Research article

Landscape patterns and agriculture: modelling the long-term effects of human practices on *Pinus sylvestris* spatial dynamics (Causse Mejean, France)

Paul Caplat*, Jacques Lepart and Pascal Marty

UMR 5175 Centre d'Ecologie Fonctionnelle et Evolutive, CNRS. 1919 route de Mende, 34293 Montpellier Cedex 5, France; *Author for correspondence (email: caplat@cefe.cnrs.fr)

Received 24 February 2005; accepted in revised form 20 October 2005

Key words: Agriculture, Bioscene, French Mediterranean, Grazing, Land-use, Landscape history, Multiagent systems, Rangeland, Scots Pine, Shifting cultivation, Time-lag

Abstract

This paper focuses on understanding human impact on landscape. Both ecological and human practices are analysed as interacting processes. An agent-based model integrating biological and historical knowledge is used to analyse the pattern of Scots Pine encroachment in a French Mediterranean upland. In the STIPA model, pine trees are autonomous agents and a cellular automaton simulates land-use. We test the effects of shifting cultivation on tree establishment at the landscape scale. This allows us to understand how agropastoral practices patterned this area from the 17th to 19th century: simulations show the importance of shifting cultivation in limiting woodland progression. Fallow duration linked to environmental heterogeneity is a significant factor for explaining pine dynamics and landscape patterning at the scale of the study region. We put this result in perspective with current rangeland management policies that often consider grazing as the most relevant tool for open landscape maintenance. Our results also show the importance of taking into account time-scale effects when linking landscape patterns to agricultural systems.

Introduction

Landscape patterns are the result of ancient, diverse and complex interactions between ecological and socio-economical systems (Lepart and Debussche 1992; Gorham 1997; Toupal 2003); they occur both on short- and long-term time scales (Bengtsson-Lindsjö et al. 1991; Motzkin et al. 1996, 1999). The widespread land-use regimes linked to grazing and cultivation (Diamond 2002) such as clearing, slash and burn and shifting cultivation systems, have strongly contributed to shaping landscapes (Childe 1971; Moore 1975;

Segerström and Emanuelsson 2002). Every landscape can thus be considered as a cultural landscape (Birks et al. 1988; Von Droste et al. 1995) according to Svobodava's definition (in Von Droste et al. 1995: 20): a transformed part of free nature resulting from man's intervention to shape it according to its particular concepts of culture.

Due to the complexity of the interactions, ecological and socio-economic systems cannot be separated: there is neither total freedom for people to organise their uses and practices in space because of ecological constraints, nor do human practices exactly match environmental conditions. Landscape patterns cannot therefore be understood only by correlations between observed patterns and the state of an abiotic or anthropogenic variable. An important point is then to analyse processes leading to particular landscape patterns. It is often necessary to reduce the complexity of human and natural systems in order to find connections relevant for the analysis of landscape dynamics and that can be easily tested and assessed. In order to find such connections we have to look at the processes that occur at the same level in both ecological and agricultural systems.

In this paper we focus on an upland Mediterranean landscape, the Causse Mejean. This area is characterised by a strong landscape contrast between a wooded western part ('wooded Causse') and a steppe-like eastern part dominated by seminatural grasslands ('bare Causse'). The striking issue is that this dual landscape was maintained from the 17th century through to the 19th century. It is only since the middle of the 20th century that a landscape change has been noticed, as trees started to colonise the eastern part of the area.

Our objective is to identify the processes that explain the long-term opposition between the 'bare Causse' and the 'wooded Causse'. Several hypotheses have been suggested to explain it. According to available scientific literature, this pattern could be a result of climatic (Martonne 1926; Flahault 1931; Thiault 1968) or geological (Marres 1935) differences between the eastern and the western part of the area. Such differences are not demonstrated by the current knowledge about *P. sylvestris* biology, and could not explain why pines are today colonising the eastern part of the area. Cultural and anthropological differences (Cohen and Alexandre 1997), and especially woodland management practices and land tenure regimes (Brun 1978) have also been suggested, but they stay correlative observations and do not provide mechanisms for explaining the landscape pattern. Finally, a hypothesis which is widely held by agronomists and policy makers emphasises the role of grazing practices. Indeed, the landscape closure that started 50 years ago was concurrent with changes in livestock breeding practices. Such changes have been well studied among farms (Osty 1978; Petit 1978; Quétier et al. 2005) but their effects on vegetation have never been demonstrated, and they do not explain the differences between the western and the eastern parts of the Causse Mejean.

None of these hypotheses address the effects of cultivation (Marty et al. 2003), although the history of cereal growing has been well documented on the Causse (Chassany 1978; Fowler 1999). Especially, during the 17–19th centuries a shifting cultivation system ('crop and fallow' cycle) was conducted on the rangelands.

Our hypothesis is that differences in fallow duration adapted to geological differences between western and eastern parts (Cazalis 1856; Laur 1929), in interaction with grazing practices, explain why the Causse Mejean dual landscape pattern was maintained during several centuries. In order to test this hypothesis we propose an agent based model (STIPA – Simulating Tree Invasion in a Past Agro pastoral system) that combines historical land-use and biological data to simulate the effect of shifting cultivation on Scots pine (Pinus sylvestris L.) colonisation.

