analysis of the sequence of aerial images confirmed that secondary forest succession following land abandonment has been the dominant process during the second half of the 20th century in the Ijuez Valley (Fig. 2). From the initial state in which 61% of the territory was cultivated, a big part of the farmland (74%) had already been abandoned around 1957 (Fig. 3). 56% of the abandoned fields remained in the shrubland stage, and only 6% of the abandoned surface had reached the incipient forest state by 1957. The other 12% of the surface had been reforested. By 1977 only 14% of the remaining farmland was maintained, while 11% presented a shrubland cover and 9% had evolved towards secondary forest. Important reforestation works were performed on this period, which affected 66% of the abandoned farmland. During the same period, 24% of the shrubland (fields abandoned in the previous interval) evolved into forest, and 65% remained in the same state. From 1977 to 2002 there was no more land abandonment, but secondary succession continued in the shrubland areas. By 2002 croplands were nearly inexistent, only appearing on the valley bottom (around 2% of the total territory). Incipient secondary forest dominated the landscape, although shrub still remained in large areas (21% of the territory; Fig 2).

From the previous analysis on the land cover changes in the valley transition matrices were calculated only for the patches that were abandoned and led to natural succession (Table 1). That is, artificial reforestation of former farmland and the continuity of crops were excluded from the analysis. The period 1957 to 1977 allows comparing the transition probabilities to secondary forest from recent and old abandoned fields (Table 1, panel b). According to the results, the transition probability is lower for the recently abandoned fields, supporting the hypothesis of a decay in the succession rate with time. The same result is found when comparing transition from shrubland to secondary forest (Table 1, panels b and c), for which it was found that the transition probability was reduced from 0.27 to 0.15 between 1957 and 2002. If this probability is referred to a period of one year to correct for the different time spans between the images, the reduction in the transition probability becomes more evident (0.0135 and 0.006). This represents a decay in the average succession rate, which was confirmed by the Anderson-Goodman test of stationarity ($\chi^2 = 1406$, $p < 0.001$).

In order to obtain transition probabilities dependent on abiotic conditions (and thus, spatially variable), three logistic models where adjusted to the transitions observed starting from abandoned fields in 1957, from shrubland in 1957 and from shrubland in 1977. The three models showed a good fit to the data, with AUC equal to 0.77, 0.83 and 0.76 for models a, b and c, respectively (Table 2).

Selection of variables by the two stepwise methods (forward and backward) was consistent, resulting in identical sets of predictor variables. According to the Wald statistic the most important variable in all the three models was potential radiation, having a negative effect on forest transition probability. This results confirm that solar radiation exerts a negative effect on secondary succession rate in our study area. Elevation was the second variable in importance in the first model (Table 2a), but it did not appear in the next two models. Slope gradient and the topographical index, showing positive relation to transition probability, appeared to be much less important in the model. After potential solar radiation, the most important variable in the second and third models was slope gradient, inversely related to transition probability (Table 2b and 2c). The topographic index showed decreased importance with respect to the previous model.

Three maps showing the spatial distribution of transition probabilities were derived from the logistic models (Fig. 4). It can be observed that locations showing high transition probabilities on one moment tend to be occupied by forest in the next step, and thus excluded from the analysis. On the contrary, locations with low transition probabilities tend to appear in subsequent maps, showing slower succession rate. This information can be presented in the form of transition times, i.e. the estimated time to reach the forest state (Fig. 5). Expected transition times to secondary forest in the study area ranged between 25 years in the most favourable areas and more than 200 years in the least favourable ones.

It must be noted that the transition probabilities show more or less the same values at the same locations in the consecutive maps (Fig. 4). The faster occupation of the cells with high transition probability is, thus, responsible for the reduction in the average transition probability which was found previously. This result supports the hypothesis that the succession process can be modelled by a stationary approach, i.e. using the transition probability map from the first observation interval. The results of one such stochastic simulations (Markov-logistic simulation) are shown in Figure 6. A good agreement was found between the simulation results and the situation observed in 2002, the success rate being 67%. For comparison, a standard Markov chain simulation with averaged transition probabilities was not able to predict the spatial distribution of succession states (Fig. 6c), and yielded a success rate of only 50%.

An important fact shown by the Markov-logistic stochastic simulation was the faster colonisation of the most favourable locations. Locations with high transition probability became scarcer as the process advances in time, which determines a decay in the average transition probabilities in the Markov-logistic simulation (Fig. 7). This contrasts with the standard Markov chain model, in which transition probabilities are constant through time. If one compares the observed proportion of secondary forest in the three aerial photos with the forest cover predicted by the two simulations (Fig. 8), a better agreement is also found between the Markov-logistic model and the observation. This has major importance if predictions are to be made about the future state of vegetation in the area, for example in the context of a decision making process through scenario testing. We prolonged the simulation up to year 2100, in order to compare the percentage of forest cover predicted by the two models (Fig. 8). Compared to the standard Markov model, the Markov-logistic simulation predicts a more realistic decay in forest recovery rate, and hence the time to total recovery is significantly higher. The decay curve can be adjusted by a logarithmic function (Fig. 8).

