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Land-use change and subalpine tree dynamics: colonization of *Larix decidua* in French subalpine grasslands

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Summary

1. In many places in Europe, trees are currently far below their theoretical altitudinal limit because of past land use. However, under the current crisis affecting mountain agriculture, trees are likely to recolonize the subalpine belt. Addressing the societal issues associated with such landscape change requires predictive tools to assess vegetation dynamics in relation to management strategies. This study aims to analyse the factors determining tree dynamics at the subalpine ecotone and to evaluate the impact of land-use change on landscape vegetation patterns.

2. We developed a hierarchical scaling approach and applied it to a European larch (*Larix decidua* Mill.) colonization in the French Alps. Our landscape case study focused on subalpine south-facing grasslands of Villar d'Arêne (France). First, we used a habitat-suitability model to delineate the climatic suitability habitats of larch in the French Alps. Then we used a landscape model (LaMoS) to determine whether larch is able to colonize these grasslands predicted to be climatically suitable, considering land use and local vegetation. The sensitivity of landscape colonization patterns to land-use scenarios (abandonment, delayed mowing or traditional mowing) and biological attributes of larch were analysed with a factorial simulation experiment.

3. The accuracy of the habitat-suitability model at the French Alps scale allowed for the prediction that the grasslands of Villar d'Arêne were highly suitable for larch.

4. Simulations highlighted the effect of land use on larch establishment at the local but not at the landscape scale. On the other hand, larch attributes such as dispersal capacity, juvenile tolerance to light interaction (competition and facilitation) and its capacity to survive on infertile soil were shown as essential for tree spatial dynamics.

5. *Synthesis and applications*. Combining a habitat-suitability model with a spatially and temporally explicit landscape model enhances the capacity to account for environmental factors acting at different overlapping scales. This modelling strategy increases the robustness and accuracy of predictions, a prerequisite for landscape management in a global change context. We conclude that ongoing and future agri-environmental policies have to be quickly adapted to protect biodiversity and ecosystem services provided by subalpine grasslands.

Key-words: climate, habitat-suitability modelling, landscape dynamics model, landscape management, mowing

Introduction

The reality of rapid anthropogenic global changes such as increasing temperatures, elevated carbon dioxide concentration, nitrogen deposition and land-use change is nowadays accepted, and these changes are expected to affect plant and animal species. Global warming appears to have already affected the ranges of species (Parmesan & Yohe 2003), with loss, expansion or relocation of habitats sometimes leading to extinctions, and many recent studies have forecast its widespread effects

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*Correspondence author. E-mail: cecile.albert@m4x.org on biodiversity and ecosystem functioning (Diaz *et al.* 2005). However, land-use change is expected to be the main influence on terrestrial ecosystems for the coming decades, followed by climate change (Sala *et al.* 2000). The direct effect of these two drivers on species distributions is not yet well understood, and interactions between them represent one of the largest uncertainties in projections of future biodiversity change (Sala *et al.* 2005).

Among the various biogeographical regions, arctic and alpine ecosystems are certainly the most temperature-constrained and thus are expected to be particularly sensitive to climate warming (Grabherr 2003). With increasing temperatures and changed patterns in snow cover, plants are expected to adapt their life cycles or to shift their ranges to more suitable habitats upwards and polewards (Walther *et al.* 2005), which is supported by accumulating observations. Walther *et al.* (2005) showed an increase in species richness on Swiss high summits between 1912 and 2003, with a mean increase in the number of species of 138%. Woody colonization at the tree line is an expected response to global changes. This climatically constrained limit (Körner 1999), separating subalpine forests from alpine meadows (≈2300 m in the Alps), is expected to be shifted upslope as global warming provides an increase in suitable habitats toward higher altitudes (Kullman 2002; Holtmeier & Broll 2005; Coop & Goivnish 2007). However, to the best of our knowledge there is no clear trend at the landscape scale of trees moving upslope (Holtmeier & Broll 2005). As land use is the key driver of tree colonization into man-made grasslands below the tree line (Rickebusch 2006), it is difficult to distinguish climate-related signals from a response to land-use change, beyond land-use legacies (Didier 2001) and atmospheric CO_2 concentration (Körner 2003). Tree colonization into grasslands is also influenced by dispersal and biotic processes (competition and facilitation) (Li & Wilson 1998; Dullinger *et al.* 2004; Kunstler *et al.* 2006).

In Europe, trees were cut long ago to make way for agricultural use, and grasslands have been prevalent on south-facing slopes since at least the 16th century (Quétier *et al.* 2007), with land-use practices precluding tree establishment. Today, decreased management intensity and land abandonment foster quick grassland recolonization (Didier 2001). Landscape changes brought on by tree encroachment into former hay meadows threaten the remarkable diversity of plants, birds, insects and mammals hosted by these habitats (Vandvik *et al.* 2005), and also alter the delivery of many other ecosystem services (Tappeiner *et al.* 2003): negatively, as in the case of recreation or water availability, or positively, for example through carbon sequestration or slope and snow stability. Management choices to move landscapes towards a desirable future, whether forested or not, therefore require forecasts of the future ranges of species under different scenarios of environmental change (Milsom *et al.* 2000).