Materials and methods

Study area

The Causse Mejean (Figure 1) is the highest (800– 1250 m a.s.l.) of the 'Grands Causses', a series of Jurassic limestone plateaux of the southern edge of French Massif Central. It is clearly defined by deep canyons isolating it from surrounding plateaux. Its 360 km² area is typical of karstic systems, with poor limestone soils including dolomitic facies, and rare arable soils located in karstic depressions. The Mediterranean climatic influence, combined with altitude and a more continental influence produce long harsh winters and hot dry summers. The annual precipitation ranges from 800 to 900 mm, and fissured limestone geology gives this area a very dry aspect.

The vegetation is mainly composed of steppelike grasslands dominated by *Stipa pennata* and *Bromus erectus*, and of open woodlands of Scots pines (*Pinus sylvestris* L.). Non-native black pine (*Pinus nigra* Arnold) plantations are located in the eastern part of the area. The arable land is scattered and mostly occurs in dolines. Landscape pattern is strongly contrasted with Scots pine woodlands in the western part, and grasslands in the eastern part. The ecotone between woodlands and grasslands, observed on a regional scale since Paul Marres' studies (1935), is progressing

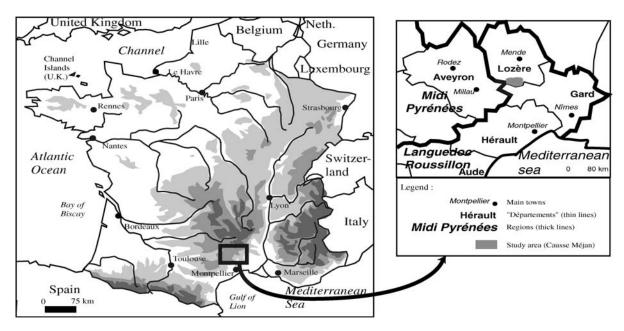


Figure 1. Location of the study area: the Causse Mejean, France.

eastwards (Figure 2). This change in landscape pattern is produced by a spontaneous encroachment by shrubs (e.g., *Juniperus communis* L., *Buxus sempervirens* L.) and trees (e.g., Scots pine) on grasslands and old-fields (Cohen and Hotyat 1995). This succession is observed in many Mediterranean upland regions in Europe (Lepart and Debussche 1992; Debussche et al. 1999). As it threatens the original flora and fauna that are linked to open habitats, it has become an important issue for conservation bodies such like the Cévennes National Park, which is in charge of the Causse Mejean environmental management.

Past land-use characteristics

Charcoal analysis of the Causse Mejean has shown that *Pinus sylvestris* forests were present before the Neolithic period (Vernet 1972; Quilès et al. 2002). Then agricultural clearings progressively opened the landscape. During the 18th century population was at its highest level in the history of the area and Scots pine forests remained only as isolated patches in the Western part, whereas the Eastern part was completely covered by grasslands (Figure 2). Numerous studies (Laur 1929; Marres 1935; Chassany 1978; Petit 1978) showed that 18th and 19th century agriculture was based on cereal cultivation. Evidences of past cultivation (walls, field patterns, and piles of stones, etc.) can be found on current landscapes (Fowler 1999). Sheep were raised above all for manure and for transferring fertility toward cultivated plots. Livestock rearing also provided wool for trade as well as some food diversity. The few dense woods were exploited for fuel wood. However, there is no historical evidence of the use of fires as a way of controlling encroachment, as it is done in other regions (Hester and Sydes 1992; Foster and Motzkin 2003).

Permanent crops, located in karstic depressions, covered about 30% of the Causse Mejean. Everywhere else, except on never cultivated small hills of dolomite rock (the *puechs*), rangelands were cultivated during 5 years, and then assigned to grazing during long fallows. As an adaptation to soil fertility, fallow periods were about 40 years on dolomite soils and about 20 years on calcareous soils (Laur 1929; Marres 1935).

It is likely that Scots Pines, initially dispersing from the canyons surrounding the Causse Mejean, established on the *puechs*, producing thus scattered, isolated seed sources (Marty et al. 2003).

(a) ca 1775 Deciduous woodland Pine woodland (b) 1840 Woodland (c) 1912 Plantations Other woodland (d) 1989 Deciduous woodland Plantations Pine woodland Sources : A) Cassini's maps of Rodez (published in 1781) and Mende (published in 1779) B) Maps from Land registry, "Département de la Lozère",1840. C) Daubrée, 1912. D) Inventaire Forestier National, 1989

Figure 2. Historical changes of the Causse Mejean landscape, from ca. 1775 to 1989.

660

Study species

Pinus sylvestris L. is the Pinus species which has the largest distribution area in the Palearctic, extending over 4000 km from southern Spain to Norway and 9000 km from west to east (Médail 2001). Scots pine flexibility regarding site conditions makes it a pioneer species (Debain 2003; Debain et al. 2003). It is one of the most precocious conifers as it reaches sexual maturity between 10 and 15 years old (Carlisle and Brown 1968). Seed dispersal occurs in spring each year, followed by germination as seeds exhibit no dormancy (McVean 1963). Even if juvenile pines are not grazed directly, strong grazing pressure an limit encroachment by accidental browsing or trampling of the seedlings; but clearing or ploughing is more efficient as it radically gets rid of trees (Lepart et al. 2001; Rousset and Lepart 2002).