Discussion

This study has shown the existence of a strong relationship between transition probability (and its reciprocal, the succession rate) and abiotic factors in a mountain landscape. This agrees with the results obtained by other authors, which show that forest succession rates can show large differences over relatively short distances in response to environmental gradients (Aragón and Morales, 2003; Carmel and Kadmon, 1999; Donnegan and Rebertus, 1999). This implies that the spatial pattern of secondary succession can be successfully modeled upon the spatial distribution of the abiotic factors.

Vegetation dynamics are very often addressed using Markov chain models, in which transition probabilities are obtained from cross-counting between two correlative vegetation surveys. Utility of Markov chains has been criticized to model future transitions because observed succession rates are seldom stationary (Usher, 1981). In practice, decay in succession rate is observed very often in natural ecosystems (Myster and Pickett, 1994; Shugart and Hett, 1973).

We demonstrate that the decay in succession rate can be modelled using a stationary first order Markov chain if factors determining transition probabilities and their spatial distribution are included in the model. Temporal differences in the succession rate can be explained by the spatial selection of the most favourable locations for secondary succession, which can only be modelled if transition probabilities are considered a continuous spatial variable.

The combination of Markov chains and multivariate analysis incorporating spatial variables related with dispersal abilities has proved to be very useful in matching observed spatial succession patterns (Augustin et al., 2001). Here, we show the utility of this methodology in predicting successional processes in environments highly dependent on abiotic constraints.

In our case study, both the transition matrices and the logistic models showed evidences of non-stationarity. We interpreted the non-stationarity of transition matrices as emerging from the process of vegetation succession in a heterogeneous landscape, in which transition probabilities differ largely from one location to another. The shortage of high favourable locations as the revegetation process advances in time is sufficient to explain the decay in the succession rate observed in the sequence of aerial photos. Accordingly, the results of our simple stochastic dynamic model based on spatially distributed transition probabilities showed a good agreement with the field observations, both in predicting the spatial distribution of secondary forest fifty years after abandonment and the timing of the process for the whole study area.

Nevertheless, we encountered a methodological problem in order to validate the results of the model, pixel-based, with the polygon maps drawn from the aerial photographs, which could affect negatively the success rate. Moreover, the model would be improved by adding neighbour information (Hersperger, 2006; Turner, 1987), seed dispersal patterns and distance from seed sources (Prevosto et al., 2003), but a fully pixel-based data would be required.

Previous models of *P. sylvestris* forest development did not take into account environmental constraints (Prevosto et al., 2003), and thus they were not applicable to a highly heterogeneous area such as the Pyrenees, where abiotic factors play a major role on determining vegetation dynamics at landscape scale (del Barrio et al., 1997). For heterogeneous areas our approach could be more useful. However, our proposed approach should include explanatory variables related to human activities (i.e. grazing and forest management) when landscapes with evidences of human use are taken into consideration.

Furthermore, the relative importance of abiotic constraints can not be directly extrapolated to other areas, as far as it is particular for the landscape analysed and the plant species involved. In our study area elevation and potential solar radiation determined the faster installation of *Pinus sylvestris* after land abandonment. Elevation determines a climatic gradient in mountains (Donnegan and Rebertus, 1999), which reproduces from bottom to top the changes in mean temperature observed from south to north. Since the Pyrenees are located in the southernmost part of the geographical range of *P. sylvestris*, high temperatures and water scarcity in summer are the limiting factors for this species (Castro et al., 2004). Dispersal and establishment determine largely survival of *P. sylvestris* (Castro et al., 2004; Prevosto et al., 2003). As seedling germination take part in spring, high solar radiation reduces water availability and decrease seedling survival during summer in Mediterranean mountains. Low summer temperatures, large water retention and less solar radiation favour the establishment of *P. sylvestris*, and thus increase secondary succession rate (Castro et al., 2004). Water availability and high temperatures are decisive in the distribution of a large amount of trees at the boundary between the summer drought Mediterranean zone and the cooler and moister mountain and northern areas (Pigott and Pigott, 1993).

Accumulation of water and nutrients due to the topography played a secondary role on determining succession rate, although in other mountain areas it has been found to be a major factor determining succession (Donnegan and Rebertus, 1999). It can be argued that in the southern limit of the geographic range of *P. sylvestris* high summer temperature and insolation play a major role and outweigh other factors, which in more temperate conditions would determine the succession rate. Also, it is likely that the broad scale used in this study affected negatively the importance of these factors.

Where conditions are favourable to *P. sylvestris*, it tends to originate nearly monospecific forest. The rapid growth rate of the pine impedes *Quercus faginea* to colonize more mesic areas. It is expected that in locations where successional rates are slower the establishment of *Q. faginea* would be allowed (Gracia et al., 2002).

Nevertheless, further study is needed to confirm this issue.

Conclusions

We propose a method to model the rate of secondary succession after farmland abandonment based on Markov chains and incorporating the effect of abiotic factors through multivariate analysis. This method was able to predict both the spatial and temporal patterns of secondary succession in our study area. For secondary forest of *P. sylvestris* in the Pyrenees, the most important factor determining rate of succession was the gradient of temperature with elevation and potential solar radiation. Water and nutrient availability due to local topographical conditions played a secondary role. The results of this research can be useful for forest managers and environmental planners, in order to decide the best practices after land abandonment. The application of this methodology is suitable anywhere where there are evidences suggesting strong abiotic constraints to secondary succession, such as mountain areas. In human-managed landscapes, the inclusion of human use as explanatory variables (i.e grazing or forest management) could improve predictive power of the model.