Three broad types of model are used to assess the likely impacts of global changes on vegetation dynamics. At a global-to-continental scale, dynamic vegetation models are based on averaged processes and are therefore of limited use for investigating species dynamics at the landscape scale (Sitch *et al.* 2003). At a regional scale, statistical habitat-suitability models are useful to quantify species–environment relationships, but do not directly include ecological processes, and are static (Guisan & Thuiller 2005). Finally, at the landscape scale, mechanistic forest-gap models or succession models are usually able to cope with spatial dynamics (dispersal), biotic interactions and survival, but do not usually include the direct influence of environmental gradients such as climate or CO_2 on the dynamics (Cousins *et al.* 2003; Schumacher *et al.* 2004).

Here we aim to analyse the factors determining tree dynamics at the subalpine ecotone and to evaluate the impact of land-use change on landscape vegetation patterns. Combining the strength of existing models at the regional and landscape scales, we developed an original approach combining hierarchically two types of model, in the case study of the European larch (*Larix decidua* Mill.) in the French Alps, and a focus on subalpine south-facing grasslands of Villar d'Arêne (France). First assuming that macroclimate drives the regional distribution of plant species (Woodward & Beerling 1997), we defined the climatically suitable habitats for European larch in the French Alps using a habitat-suitability model (Guisan & Zimmermann 2000). This model gave a potential distribution representing Hutchinson's realized niche for larch without directly including biotic and biological factors that might prevent a species from occupying its entire suitable habitat (e.g. competitive exclusion, dispersal limitation). Then, scaling down to the landscape level in one of these climatically suitable sites, Villar d'Arêne south-facing grasslands, we determined whether larch could colonize those grasslands under three land-use scenarios, considering the dispersal ability of larch and its ability to compete against the local vegetation. For this purpose we used a landscape dynamic succession model (LaMoS Landscape Modelling Shell; Cousins *et al.* 2003), parameterized using both literature and experimental data. The sensitivity of landscape colonization patterns to land-use scenarios (abandonment, delayed mowing or traditional mowing) and biological attributes of larch was analysed using a factorial simulation experiment. The results are discussed considering the relevance of such a modelling approach for guiding management in the context of global change.

Materials and methods

STUDY SPECIES

Larix decidua (European larch) is a deciduous tree of montane forests and montane-subalpine grasslands (500–2600 m). European larch is often described as a heliophile pioneer species (Rameau *et al.* 1993). Its establishment is quickly followed by trees such as *Pinus cembro* and *Pinus uncinata* in the high subalpine belt, *Picea abies* and *Abies alba* in the low subalpine belt, and *Fagus sylvatica* below.

The life span of larch can reach 400 years (Carrer & Urbinati 2004), but we used a mean value of 200 years, which is enough to contrast with the life span of graminoids. Larch becomes mature after 20–30 years and has mast seeding years approximately every

Table 1. Eleven environmental variables: 10 bioclimatic variables from the meteorological model Aurelhy at a resolution of 200 m × 200 m and one soil texture variable from the *European soil database*

Type	Variable	Five PCA-selected variables
Bioclimatic (200 × 200 m)	Relative humidity	×
	Solar radiation	×
	Vapour pressure deficit	
	Degree days above 5 °C (°C)	×
	Number of frost events	×
	Total precipitations of the year (mm)	
	Summer precipitations (mm)	×
	Average maximal temperature (°C)	
	Average minimal temperature (°C)	
	Minimal temperature in winter (°C)	
Soil (1 × 1 km)	Soil texture	

10 years, with seed life span ranging from 3 to 7 years. Seeds are mostly dispersed by wind and birds (Rameau *et al.* 1993).

A HIERARCHICAL APPROACH AT TWO SCALES

Assuming that climate is driving the regional distribution of plant species, and that dispersal, biotic interactions and land-use change are the most important factors determining landscape-scale distribution, we developed an original approach based on a hierarchical approach at two scales. The first model was applied at the regional scale (French Alps) to quantify the ecological niche of larch, and then by GIS mapping to identify areas of high habitat suitability. The second model investigated at the landscape scale whether larch could migrate and establish in interaction with the current vegetation (grass-dominated) according to different scenarios of land-use change.

Regional-scale suitability

To delineate the niche space of larch, we used habitat-suitability modelling (Guisan & Zimmermann 2000), which links species occurrence data with selected environmental factors (Austin 2002).

We used presence and absence data for larch from the botanical database SOPHY (http://sophy.u-3mrs.fr/sophy.htm; Brisse *et al.* 1995), which contains more than 3 million observations of plants in France for 4500 taxa. The 2156 plots of *L. decidua* (375 observed presences and 1781 observed absences) in the French Alps were used for this study. Each plot is characterized by its geographical coordinates with an accuracy between 100 m and 1 km, the altitude of the plot and the cover-abundance index of the plant (from 1 to 6), according to the Braun–Blanquet methodology (Mueller-Dombois & Ellenberg 1974).

To describe the environmental niche of larch, we used 11 variables (Table 1): a set of bioclimatic variables obtained from a digital elevation model and from the meteorological model Aurelhy (Benichou & Le Breton 1987), based on interpolated measurements at a resolution of 200 m × 200 m and soil texture data from the *European soil database* (http://eusoils.jrc.it/ESDB/index.htm) at a resolution of 1 km × 1 km. A condensed set of five variables (relative humidity, summer precipitation, number of frost events, solar radiation, number of degree days above 5 °C) was determined using principal components analysis to limit the collinearity within the environmental drivers.

Among the species distribution models commonly used, generalized linear models (GLM) and generalized additive models (GAM) have proven to be one of the best compromises between interpretability and predictability (Guisan & Thuiller 2005).