Simulating tree invasion on a past agropastoral system: the STIPA model

Our aim was to test if the difference in fallow duration that characterised the two systems 'bare Causse' and 'wooded Causse' could explain a longterm difference in landscape between these two parts of the Causse Mejean. We then needed a model focusing on the interactions between pine tree and agricultural practices. Mechanistic models have been widely used to study forest dynamics (Botkin et al. 1972; Bugmann 2001); particularly, individual-based models have demonstrated their capabilities to address spatial issues in the context of woody plant colonisation (Higgins and Richardson 1998; Grimm et al. 1999; Prévosto et al. 2003). We looked for such an approach that could be combined with a model of land-use. Consequently, we used a multi-agent system (see Bousquet and Le Page 2004), simulating agricultural patterns with a cellular automaton grid, while invading pine trees were considered as independent located agents (their location refers to a precise cell in the grid). This choice was aimed at emphasizing the importance of dispersion for describing its effect on landscape patterns. We worked with Cormas, a software platform based on the VisualWorks[®] environment for programming in Smalltalk object-oriented language (Bousquet et al.

1998; see also Becu et al. 2003; Mathevet et al. 2003). Cormas is an agent-based platform, and provides great flexibility in simulating autonomous objects with clear and simple behaviour rules. The model description follows the international standard rules for oriented-objects models (Unified Modelling Language).

In STIPA, a closed grid of 100×80 hexagonal cells simulates a 137 ha rectangular portion of theoretical landscape subject to Scots pine colonisation from an isolated seed source. Simulations last 150 years, each time-step corresponding to 1 year. A hexagonal shape of cells aims to equalise distances between neighbours.

Each cell represents a 170 m^2 unit of the landscape. Two types of cells correspond to the agropastoral system of the 19th century. The permanent crops are clusters of about 1400 m² and distributed randomly over the grid. They represent 'dead zone' for pine as they are cultivated each year. The remaining cells are rangelands and their behaviour is based on the typical 'crops and fallow' cycle (Figure 3).

At the beginning of the cycle, each cell is cultivated during a crop duration of 5 years (Temp-Crop state). Then it is assigned to Fallow for a fallow duration (thereafter referred as T parameter) during which it is subjected to pine encroachment. In order to assess landscape changes due to pine progression, cells in Fallow state exhibit a *cover* attribute, changing from grassland to woodland when cells are colonised by pines: if covered with more than 40 pine individuals (corresponding to a realistic density of 3000 trees per hectare; Balandier et al. 2002) a cell becomes a 'young wood', and if covered with more than 40 adult individuals it becomes a 'mature wood'.

Adding to these land-uses, a cell located on the left side of the grid simulates an isolated wood, and acts as 'seed source' during the whole simulation.

Pines are independent, located agents following a realistically biological life cycle (Figure 4).

Each pine individual grows old (Figure 4a), becomes mature after 15 time-steps, reproduces and stops reproducing when the cell where it stands is completely surrounded by woods. The method for reproducing is detailed in the Figure 4b. An individual of *P. sylvestris* produces several thousands of seeds per year but they are

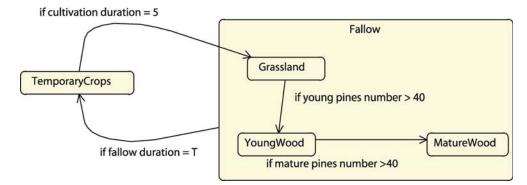


Figure 3. State-transition diagram of the shifting cultivation system cells in the STIPA model, in standard UML figuration. Cells change from a state (figured with a box) to another, based on decision rules.

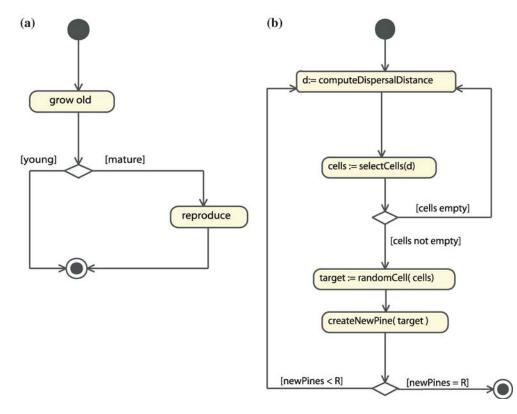


Figure 4. Activity diagrams of the pine in the STIPA model, in standard UML figuration. (a) General activity diagram. (b) 'Reproduce' method. Pine life cycle begins at the black spot and follows several 'methods' defining pine behaviour, calling on decision rules (in square brackets) if required, then stops at the ringed spot.

subjected to low emergence rate; then seedlings experience a high mortality (>75%) during the first 5 years (McVean 1963; Castro et al. 1999; Médail 2001). As modelling these stages would be very memory-consuming, we only considered the recruitment of 5 years old seedlings (thereafter referred as R), as suggested by Prévosto et al. (2003). Thus, at each time-step of the simulation each mature pine reproduces and disperses R seedlings (new pines). For each new pine a dispersal distance is computed using a function assessed by Debain (2003) for *P. sylvestris* from

field data from the Causse Mejean. The density of probability for a single seed is given for d (distance from the seed source) by the following:

$$f(d) = p/(2a)x \exp(-|d/a|) + (1-p)/(2b)x \exp(-|d/b|)$$
(1)