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Table 1. Transition matrices for natural secondary succession on abandoned farmland between around 1950 and 1957 (a), 1957 and 1977 (b), 1977 and 2002 (c).

a	Shrubland	Forest
Abandoned fields	0.90	0.10

b	Shrubland	Forest
Abandoned fields	0.55	0.45
Shrubland	0.73	0.27

c	Shrubland	Forest
Shrubland	0.85	0.15

Table 2. Logistic models specifications: *a*, transition from abandoned fields to forest 1977; *b*, transition from shrublands 1957 to forest 1977; *c*, transition from shrublands 1977 to forest 2002.

a	Variable	B	se	Wald	sign.
	Intercept	-1.007	0.164	37.5	<0.001
	elevation	5.136	0.114	2039.8	<0.001
	slope gradient	1.767	0.261	46.0	<0.001
	topographic index	0.134	0.012	127.6	<0.001
	potential radiation	-0.604	0.013	2157.3	<0.001
b	Parameter	B	se	Wald	sign.
	Intercept	9.711	0.232	1757.0	<0.001
	slope gradient	-7.036	0.361	380.7	<0.001
	topographic index	0.050	0.014	12.4	<0.001
	potential radiation	-0.870	0.017	2473.1	<0.001
c	Parameter	B	se	Wald	sign.
	Intercept	7.539	0.255	871.6	<0.001
	slope gradient	-6.328	0.385	270.3	<0.001
	topographic index	-0.123	0.018	48.7	<0.001
	potential radiation	-0.622	0.019	1101.7	<0.001

se: standard error

Figure captions

Figure 1. Location of the study area and relief. Contour interval is 100 m. The area under study (abandoned farmland that undergone natural succession) is shown in grey.

Figure 2. Land cover maps from 1950 (*a*, inferred from 1957 photo and Ibarra & de la Riva (1996), 1957 (*b*), 1977 (*c*) and 2002 (*d*). Legend: 1, mature forest; 2, arable lands; 3, shrubland; 4, secondary forest; 5, reforestation; 6, other.

Figure 3. Transitions tree. In black, the transitions considered in the model.

Figure 4. Forest transition probability maps. *a*, transition from abandoned fields to forest (1977); *b*, transition from shrubs (1957) to forest (1977); *c*, transition from shrubs (1977) to forest (2002).

Figure 5. Expected transition time (years to forest state).

Figure 6. Secondary succession on abandoned fields, land cover in 2002: *a*, observed; *b*, simulated, Markov - logistic model; *c*, simulated, standard Markov chain model. Legend: 1, secondary forest; 2, shrubland.

Figure 7. Average transition probabilities for the standard Markov model (plain line) and the Markov-logistic simulation (dots). Dashed line: adjusted power curve ($y = 5.22 * 10^{40} x^{-12.32}$).

Figure 8. Rate of forest recovery, percentage of the abandoned surface. Big squares, observed; small squares, standard Markov model; dots, Markov-logistic simulation; dashed line, adjusted logarithmic curve ($y = -0{,}67 + 0{,}29 \ln(x-1938{,}7)\ \forall\ x-x_0 > 0$).

Table 1. Transition matrices for natural secondary succession on abandoned farmland

between 1950 and 1957 (a), 1957 and 1977 (b), 1977 and 2002 (c).

a	Shrublands	Forest
Abandoned croplands	0.91	0.09

b	Shrublands	Forest
Abandoned croplands	0.35	0.65
Shrublands	0.73	0.27
Forest	0	1

c	Shrublands	Forest
Shrublands	0.85	0.15
Forest	0	1

Table 2. Logistic models specifications. *a*, transition from abandoned fields to forest 1977; *b*, transition from shrublands 1957 to forest 1977; *c*, transition from shrublands 1977 to forest 2002.

a	Parameter	B	se	Wald	sign.
	Intercept	-1.007	0.164	37.5	<0.001
	elevation	5.136	0.114	2039.8	<0.001
	slope gradient	1.767	0.261	46.0	<0.001
	topographic index	0.134	0.012	127.6	<0.001
	potential radiation	-0.604	0.013	2157.3	<0.001
b	Parameter	B	se	Wald	sign.
	Intercept	9.711	0.232	1757.0	<0.001
	slope gradient	-7.036	0.361	380.7	<0.001
	topographic index	0.050	0.014	12.4	<0.001
	potential radiation	-0.870	0.017	2473.1	<0.001
c	Parameter	B	se	Wald	sign.
	Intercept	7.539	0.255	871.6	<0.001
	slope gradient	-6.328	0.385	270.3	<0.001
	topographic index	-0.123	0.018	48.7	<0.001
	potential	-0.622	0.019	1101.7	<0.001