Both GLM and GAM models were implemented with a LOGIT link function, specifically for binomial variables such as presence/absence of a species. We first used GAM in an exploratory way, to identify the most probable shapes of the response curves, which were then fitted within a GLM. The shapes of the response curves were identified using a cubic spline smoother and a two-sided stepwise procedure based on the Akaike information criterion (AIC; Akaike 1974) to choose the most parsimonious model. We then estimated the mathematical formula (linear, quadratic or polynomial) corresponding to the response curve of each significant explanatory variable, and built a GLM with those terms. The goodness of fit was estimated by a measure of deviance reduction (adjusted D^2) given by (Guisan & Zimmermann 2000):

$$\text{adjusted } D^2 = 1 - [(n-1)/(n-p)] \times [\text{residual deviance/null deviance}], \qquad \text{eqn 1}$$

where n is the number observations and p is the number of parameters.

The model was calibrated on a random fraction of the original data (70%) and its predictions were tested on the remaining data (30%), assuming the two random fractions to be quasi-independent. In order to assess the predictive capacity of the model, model predictions were compared with real observations using the area under the curve (AUC) of a receiver-operating characteristics plot (Swets 1988; Fielding & Bell 1997). This AUC measure allows us to test whether the obtained predictions differ significantly from a random prediction. We used the following rough guide (Swets 1988): poor predictions for AUC were contained in the range 0·5–0·7; useful predictions for AUC in the range 0·7–0·9; and good to excellent predictions when AUC is >0·9. A threshold was then calculated to optimize the separation in a contingency table of the true presences and true absences, and the outputs of the model were then transformed with this threshold into binary results for presences and absences.

The final model gave the habitat suitability index of the species as a function of abiotic conditions and allowed us to determine geographically potentially highly suitable locations. We projected the model over the French Alps, with zeros where the index was below the selected threshold and the nough value of the index where it was above the threshold. Zooming down allowed us to observe the local habitat-suitability patterns and to determine high-suitability areas for larch.

Landscape dynamics and land-use change scenarios

Case study site

The Villar d'Arêne study area (45·04°N, 6·34°E; altitude 1650–2500 m) is located in the central French Alps, on a south-facing slope near the Lautaret pass. This area covers 1292 ha characterized by subalpine climatic conditions with mean temperatures reaching –7·4 °C in February and +19·5 °C in July, total annual precipitation averaging 956 mm, and prevailing winds mainly coming from the west.

This site was selected from the outputs of the regional model as a typical location within the subalpine belt with high habitat suitability for larch, but still devoid of trees. Its vegetation patterns, floristic composition and land-use dynamics are well documented, making it an ideal site for detailed landscape modelling.

Until the 12th century, the area used to be covered with a dominant pine species (*P. uncinata*) before trees were removed for agriculture and grazing (Ali *et al.* 2003). The site was then terraced and ploughed in its lower section and mown and/or grazed in its upper section. Cropping was abandoned after World War II, and management then involved summer mowing with or without fertilization on both terraced and unterraced fields. More recently, mowing has been abandoned in the steeper and least accessible parts of the landscape. Nowadays grazing pressure has decreased and a smaller area is still mown for conservation purposes (NATURA 2000 directive; Quétier *et al.* 2007).

Current land cover is exclusively grasslands, dominated by four grass functional types with high local abundance and, respectively, represented by the most common species: *Bromus erectus*, *Dactylis glomerata*, *Festuca paniculata* and *Sesleria caerulea.* Their landscape-scale distribution and dominance patterns are determined by past and current land use (Quétier *et al.* in press). The main tree species in Villar d'Arêne is *L. decidua*, which is colonizing the north-facing slope; however, few individual trees currently occur in the grassland area with a patchy distribution.

Landscape dynamics model

Once a climatically suitable site had been chosen, a second approach at the landscape scale aimed to study the potential establishment of larch in the existing communities according to various scenarios of land-use change. To analyse larch dynamics on a landscape scale, including biotic and biological processes, we used a landscape dynamics model: LaMoS (Cousins *et al.* 2003). LaMoS is based on the concept of plant functional type (PFT; Lavorel *et al.* 1997), defined as a group of species with similar responses to and/or effects on their environment. It assumes that abiotic conditions are suitable for each PFT in the area where they are studied.

LaMoS is a spatially and temporally explicit model that accounts for basic vegetation dynamic processes resulting from the interactions between plant functional types (or species), habitat conditions, disturbances and spatial patterns (Cousins *et al.* 2003). Within LaMoS, the landscape is described as a raster grid, in which landscape dynamics is modelled by three interacting modules. First, a succession model drives within-pixel yearly successional dynamics. We used a modification of the FATE model (Moore & Noble 1990), which determines the abundance of competing PFTs represented as age cohorts based on a simple set of traits relating to plant life history, tolerance to light interaction at different life stages, and recruitment (for details see Cousins *et al.* 2003; Quétier *et al.* in press) (Table 2). Second, a dispersal model distributes seeds across the landscape. We used a negative exponential model (Table 2) coupled with a random long-distance dispersal function (Table 2), which is also exponentially correlated with distance to seed source but allows a very small (10^{-4}) fraction of seeds to be dispersed much further (1·8 km). Third, a disturbance model establishes the potential disturbed fraction of abundance (output from the succession model) for each PFT and affects each PFT specifically, leading to death, resprouting or no effect on the different defined age classes. We used a uniform mowing disturbance within fields still in use under various land-use scenarios.