The first term gives probability of seeds being dispersed at short distance (proportion p of the seeds), while the second represents long distance dispersal (proportion (1-p) of the seeds). Coefficients a, b and p values were estimated, respectively as 3.6, 82.7 and 0.938 by Debain (2003) from field data with a maximum likelihood procedure. This mixed function (Bullock and Clarke 2000) fits very well with field results concerning the importance of long distance dispersal events (Debain 2003). An inversion formula is used to integrate the equation (1) into the model as a random generator, attributing to each seed a dispersal distance from an uniform [0 1] random probability (Figure 4b, method 'compute Dispersal Distance'). The direction of dispersal is randomised for each seed, as we were not able to assess this parameter effect (Higgins and Richardson 1998).

Finally, pines located in permanent or temporary crops are killed at the beginning of the following time-step.

In order to reduce the model sensitivity to initial conditions, at the beginning of each simulation the spatial configuration of permanent crops is set randomly, and each cell of the shifting cultivation system is set at a stage chosen randomly from the 'crop and fallow' cycle.

Parameter calibration and simulation plan

We evaluated how Scots pine encroachment was favoured or limited by the shifting cultivation system in testing the effects of the parameter T; however, we expected the recruitment (R) to be also a key factor as it determines the number of individuals that can colonise the grasslands. Then the effect of R was first tested in running simulations without any cultivation limiting tree encroachment (referred to as 'pastoral' system), with recruitment parameter R taking a realistic range of values (0.2, 0.6, 3, 5) following Prévosto et al. (2003) who worked in similar conditions. Then we introduced a shifting cultivation system,

Model simplifications

Focusing on processes relevant for testing the relative effect of shifting cultivation in landscape patterning, we assume two main simplifications in the STIPA model:

(i) We did not take into account fine scale heterogeneity in pine recruitment (interactions with plants, grazing spatial variability). However, the geological heterogeneity is reflected in the differences of land-use: permanent crops are situated on the arable soil of karstic depressions, shifting cultivation is conducted on dolomitic soils ('T20' system) or calcareous soils ('T40' system).

(ii) We ignored temporal variability in pine reproduction, establishment and mortality. Sensitivity of grasslands to pine encroachment was considered to be homogeneous, even if some field observations suggest that post-cultural stages favour seed germination and sapling growth by reducing competition with grass.

Model outputs analysis

For each year of each simulation we recorded the number of young woods and the number of mature woods.

In order to analyse the effect of parameters on final woodland cover, we performed with Splus 6.2 software a k-factors analysis of variance of 10 repetitions of the whole simulation plan (Higgins and Richardson 1998; Mathevet et al. 2003).

Results

Global effects of parameters on final woodland area

The full analysis of variance revealed that the 2 parameters tested (system-pastoral, *T*20, *T*40 and recruitment *R*) had a significant effect (p < 0.01) on wood cover at year 150). No sensitivity to the

initial configuration of permanent crops was found.

Effect of R on pine progression

Changes in *R* values simulated changes in grazing pressure. Increasing the recruitment parameter *R* significantly increased final woodland cover (with p < 0.005 in the full analysis of variance) and reduced the time necessary to reach this *maximum* (Figure 5a).

Curves show three stages in the increase of young woods establishment: (1) establishment limited to the periphery of seed sources, (2) a strong increase and (3) strong decrease corresponding to a transformation of young woods into mature woods (Figure 5b). Curves R = 3 and R = 5 show an early take-off for young wood establishment. A decrease in young woods and replacement by mature woods occurred at Y (year in simulation) = 100 and Y = 120 and mature woods occupied the whole grid at the end of the cycle. Curves R = 1 and R = 0.6 reached a maximum at Y = 110 and Y = 130; the curve of mature woods does not reach an equilibrium as for R = 3 and R = 5. Finally, even a very low recruitment (R = 0.2) simulating a very strong grazing pressure did not stop pine encroachment. But pine colonisation was slow and the final number of woods was lower than in the other simulations.

As predicted by the pine dispersal function, rare long distance establishment produced a limited number of isolated patches in the first stages (Figure 6).

After 50 years, patches coalesced. Even if progression started slowly and did not strongly affect landscape pattern at Y = 50, a strong colonisation occurred in the following steps.

Effects of shifting cultivation system

The shifting cultivation system changed pine dynamics as the reproduction period was reduced to a maximum of 25 years for long fallows ('T40') and 5 years for short ones ('T20'). At the landscape level, this effect was significant (p < 0.005).

Figure 7 shows the results of young and mature wood encroachment within the 'T20' and 'T40' systems.

At constant recruitment value, the parameter T strongly affected pine colonisation. A 20 years fallow duration minimised wood progression (Figure 7a–c). With R values lower than 3 a cyclic wood progression was observed, due to colonisation/cultivation of the 2 or 3 cells contiguous to the seed source. Even with R = 5, colonisation started slowly (10 'young woods' at Y = 50) and only reached ca. 390 young woods at Y = 150 (representing about 5% of the whole grid).