radiation

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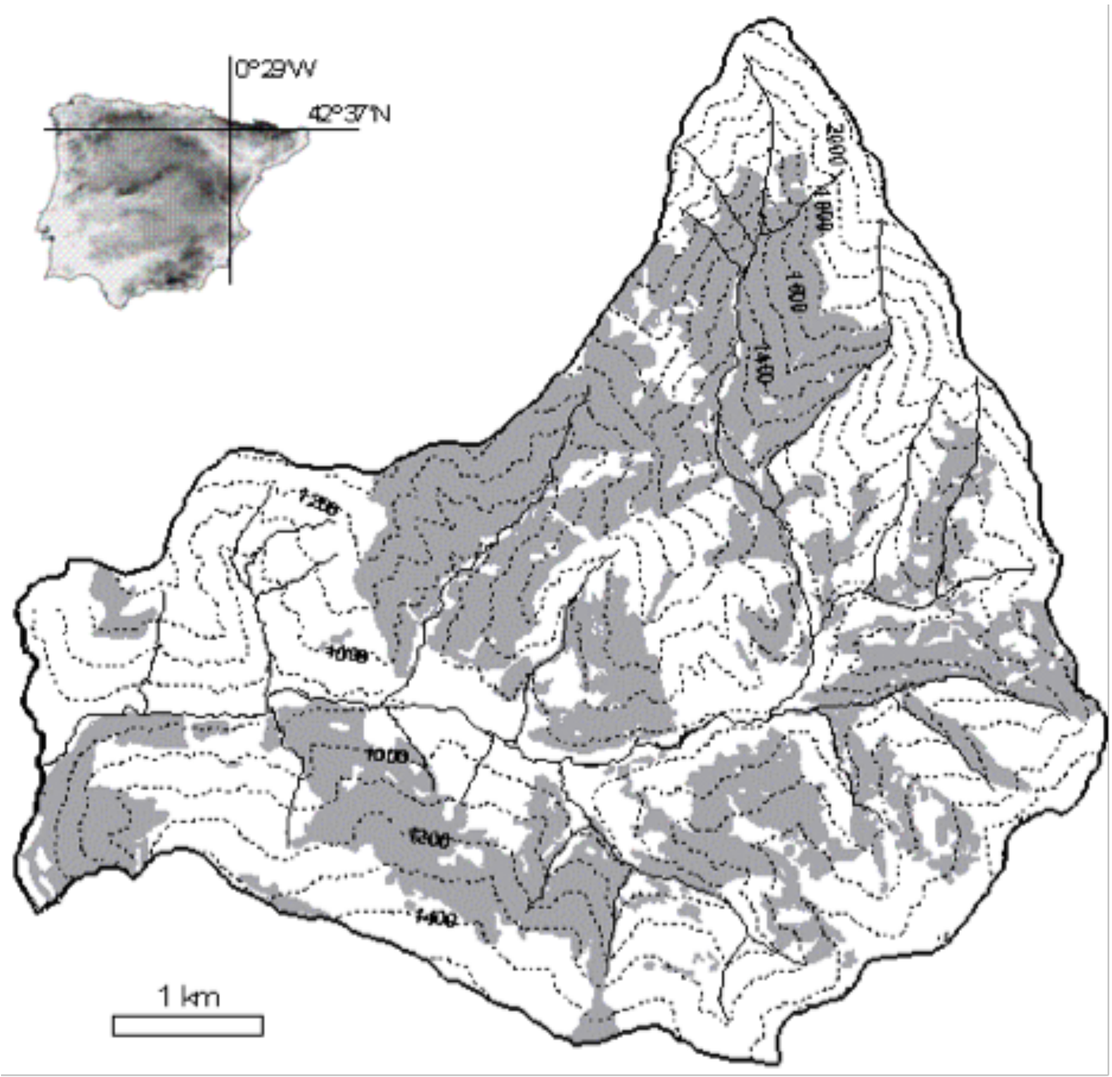
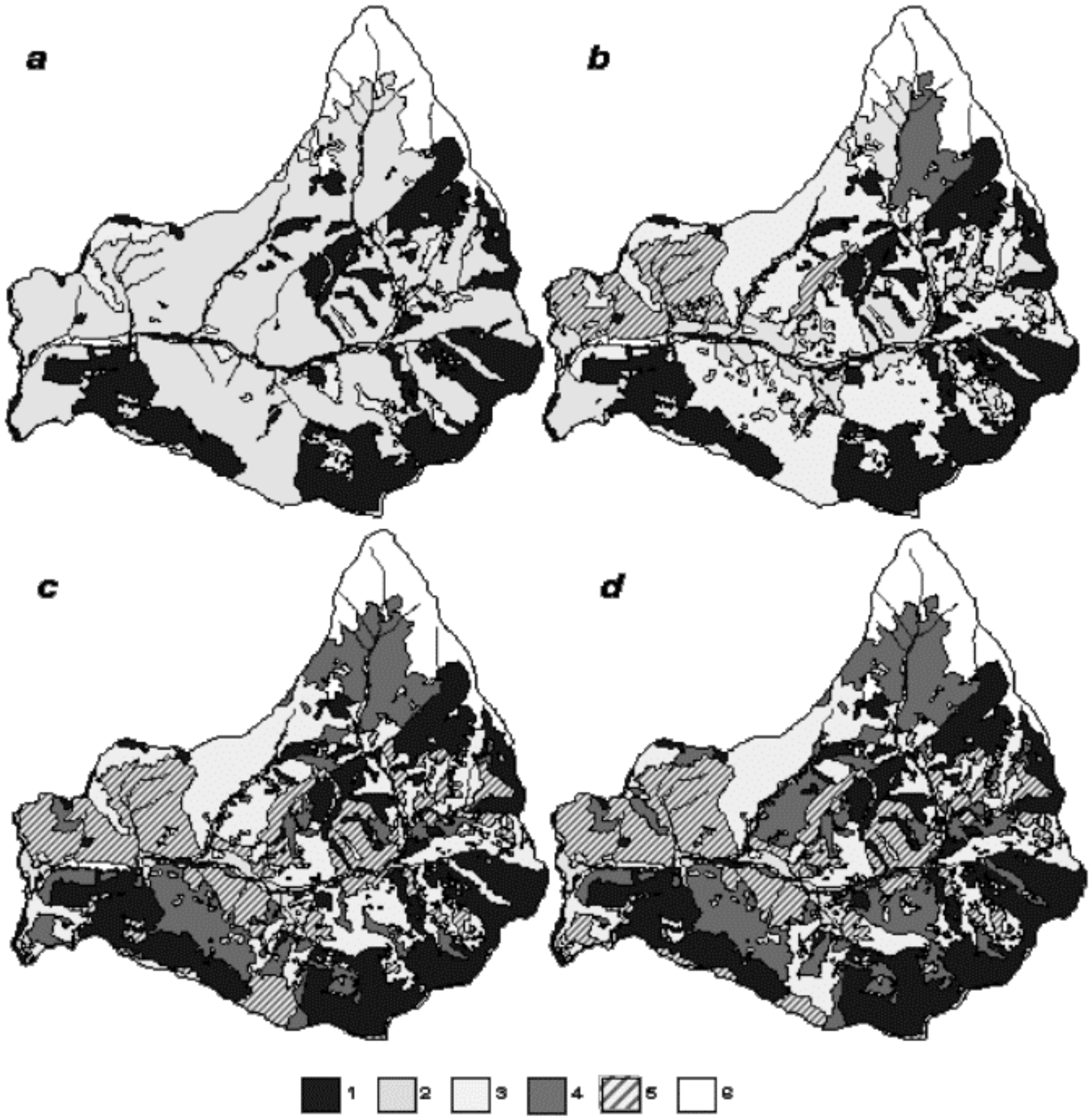