Villar d'Arêne grasslands have already been modelled with LaMoS, including four leaf-height-seed (LHS)-based PFTs, classifying the dominant graminoids in contrasting nutrient economies and competitive effects and responses after Westoby's (1998) LHS plant strategy scheme. This method uses three plant traits (leaf area, plant height and seed weight) to determine species' strategies for growth, persistence and regeneration. The four LHS-based PFTs resulting from field work, named after the archetype species in each cluster, are Bromus PFT, representing medium-sized, disturbance-tolerant species; Dactylis PFT, representing tall, acquisitive species; Festuca PFT, representing tall, competitive and conservative species; and Sesleria PFT, representing small-sized, stress-tolerant species (unpublished data). The model including the four contrasting grass PFTs was calibrated under past conditions, run until the present with historical land use, and validated under current conditions.

The four PFTs are thought to have contrasting nutrient economies and contrasting competitive effects and responses, and were parameterized with both field and experiment data.

Future land-use scenarios

We added to this model a tree PFT, parameterized to represent larch. Most of the necessary parameters were found in the literature, but germination rates under different light levels, representing light interaction (competition and facilitation), were determined with a controlled experiment (see below). Three sensitive parameters remained undefined and were tested with simulations: dispersal ability; resource-uptake efficiency, which determines the demographic response to pixel fertility; and juvenile response to light interaction.

To test the impact of land-use change on tree dynamics, we used three scenarios of land-use change representing local land-use projections by 2050, developed by Quétier (2006). These were based on local projections of Europe-wide scenarios of land-use change (Rounsevell *et al.* 2006), formulated on the basis of the Intergovernmental Panel on Climate Change (IPCC) global storylines (Nakicenovic & Swart 2000). The first scenario represents a global, economically growing world, leading to land abandonment because isolated mountain lands are no longer profitable. The second scenario represents a global, sustainably developing world. It leads to delayed mowing, maintained in isolated regions only for environmental purposes as a way of protecting biodiversity, but this non-profitable activity is delayed until the end of summer (August). The third scenario represents a regional, sustainably developing world, leading to the persistence of traditional agriculture. The environmental value and regional identity of Villar d'Arêne allow protection of the strong local agriculture, including the early (June or July) mowing of grasslands. This early mowing disturbance prevents the Festuca PFT from producing seeds (Quétier *et al.* in press).

Table 2 LaMoS parameterization for larch species

Parameter	Value
(a) Life parameters	
Low resource threshold*	0·20 or 0·60
Maximum biomass	10 000 t ha^{-1}
Maximum abundance	8000 trees ha^{-1}
Life of active pool	5 years
Immature stratum	Medium
Mature stratum	High
Time to maturity	30 years
Maximum abundance	Leads to a medium extinction of light
Potential fecundity	200 000 seeds per tree every 10 years
Life span	200 years
Stage tolerance to available light:	
Germinants	Medium and high light level
Juveniles*	High light level or medium and high light level
Matures	High light level
Germination rate for different light availability**:	
Low light level	High
Medium light level	Medium
High light level	Low
(b) Dispersal and disturbance response parameters	
Long-distance dispersal*	Yes or no
Long-distance dispersal fraction	0·0001
Mean dispersal distance	0·4
Maximum long-distance throw	1·8 km
Type of disturbance	Constant severe harvest (60% of biomass)
Frequency	Once a year
Response of larch:	
Germinants	All killed
Juveniles	All killed
Matures	All killed

*The three parameter tested with the simulations.
**Parameter of germination rate determined with the controlled experiment.

Simulations

The LaMoS model has already been shown to be sensitive to several parameters, including seed dispersal, germination rate, resource-uptake efficiency, and juvenile tolerance to light availability (Cousins *et al.* 2003; Grigulis *et al.* 2005; Quétier *et al.* 2007). Among these key parameters only germination was estimated by experiments, the others being tested with simulation runs. We used a factorial simulation design to test the sensitivity of larch colonization to three of the critical auto-ecological parameters: with vs. without long-distance seed dispersal ability (Table 2); shade-tolerant vs. intolerant juveniles (Table 2); and high vs. low resource-uptake efficiencies (Table 2), under the three scenarios of land-use change (A1 = abandonment, B1 = late mowing, B2 = early mowing) (Fig. 2b), yielding a total of 24 different simulations. Simulations were run on a 43 × 75-pixel (90 × 90-m) landscape representing the altitudinal fertility gradient at the site (five values from 1 at the bottom to 0·2 at the top), with a maximal value (fertility = 1) for formerly cropped and fertilized grasslands (Fig. 2a) (Quétier *et al.* in press). Land-use scenarios were translated into disturbance maps, contrasting areas with annual mowing and abandoned areas where successional development proceeded undisturbed. Each simulation was run for 230 years post-land-use change to observe at least one complete generation of trees, using current conditions as the initial state (Fig. 2c), with a line of trees with maximum abundance introduced on the north-facing slope of Villar d'Arêne (initial conditions for larch; personal observations). We recorded maps of mature abundance of each PFT every 30 years. Simulations were not repeated because the model was stable and deterministic.