With a 40 years fallow duration (Figure 7b–d) only a low recruitment value (R = 0.2) severely contained pine encroachment. Nevertheless, shifting cultivation helped maintain woodland cover at levels lower than those observed within the 'pastoral' system: with T = 40 years fallow duration and R = 3, the 1000 young wood value was reached at Y = 90 vs. Y = 60 without shifting cultivation (Figure 7b).

The mature woods progressions (Figure 7c and d) confirm that no real woodland progression occurred with short fallow time (T = 20), except simulations with a high R (R = 5). With T = 40, mature woods progression started with a moderate recruitment (R = 1), even if it did not reach the values obtained within the 'pastoral' system.

Discussion

Bare Causse vs. wooded Causse: a combination of grazing and cultivation

The simulations with the STIPA model revealed that only a combination of short fallow duration (T = 20) and a recruitment value lower than 5 allowed to control efficiently the pine progression. Such a system was then able to produce the open landscape that characterises the 'bare Causse'. On the opposite, with long fallows (T = 40), only recruitment values lower than 0.2 allowed to control pine progression. In consequence we showed that within a wide range of recruitment values (from 0.2 to 5) differences in fallow duration can produce a contrasted landscape.

The differences in fallow duration are well documented (Cazalis 1856; Marty et al. 2003); what about recruitment conditions? Values of

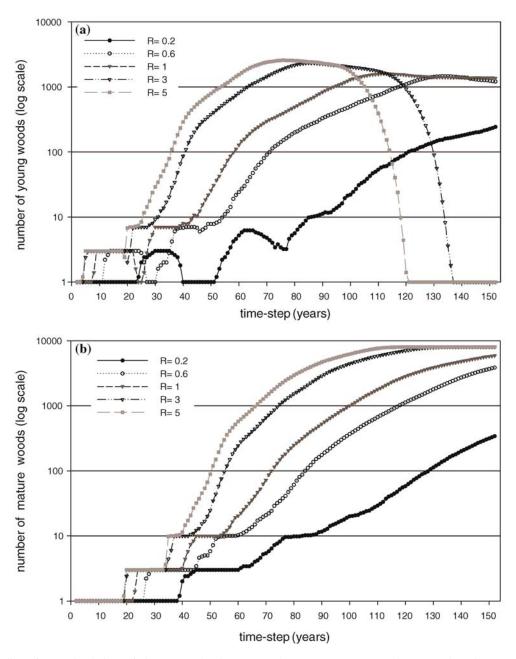


Figure 5. Effect of R on simulations of pine progression in a 'pastoral' system (a) 'young woods' progression; (b) 'mature woods' progression; log transformed.

P. sylvestris recruitment of 5 years old seedlings range widely in temperate areas, from 0.7 to 5 in a dense *Calluna vulgaris* moorland (Prévosto et al. 2003) to 34 in a xerophilous grassland of the northern France (Guittet and Laberche 1974); on Causse Mejean, a *P. sylvestris* recruitment value of 8 was found by Debain (2003) in low grazing conditions. Different factors can reduce pine recruitment such as a competition with the herbaceous layer (Castro et al. 2002), summer droughts (Castro et al. 2004), or grazing (Zamora et al. 2001). From historical data (Chassany 1978; Marty et al. 2003) it is known that grazing was conducted on the Causse Mejean rangeland during

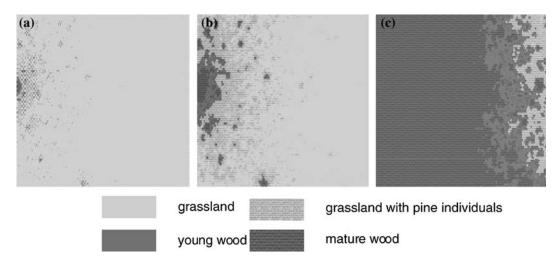


Figure 6. Spatial patterns for one simulation of pine progression in a 'pastoral' system with R = 1. (a) year 50; (b) year 75; (c) year 150.

fallows and that sheep diet was totally based on rangelands resources. In those conditions grazing was likely to reduce pine recruitment to values lower than 6 which allow, under *T*20 system in our simulations, to control woodland progression.

Otherwise, our modelling results indicate that in absence of cultivation, or in a system with long fallows (*T*40), it is necessary to decrease Scots pine mean recruitment to values lower than 0.2 or 0.6 to keep open grasslands during decades. One could hypothesise that during the 17–19th centuries the grazing pressure would have decreased pine recruitment to such values, but as there is no evidence for a difference in grazing pressure between the eastern and the western parts of the Causse Mejean during the 17–19th centuries (Marres, 1935), that hypothesis would not explain why woodlands have maintained on the western part of the Causse.

Introducing the shifting cultivation as a mechanism limiting pine colonisation appears then to be a good alternative to the 'grazing' dominance hypothesis (Le Brun 1957; Le Houérou 1981; Thirgood 1981). Until now, despite the work of Liou (1929) who suggested a dominant role of cultivation, grazing pressure has been seen as the key historical driver of the Causse Mejean landscape. The STIPA model contributes towards critics of the idea of overgrazing as one of the major causes of upland deforestation (Perevolotsky and Seligman 1998; Grove and Rackham 2001).

Time lags between ecological and historical analysis

Our simulations illustrated a phenomenon described in studies on biological invasions (see Hastings et al. 2005 for a review on this subject): the existence of a time-lag during which invasive plant density is low, often under a threshold of detection. In the case of Causse Mejean landscape, such a time-lag can lead to misinterpretation of the links between human activity and landscape patterns.