Fig. 1



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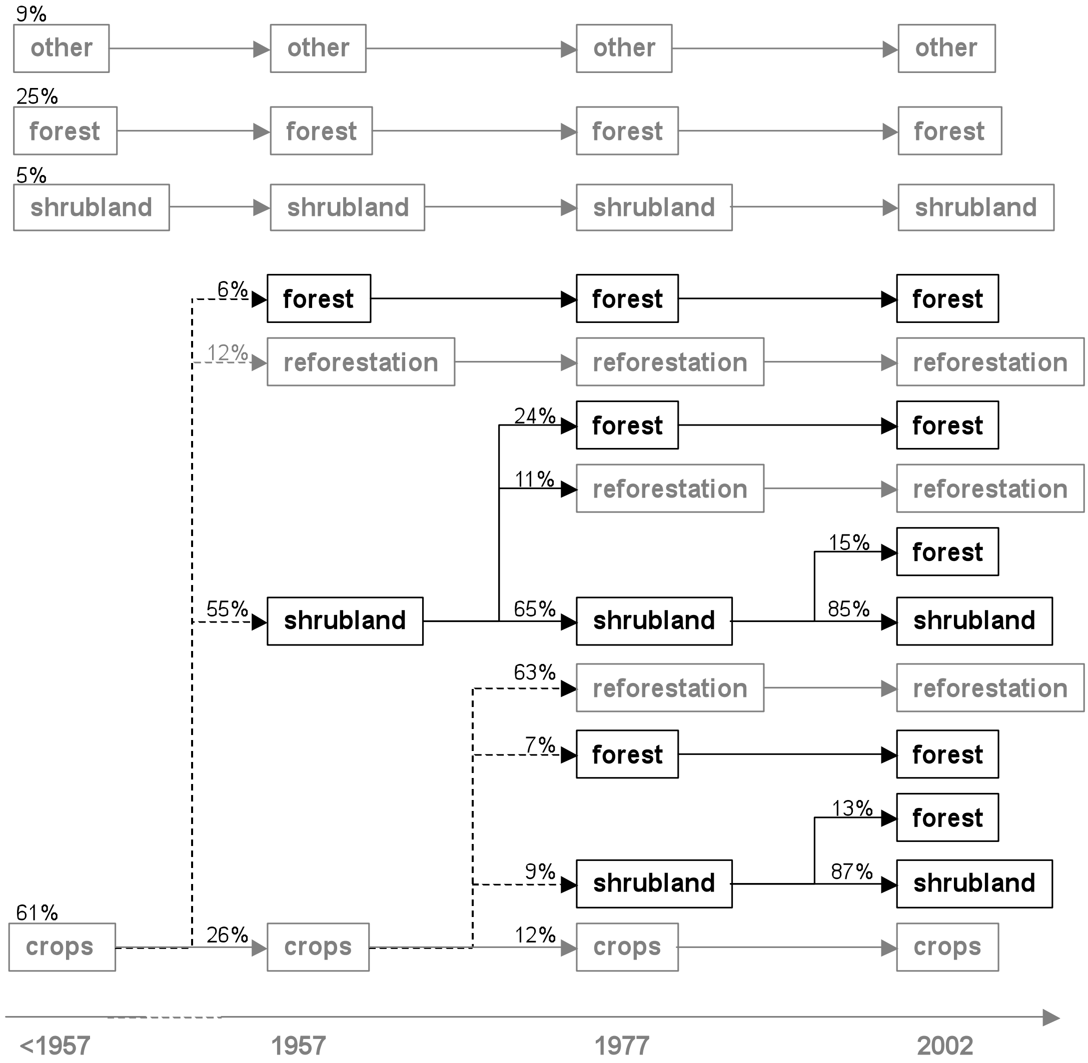
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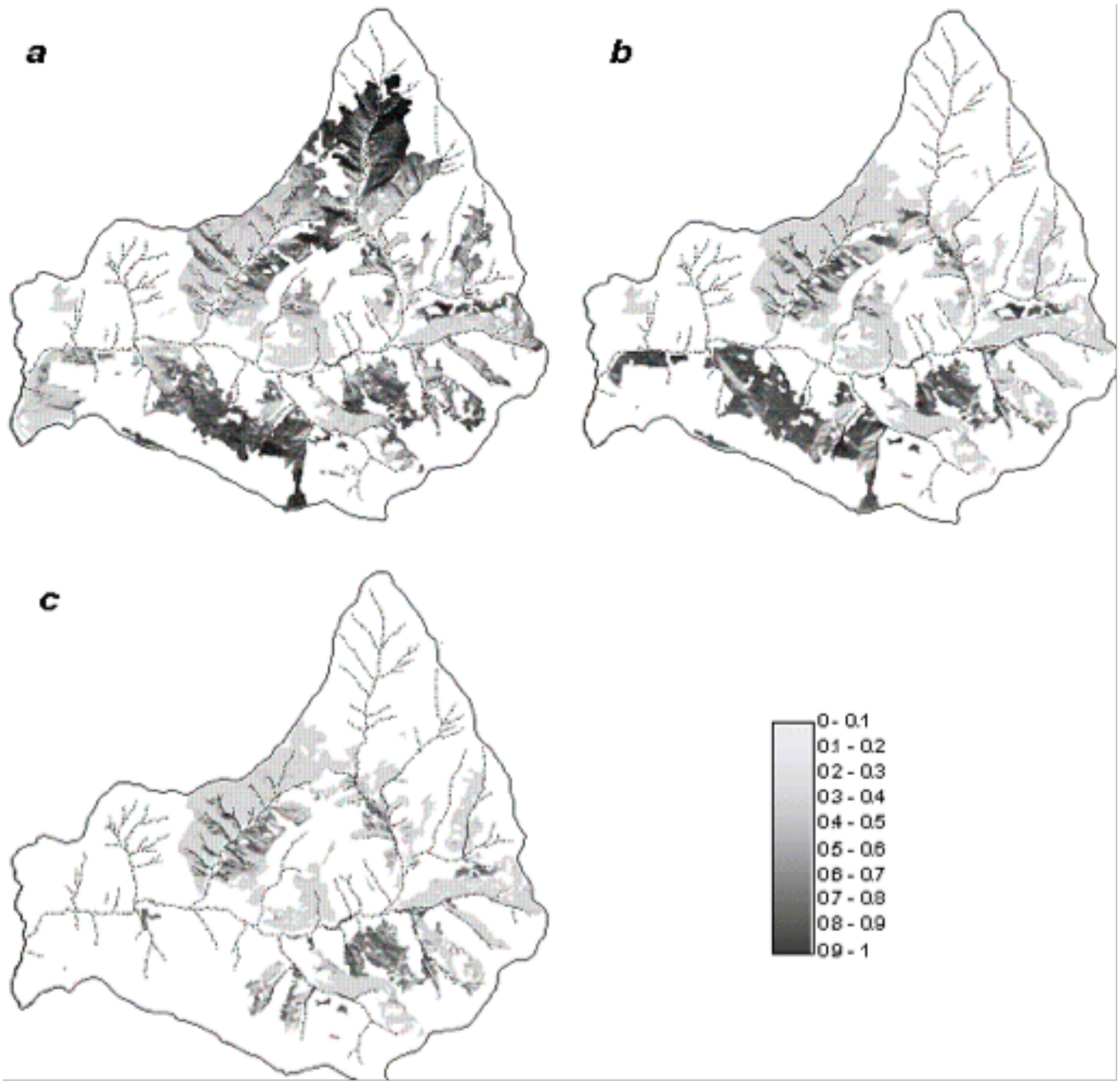