LARCH SEED GERMINATION UNDER DIFFERENT LIGHT CONDITIONS

We quantified the effect of light conditions on seed germination using a controlled experiment. Our experiment was set up under unlimited conditions of water supply, because both light and water are usually expected to influence the germination rate (Broncano *et al.* 1998). We used seeds of *L. decidua* from the northern internal Alps, provided by the French Office National des Forêts. After the seeds had been stored in cold conditions (2–3 °C) from 8 March to 4 April 2006, on 5 April they were placed in five pots, which received three different light treatments (measured light: 100, 36 or 0% of total full sunlight) applied with shade cloth to (partially) shade the pots containing 50 seeds. The seeds were monitored every 2 days until 8 May, and the first root's appearance was recorded as the sign of a successful germination.

All statistical models and analyses were carried out with the free-source software R (ver. 2·3·1; Ihaca & Gentleman 1996). All map treatments were realized using ARCGIS ver. 9·1 (ESRI, Redlands, CA, USA).

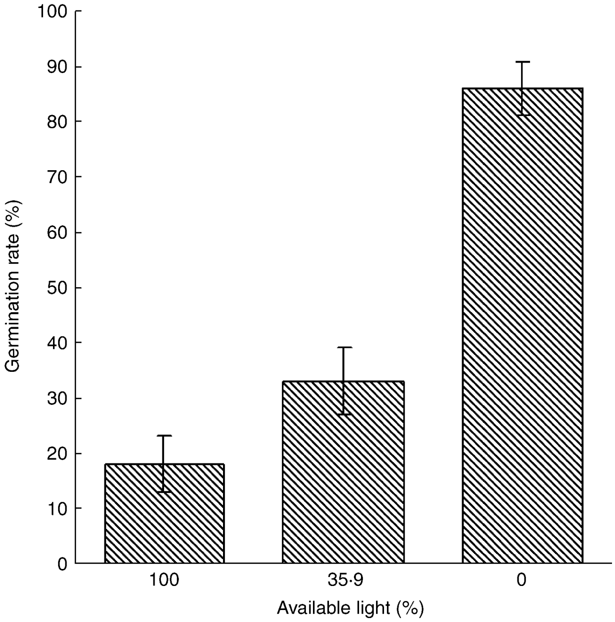

Fig. 1. Effects of light availability on germination rate of *Larix decidua*.

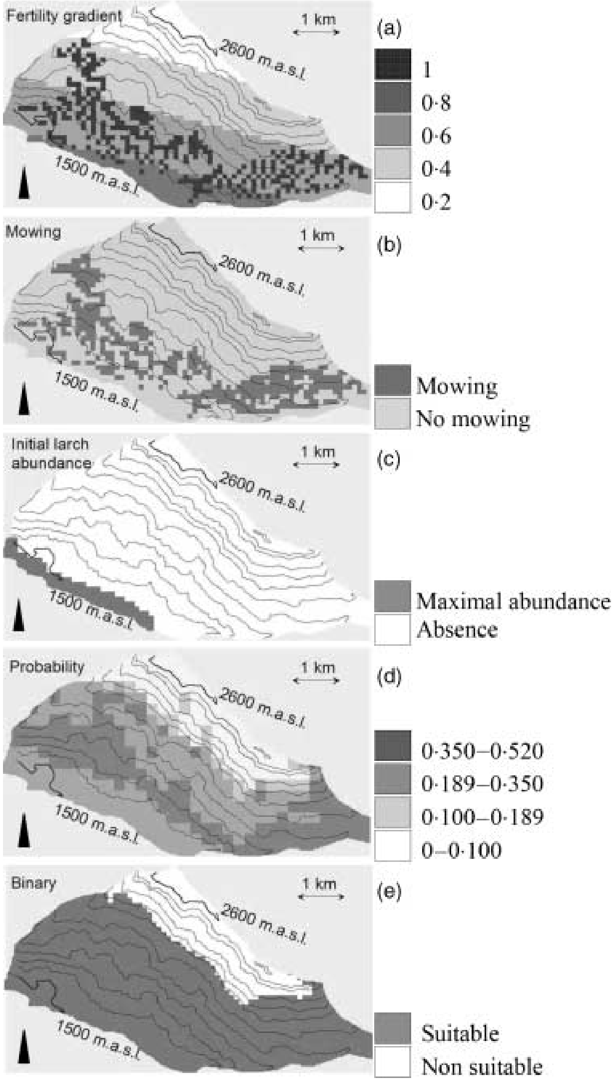

Fig. 2. Map layers of the grasslands of Villar d'Arêne along an altitudinal gradient: (a) relative soil fertility from 0·2 to 1. (formerly fertilized grasslands = dark patches); (b) current mowing disturbance; (c) current location of *L. decidua*; (d) larch habitat suitability (200 m× 200 m); (e) binary larch potential distribution (0 below the threshold of 0·189 and 1 above).

Results

PARAMETERIZATION OF GERMINATION WITH EXPERIMENTAL RESULTS

There was a negative relationship between light availability and germination (Fig. 1), showing the relatively high ability of larch seeds to germinate under a completely dark cover, although saplings needed light to grow subsequently. This experiment allowed us to parameterize the germination rate in LaMoS under three different light levels (low, medium, high) as required by the LaMoS model (Table 2).

HABITAT SUITABILITY FOR LARCH IN THE FRENCH ALPS

The stepwise GAM identified that the response of species to the selected environmental variables was quadratic. Soil type was not selected by the stepwise procedure as a pertinent variable to explain larch distribution.

We then built a GLM using the variables selected by the stepwise GAM and the predetermined parametric shapes. The explanatory and predictive powers of the final model were fairly high ($D^2 = 43\%$, AUC evaluation = 0·92, AUC calibration = 0·92).