When a socio-economical system changes, the ecological system does not respond immediately. Ecological dynamics like the establishment of Scots pine woodlands occur over several decades. Our results show that in all simulations, the first years are characterised by a low level of pine progression, limited to the neighbourhood of seed sources without important changes in landscape pattern (e.g., Figure 5). A strong invasion can be very unobtrusive for a long period, and be noticed only when a 'point of no return' is reached. For example, if we look at wood progression curves at a given time-step (for example year 50), it is impossible to guess how the landscape will evolve without knowing the underlying dynamic (T = 20) or T = 40). There is therefore a risk in assigning a particular state of the landscape to the features of the contemporary social organisation whereas the landscape structure is inherited. In the Causses region and on the Causse Mejean in particular, the time lag is not a latency or acclimation time for an

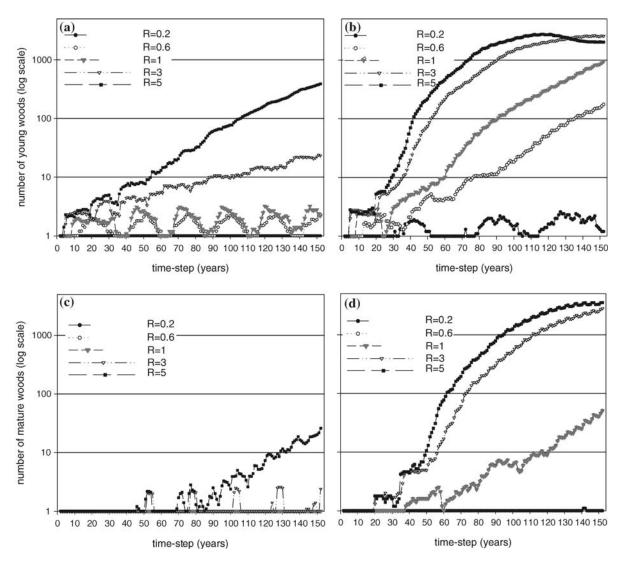


Figure 7. Effect of R on simulations of pine progression in a shifting cultivation system (a) T = 20; (b) T = 40; 'young wood' progression log transformed; (c) T = 20; (d) T = 40; 'mature wood' progression log transformed.

introduced species: the Scots pine has been known to occur since at least 5000 BP (Quilès et al. 2002). The time lag is the start of the curve of fast growth in the establishment of the pine forest. This time lag was rather long so that the awareness of the invasion took place at a time (ca. 1980) when the cereal cultivation in the recent past had been forgotten and when observers thought that the grassland landscape was in equilibrium with grazing. The progression of pine was attributed to decreased grazing pressure related to the modernisation of the livestock rearing system in the 1960s and 1970s. But our results suggest that it was a much older socio-economic change, the halt of cereal cultivation and the specialisation in livestock at the end of the 19th century that triggered the colonisation. This colonisation was very slow and did not greatly change the landscape between 1900 and 1950.

Taking into account this time lag can avoid misinterpretation of encroachment dynamics. It emphasises the limits of a descriptive knowledge of past landscape features and past land-use systems and suggests that it is fundamental to study ecological and human social systems as a multi-scale interaction. 668

Unsustainable practices for a sustainable landscape?

Current management objectives for the Causse Mejean, as found in the Cévennes National Park policies, are looking for maintaining the open landscape inherited from previous centuries. This position is justified from a biodiversity, a cultural and an agronomic point of view: open landscapes are habitats for priority species, cultural landscape with heritage value and resources for farmers. To reach this objective they support grazing practices that are supposed to stop pine colonisation (PNC 1999; Etienne 2001). This is a view close to a 'virtuous circle': grazing maintains an open landscape of interest for biodiversity and environmental quality is a key factor for a high quality farming based on the use of local resources. However, it is clear in our simulations that a very low recruitment is necessary to limit pine encroachment. Yet the grazing pressure necessary on a long-term basis to reach such recruitment values would probably be incompatible with most sheep breeders' strategies today (Quétier et al. 2005).

Controlling Scots pines progression is a 'sustainable development' objective that could be obtained by agricultural practices such as the ones documented for the 18th and 19th century. Even though effective to maintain open landscapes, they cannot be considered as sustainable. The 19th Causse Mejean system would today appear as a completely unsustainable system: demographic pressure and human competition for food caused high mortalities, rural poverty, strong social inequalities, overexploitation of natural resources, soil erosion, exploiting rangelands until it caused the degradation of the soil. Even for biodiversity, strong grazing pressure and overexploitation of trees and shrub for heating/cooking, may not have delivered biodiversity goods as does current landscape.

Nowadays, woodlands and rangeland clearings for cultivation purpose are a common practice among farmers who want to increase their available arable land. Supporting clearing could be a management measure suitable for maintaining open landscapes. This would require shifting from cultivation to grazing after several years. Nevertheless, the cost effectiveness of such a method needs to be assessed. By now, pine cutting begin to be adopted by rangelands managers (Carrère et al. 1999) who are confronted with the failure of 'grazing-based' agri-environmental solutions for controlling encroachment (Bartolomé et al. 2000).