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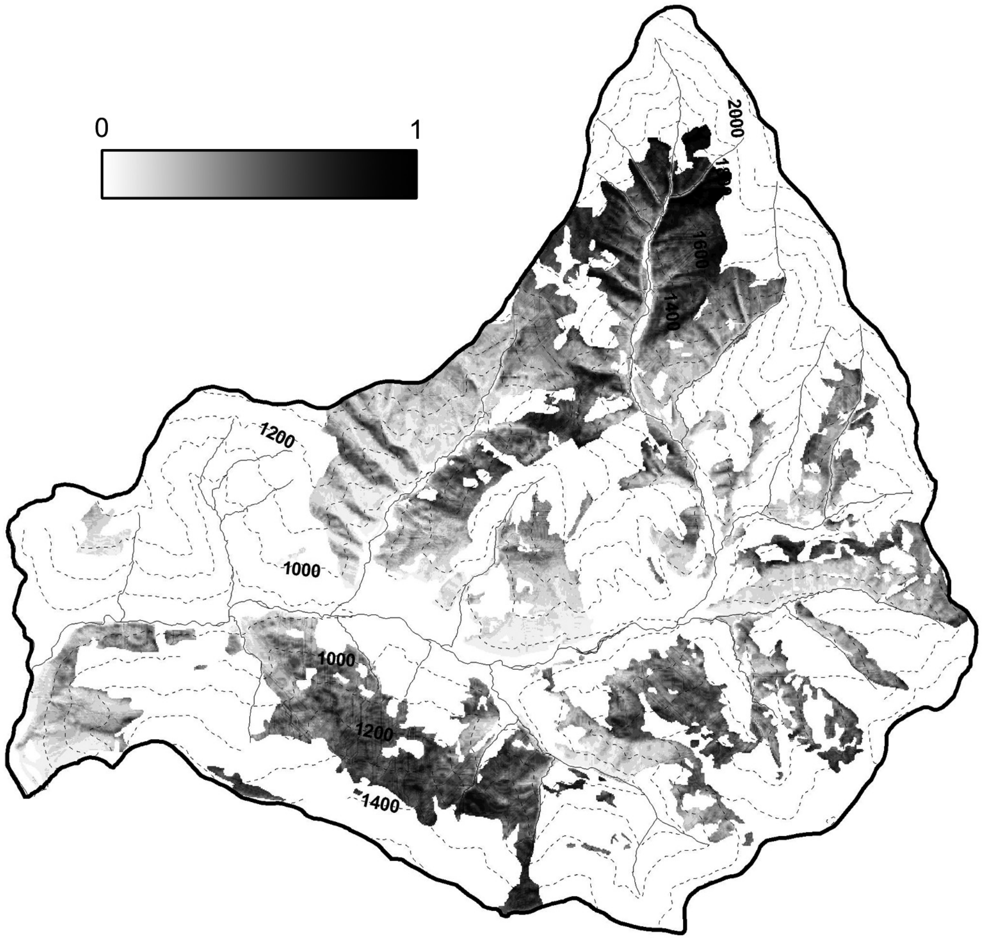

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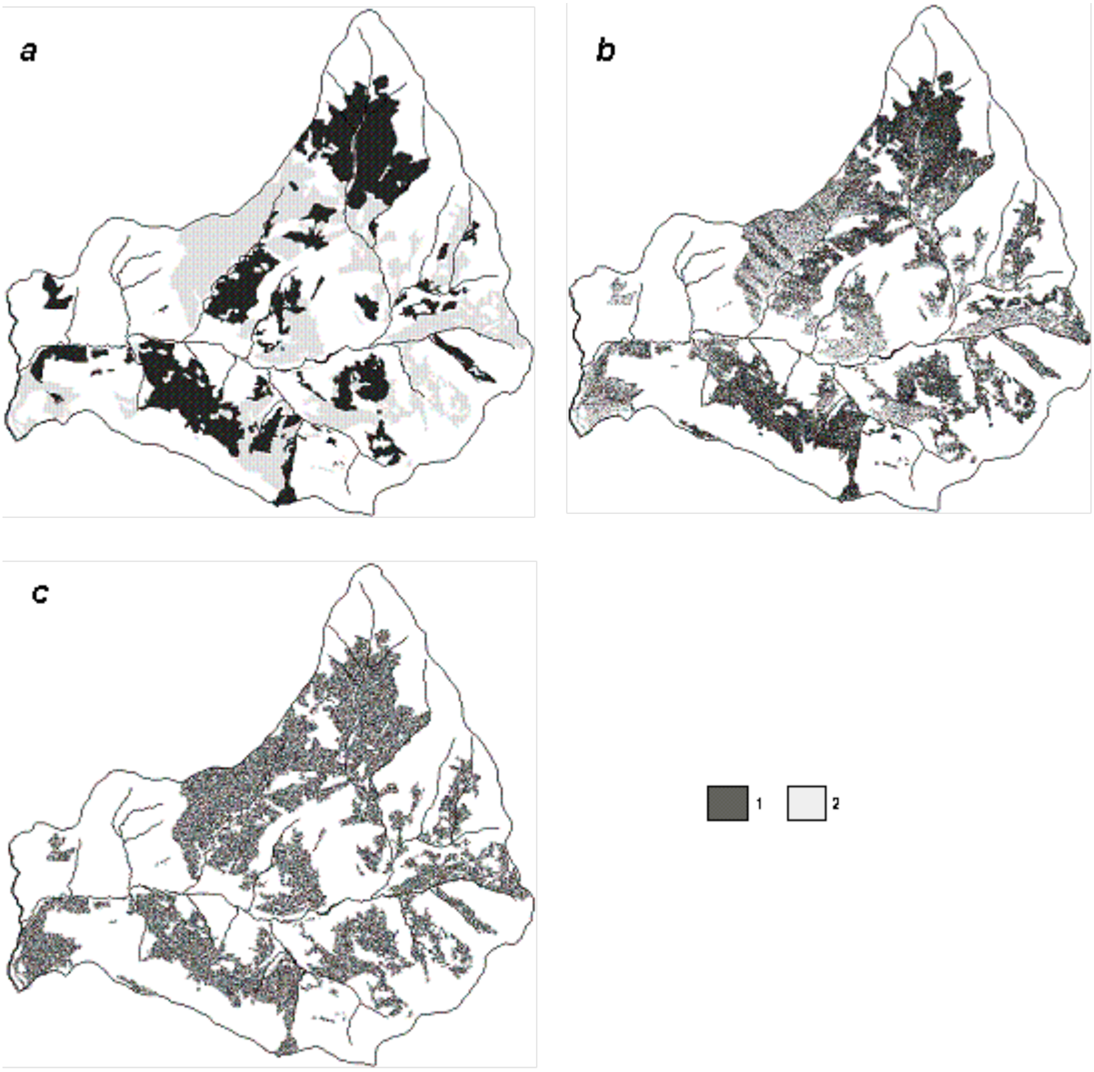