The geographical projection (Fig. 3) showed that under current climatic conditions, larch was predicted potentially to occupy a relatively narrow altitudinal range within mountainous areas. A zoom of the projection identified the south-facing grasslands of Villar d'Arêne as fairly suitable for larch (Fig. 2d,e). The binary-converted results (threshold = 0·189) led us to consider the high part of the grasslands as unsuitable for larch.

EFFECTS OF AUTOECOLOGY AND LAND-USE CHANGE ON LARCH DYNAMICS AT THE LANDSCAPE SCALE

The low part of Villar d'Arêne grasslands was potentially suitable for larch. We then determined whether larch could colonize grasslands by dispersing seeds from its current distribution area on the north-facing slope, germinating and recruiting in local vegetation under the effects of soil-fertility patterns and different land-management regimes (mowing vs. abandonment) (Fig. 4). The LaMoS simulations allowed us to highlight key drivers for the ability of larch to establish in Lautaret grassland. Juveniles appeared outside the initial population source after 20 years, and mature trees about 50 years after land-use change.

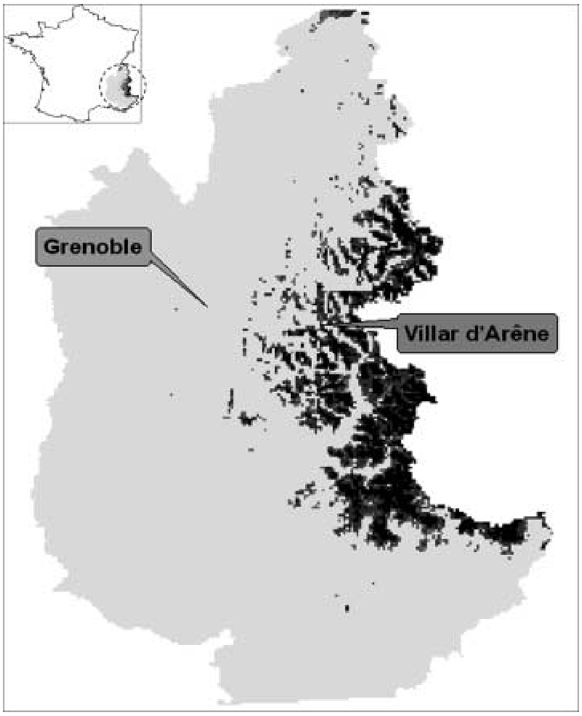

Fig. 3. Larch suitability map at the regional scale (French Alps). Dark to light, from high to low suitability index.

Simulations showed that land use partly drives larch distribution. In particular, mown grasslands were devoid of larch because the mowing disturbance directly prevented trees from growing. Further, if larch had a low dispersal ability (no long-distance dispersal), mowing dramatically reduced colonization by larch (results not presented here), potentially leading to local extinction (see Appendix S1 in Supplementary material).

However, the ecological attributes of larch appear to be of crucial importance in predicting its potential colonization into the subalpine landscape. Maps of mature tree abundance showed three main landscape patterns. (1) When larch had high resource-uptake efficiency, shade-tolerant juveniles and a long-distance dispersal capacity, colonization was efficient over the whole landscape, even in poor soils at higher altitude, and was nearly independent of land use (Fig. 4b,e,h). (2) With shade-tolerant juveniles, but no long-distance dispersal ability, colonization was patchy, with two different patterns. Either larch had low resource-uptake efficiency, so that patches coincided with fertilized meadows (see Appendix S1), or larch had high resource-uptake efficiency and was limited only by biotic interactions (Fig. 4a,d,g). (3) With shade-intolerant juveniles and no long-distance dispersal, larch colonization was limited to a few individuals and a small spatial extent (see Appendix S1), or led to local extinction; on the other