Conclusion

Landscape patterns are historical co-productions of human land-use strategies and ecological processes. Understanding landscape patterns does not require studying the effect of land-use on ecological processes or *vice versa*, but analysing the mutual interactions between socio-economic systems and ecological systems. In this context, agentbased modelling approaches like STIPA are relevant tools to integrate land use practices and natural processes.

Acknowledgements

We thank Raphaël Mathevet, Pierre Bommel, Robert Britton and two anonymous referees for their fruitful comments on the manuscript. This work is linked to the BIOSCENE project (Scenarios for reconciling biodiversity conservation with declining agricultural use in the mountains of Europe) project (No.: EVK2-2001-00354), under the EU 5th Framework Energy, Environment and Sustainable Development, supported by the European Commission. P. Caplat was funded by the BIOSCENE project coordinated by Jonathan Mitchley. This research was also supported by the DIVA programme of the French Ministry of Ecology and Sustainable Development, coordinated by Jacques Baudry and is included in the programme of the long-term Research Area 'Mediterranean Backcountry' funded by the CNRS.

References

- Balandier P., Rapey H., Ruchaud F. and de Montard F.X. 2002. Agroforesterie en Europe de l'Ouest: pratiques et expérimentations sylvopastorales des montagnes de la zone tempérée. Cahiers d'études et de recherches francophones/ Agricultures 11(2): 103–113.
- Bartolomé J., Franch J., Plaixats J. and Seligman N.G. 2000. Grazing alone is not enough to maintain landscape diversity in the Montseny Biosphere Reserve. Agric. Ecosyst. Environ. 77: 267–273.
- Becu N., Perez P., Walker A., Barreteau O. and Le Page C. 2003. Agent based simulation of a small catchment water

management in northern Thailand: description of the CATCHSCAPE model. Ecol. Model. 170: 319–331.

- Bengtsson-Lindsjö S., Ihse M. and Olsson E.N.A. 1991. Landscape patterns and grassland plant species diversity in the 20th century. In: Berglund B.E. (ed.), The cultural landscape during 6000 years in southern Sweden – the Ystad Project. Ecological Bulletins, pp. 388–396.
- Birks H.H., Birks H.J.B., Kaland P.E. and Moe D. (eds), 1988. The Cultural Landscape. Past, Present and Future. 2nd edition. Cambridge University Press, Cambridge, UK.
- Botkin D.B., Janak J.F. and Wallis J.R. 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60: 849–873.
- Bousquet F., Bakam I., Proton H. and Le Page C. 1998. Cormas: common-pool resources and multi-agent systems. Lecture Notes Artif. Intel. 1416: 826–837.
- Bousquet F. and Le Page C. 2004. Multi-agent simulations and ecosystem management: a review. Ecol. Model. 176: 313–332.
- Brun A. 1978. Le Causse Mejean. De la crise des années 50 aux perspectives actuelles. INRA-ESR, Paris, France.
- Bugmann H. 2001. A review of forest gap models. Climat. Change 51: 259–305.
- Bullock J.M. and Clarke R.T. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. Oecologia 124(3): 506–521.
- Carlisle A. and Brown A.H.F. 1968. Biological Flora of the British Isles. *Pinus sylvestris* L. J. Ecol. 56(1): 269–307.
- Carrère P., Orth D., Kuiper R. and Poulin N. 1999. Development of Shrubs and Young Trees Under Extensive Grazing. Proceedings of the International Occasional Symposium of the European Grassland Federation, Thessaloniki, Greece.
- Castro J., Gomez J.M., Garcia D., Zamora R. and Hodar J.A. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. Plant Ecol. 145: 115–123.
- Castro J., Zamora R., Hodar J.A. and Gomez J.M. 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J. Ecol. 92(2): 266–277.
- Castro J., Zamora R. and Hodar J.A. 2002. Mechanisms blocking *Pinus sylvestris* colonization of Mediterranean mountain meadows. J. Veg. Sci. 13: 725–731.
- Cazalis F. 1856. Quelques mots sur l'état de l'Agriculture dans le Larzac et sur le Causse Mejean; améliorations à introduire dans le système d'exploitation de ce dernier pays. Bulletin de la Société d'Agriculture, Industrie, Sciences et Arts du département de la Lozère 1959: 440–455.
- Chassany J.-P. 1978. Le Causse Mejean. Eléments d'histoire agro-écologique. INRA-ESR, Paris, France.
- Childe V.G. 1971. The neolithic revolution. In: Struever S. (ed.), Prehistoric Agriculture. Natural history press, New York, USA, pp. 15–21.
- Cohen M. and Alexandre F. 1997. Embroussaillement, pratiques et représentations sociales: une recherche de corrélations. L'exemple des territoires de Rieisse et de Rouveret (causse Mejean, Lozère). Nat. Sci. Sociétés 5(1): 31–44.
- Cohen M. and Hotyat M. 1995. Embroussaillement et boisement sur le Causse Mejean entre 1965 et 1992: une approche par photo interprétation diachronique. In: Saussol A. and Bonniol J.-L. (eds), Grands Causses, nouveaux enjeux, nouveaux regards. Fédération pour la vie et sauvegarde du Pays des Grands Causses, Millau, France, pp.113–124.