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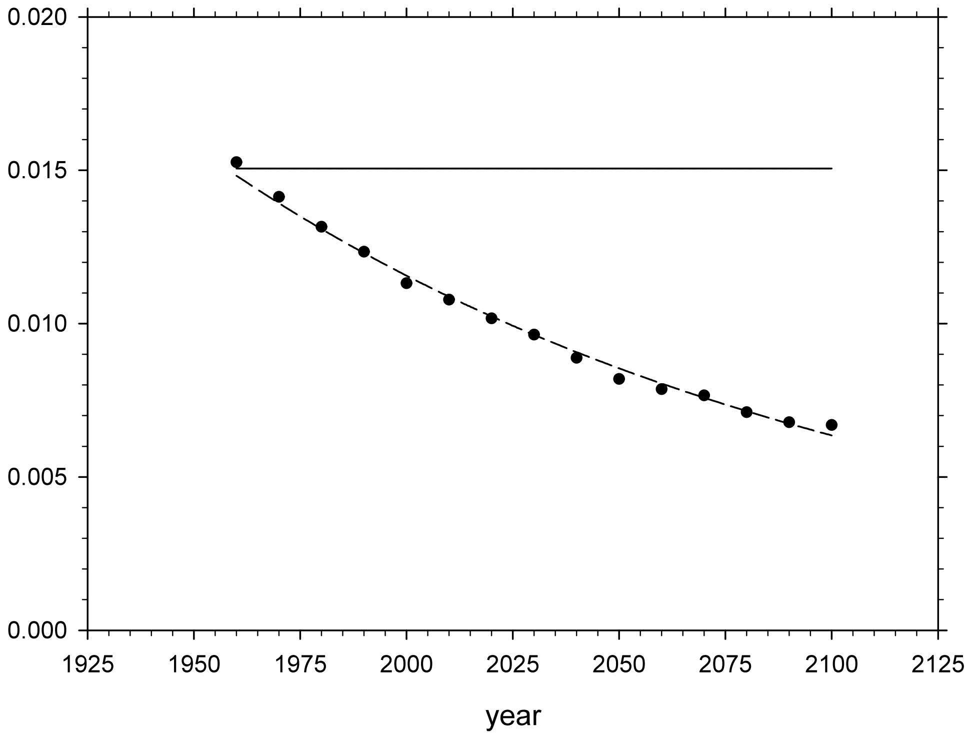
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Fig. 7

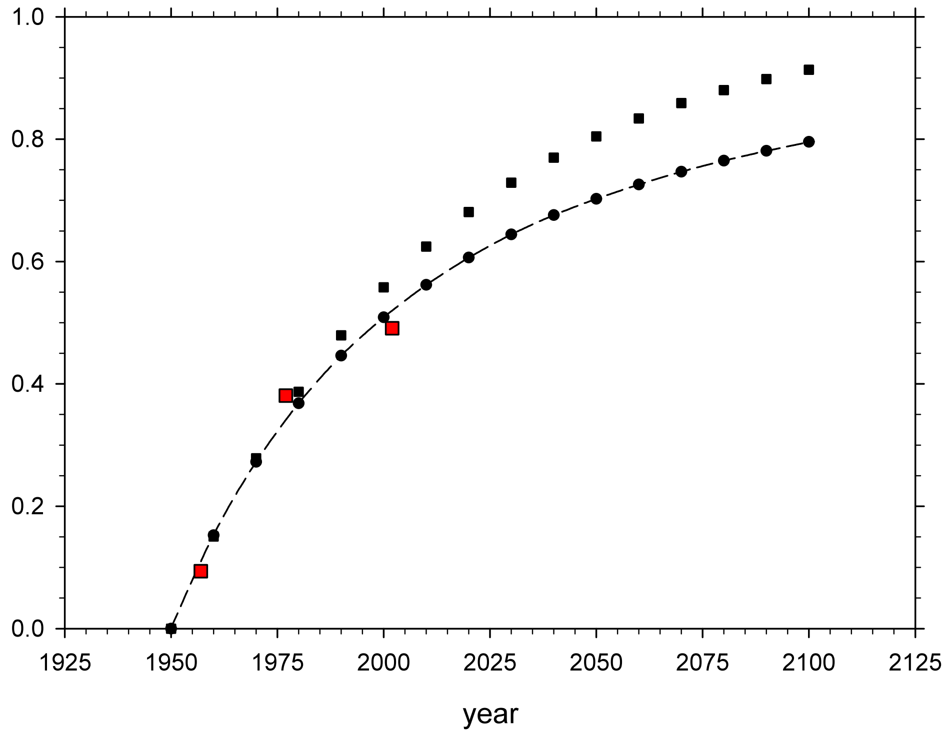
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Fig. 8