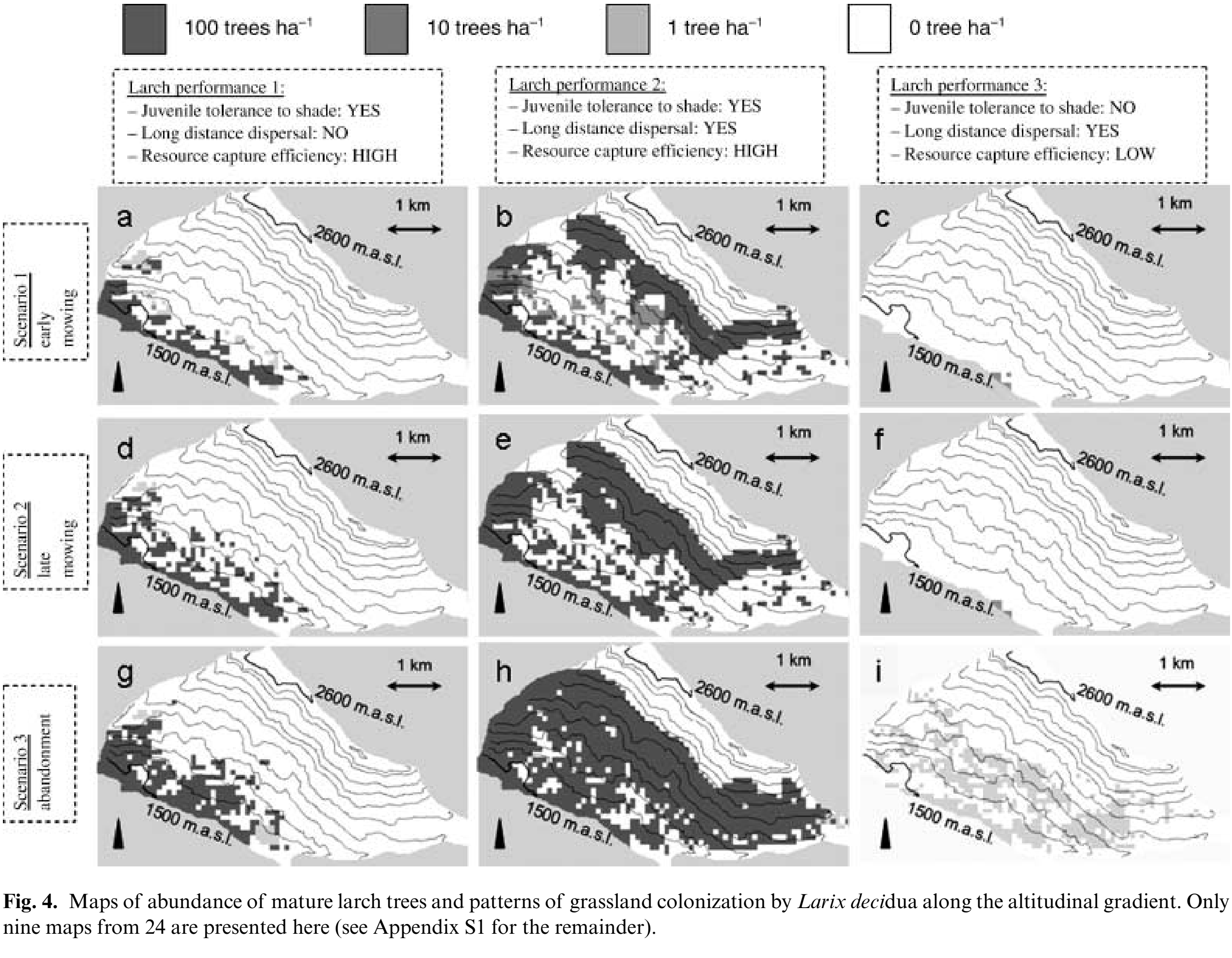

Fig. 4. Maps of abundance of mature larch trees and patterns of grassland colonization by *Larix decid*ua along the altitudinal gradient. Only nine maps from 24 are presented here (see Appendix S1 for the remainder).

hand, with shade-intolerant juveniles and a long-distance dispersal ability, colonization was spatially broad but limited to few individuals, or also led to local extinction (Fig. 4c,f,i).

Discussion

MODELLING THE SIMULTANEOUS EFFECTS OF CLIMATE AND LAND-USE CHANGE ON LANDSCAPES

The new approach proposed here, relying on combined models at the regional and landscape scales, offers several assets for predicting future landscape dynamics. First, the use of habitat-suitability modelling as a first step fulfils the most important assumption of LaMoS, which is the suitability of the study site for modelled species. Including both abiotic and biotic conditions in landscape dynamics thereby increases the realism of projections. Second, this method combines two different study scales, and uses state-of-the-art models at each scale. As a first step, habitat-suitability models can be established at regional or global scales, given a suitable sample size of presence records to train the model reliably (Stockwell & Peterson 2002). Under these conditions one of the most important assumptions of these models can be fulfilled: pseudo-equilibrium between the species of interest and the current environment (Guisan & Thuiller 2005). This does not mean that the species occupies its whole niche (Pulliam 2000), because habitat-suitability models provide a geographical representation of the entire niche, including truly occupied locations and those that could be occupied but are not currently because of competitive exclusion, land use or low dispersal ability (Pulliam 2000). The Villar d'Arêne landscape is an example of such a climatically suitable but unoccupied locality. As a second step, landscape models such as LaMoS are appropriate for a local analysis on a well known site identified as climatically suitable. This approach is more parsimonious than attempting to run landscape models at large scales, a time-consuming exercise with numerous parameters that are difficult to obtain at a large scale (e.g. former land use). The proposed approach appears promising for addressing scaling problems, including limitations of models at each scale (Peters *et al.* 2004). It may also reduce uncertainties in trying to address climate and land-use changes, and their interactions, simultaneously. As far as we know, few model combinations have already been implemented in such a way (Guisan & Thuiller 2005). They are some examples for animal species where landscape models are used as variables for the niche-based models (Wintle *et al.* 2005). Concerning plants, there are very few studies presenting such a combination. Dullinger *et al.* (2004) carried out a similar analysis without explicitly using a hierarchical approach, but by building a spatially explicit model incorporating both climate, biotic interactions and dispersal. Recent developments of forest gap models implicitly combined these niche-based models and landscape models, but they are only applicable to trees and ignore grasslands or open habitats (Schumacher 2004).

IDENTIFYING DRIVERS OF LARCH EXPANSION IN SUBALPINE GRASSLAND LANDSCAPES

Our simulations suggest that European larch is likely to establish viable populations in the Villar d'Arêne grasslands within the next 50 years under the various scenarios implemented. This potential colonization by trees of abandoned or less-used grasslands is not surprising, as similar colonization patterns have already been observed in old fields from mountain (Didier 2001) and lowland regions (Debussche & Lepart 1992).

The patterns of colonization depend on both future land management and larch ecological characteristics. Our simulations suggest that, under current and projected management practices, the landscape-scale distribution of trees is ultimately driven by the ecological characteristics of larch rather than by the ability of management to contain colonization. This result confirms a previous simulation study that demonstrated that colonization of the Villar d'Arêne landscape by the undesirable grass *F. paniculata* was primarily driven by constraints on its recruitment into formerly ploughed grasslands, rather than by current management (Quétier *et al.* in press). Likewise, Tasser & Tappeiner (2002) demonstrated that current tree colonization patterns are determined primarily by dispersal (e.g. distance to seed source) and secondarily by current management.

Although mowing could prevent tree establishment locally, its effects appeared limited at the landscape scale because of its small extent, even under the most intensive scenarios (scenarios 2 and 3, 15% of landscape area mown). Under such patchy land use, trees were shown to establish between mown patches. None of our scenarios considers an extension of the mown area that could contain tree establishment; at best, mowing is conserved to its current, relatively small extent.

Under these land-use conditions, we show that the most important traits determining the colonization of subalpine grasslands such as those of Villar d'Arêne are related to the three main phases of colonization: dispersal of seeds to reach a new location (dispersal ability); ability of the species to develop in this new location (resource-uptake efficiency); and ability of the species to sustain competition from colonized communities (juvenile tolerance to light interaction). These results corroborate those of many experimental and modelling studies (Bleher *et al.* 2002; Dullinger *et al.* 2004) showing the importance of dispersal ability (mean distance and distribution) and inter- and intraspecific competition in tree colonization patterns. Likewise, Quétier *et al.* (in press) showed that the response of the Villar d'Arêne landscape to land-use scenarios depended on the ability of the Festuca PFT to disperse seeds. These traits are not always easy to quantify, but experiments such as the one we conducted for germination could be used to reduce uncertainty in their estimation.

Finally, our simulations are informative in estimating the time-scale of colonization. For instance, abandoned grasslands could turn into woody communities within a few decades. This study also shows the importance of land-use legacies

(Donohue *et al.* 2000; Quétier *et al.* 2007), and how the knowledge of former land use could aid the prediction of future landscape dynamics.

IMPLICATIONS FOR FUTURE LANDSCAPES AND ECOSYSTEM SERVICES

Results from simulation studies such as this can offer guidance for management of semi-natural mountain grasslands in the context of global change. At the landscape scale, agricultural land use can have either a positive or a negative effect on biodiversity and associated goods and services (Tscharntke *et al.* 2005; Bolliger *et al.* 2007). Mowing, as carried out for several centuries, plays a crucial role in maintaining a high level of biodiversity (Maurer *et al.* 2006) by creating an intermediate disturbance intensity that prevents competitive exclusion by late-successional species (shrubs, trees) or large perennial tussock grasses (Quétier *et al.* 2007). This diversity, and the corresponding functional composition of the vegetation, are associated with the delivery of multiple services that are important to local stakeholders. Our results suggest that current patterns of agricultural use may not be able to sustain desirable levels of biodiversity associated with open landscapes, and we highlight some possible alternatives.

We examined three plausible scenarios of land use that lead to three possible futures for the next few decades, depending mostly on uncertainties about larch autoecology. Knowledge of these futures should inform management decisions that are required to adapt to future changes or mitigate them if they are found to be undesirable.

(1) Persistence of open and species-rich grasslands in Villar d'Arêne and similar localities. The current management regime does not seem intense enough for this, and more intense and/or widespread disturbances are needed to resist colonization by larch, as well as by undesirable grassland species (Quétier *et al.* in press). Maintaining the current open landscape would require mowing a larger area, as was done until World War II. The introduction of targeted grazing management, focusing more intensively on unmown grasslands and applied early in the season, would also be required to restore species-rich grasslands (Jouglet 1999).

(2) Establishment and management of a larch forest. This alternative scenario might be favoured for multifunctional agriculture, as the light cover provided by larch forest sustains a high diversity of plants and animals (Rameau *et al.* 1993). Larch forests already occur in the Guisane valley, southward from the Lautaret pass, and provide useful protection against landslides and avalanches. They can also provide shelter and some fodder for stock. The downside is that this type of forest needs to be managed because it is not a stable successional stage, and larch would quickly be superseded by other tree species such as some pines (Ozenda & Borel 1995). Under this scenario, the effects of forest establishment on current grassland communities should be investigated further. Landscape simulations predict the disappearance of the Sesleria and Dactylis PFTs in favour of the dominant and abundant Festuca PFT when land is abandoned (Quétier *et al.* in press) and when larch colonization occurs. Such a change in grassland functional composition would inevitably lead to some fundamental changes in ecosystem function and associated goods and services, such as the availability of fresh water, carbon sequestration or soil conservation. For example, dominance by the Festuca PFT is associated with an increase in biomass production, but a decrease in fodder quality and strong litter accumulation, with a loss of flower diversity and thus of aesthetic value (Quétier *et al.* in press).

(3) Establishment of mountain forest to prevent soil erosion and avalanches. In this case, no specific management is required and trees might be left to expand their range. This change may come at the cost of biodiversity and water availability (Tscharntke *et al.* 2005), but with positive consequences for carbon storage.

The effects of each of these futures on tourism should also be considered, as tourism is currently, and is likely to remain, a key sector sustaining the mountain economy.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Maps of the abundance of mature larch trees and patterns of grassland colonization by *Larix decidua* along the altitudinal gradient for the 24 simulations combining land-use scenarios and larch autoecology

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2664.2007.01416.x.
(This link will take you to the article abstract).