- Daubrée M. 1992. Statistique et atlas des forêts de France, Paris, France.
- Debain S. 2003. *Pinus sylvestris* et de Pinus nigra sur le Causse Mejean: paramètres démographiques et interactions biotiques. Ph.D. Thesis ENSAM, Montpellier, France, 142p.
- Debain S., Curt T., Lepart J. and Prévosto B. 2003. Reproductive variability in *Pinus sylvestris* in southern France: implications for invasion. J. Veg. Sci. 14(4): 509–516.
- Debussche M., Lepart J. and Dervieux A. 1999. Mediterranean landscape changes: evidence from old postcards. Global Ecol. Biogeogr. Lett. 8: 3–15.
- Diamond J. 2002. Evolution, consequences and future of plant and animal domestication. Nature 418: 700–707.
- Etienne M. 2001. Pine trees invaders or forerunners in mediterranean-type ecosystems: a controversial point of view. J. Mediterranean Ecol. 2: 221–231.
- Flahault C. 1931. A propos de la géographie botanique des Causses. Bulletin de la Société Languedocienne de Géographie (2): 89–100. (II1931)
- Foster D.R. and Motzkin G. 2003. Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. Forest Ecol. Manage. 185: 127–150.
- Fowler P. 1999. A limestone landscape from the air: le Causse Mejean, Languedoc, France. Antiquity 73: 411–419.
- Gorham E. 1997. Human impacts on ecosystems and landscapes. In: Nassauer J.I. (ed.), Placing Nature. Culture and Landscape Ecology. Island Press, Washington & Covelo, USA, pp. 15–32.
- Grimm V., Wyszomirski T., Aikman D. and Uchmanski J. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecol. Model. 115: 275–282.
- Grove A.T. and Rackham O. (eds) 2001. The Nature of Mediterranean Europe. An ecological history. Yale University Press, New Haven and London, UK.
- Guittet J. and Laberche J.-C. 1974. L'implantation naturelle du pin sylvestre sur pelouse xérophille en forêt de Fontainebleau. Oecol. Plant. 9(2): 111–130.
- Hastings A., Cuddington K., Davies K.F., Dugaw C.J., Elmendorf S., Freestone A., Harrison S., Holland M., Lambrinons J., Malvadkar U., Melbourne B.A., Moore K., Taylor C. and Thomson D. 2005. The spatial spread of invasions: new developments in theory and evidence. Ecol. Lett. 8: 91–101.
- Hester A.J. and Sydes C. 1992. Changes in burning of Scottish heather moorland since the 1940s from aerial photographs. Biol. Conserv. 60: 25–30.
- Higgins S.I. and Richardson D.M. 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecol. 135: 79–93.
- Inventaire Forestier National. 1989. Inventaire forestier de la Lozère, Paris, France.
- Laur F. 1929. Le plateau du Larzac. Contribution à l'étude de la vie économique de la région et à l'histoire des bien communaux avant et après la Révolution. Imprimerie de la charité, Montpellier, France.
- Le Brun P. 1957. Un siècle de floristique à travers les Alpes françaises. Bull. Soc. Bot. de France CIV: 339–359.
- Le Houérou H.N. 1981. Impact of man and his animals on Mediterranean vegetation. In: Di Castri F. and Specht R.L. (eds), Mediterranean-Type Shrublands: Ecosystems of the World. Vol 11. Elsevier, Amsterdam, Neth, pp. 479–521.

- Lepart J., Martin A., Marty P. and Debain S. 2001. La progression des pins sur les Causses. Un phénomène difficilement contrôlable. Forêt Méditerranéenne 22(1): 23–28.
- Lepart J. and Debussche M. 1992. Human impact on landscape patterning: mediterranean examples. In: Hansen A.J. and Di Castri F. (eds), Landscape Boundaries. Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, Paris, Berlin, pp. 76–105.
- Liou T.N. 1929. Etudes sur la géographie botanique des Causses. Archives de Botanique III, 220p.
- Marres P. 1935. Les Grands Causses, étude de géographie physique et humaine. Arrault et Cie, Tours, France.
- Martonne E.D. 1926. Les grandes régions de France. Cévennes et Causses, Paris, Payot.
- Marty P., Pélaquier E., Jaudon B. and Lepart J. 2003. Spontaneous reforestation in a peri-Mediterranean landscape: history of agricultural systems and dynamics of woody species. In: Fouache E. (ed.), Environmental Dynamics and History in Mediterranean Regions. Elsevier, Paris, France, pp. 179–186.
- Mathevet R., Bousquet F., Le Page C. and Antona M. 2003. Agent-based simulations of interact-ions between duck population, farming decisions and leasing of hunting rights in the Camargue (Southern France). Ecol. Model. 165: 107–126.
- McVean D.N. 1963. Ecology of Scots pine in the Scottish highlands. Nat. Conservancy 1963: 671–686.
- Médail F. 2001. Biogéographie, écologie et valeur patrimoniale des forêts de pin sylvestre (*Pinus sylvestris* L.) en région méditerranéenne. Forêt Méditerranéenne 22: 5–22.
- Moore P.D. 1975. Origin of blanket mires. Nature 256: 267-269.
- Motzkin G., Foster D., Harrod J. and Boone R. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecol. Monogr. 66: 345–365.
- Motzkin G., Wilson P., Foster D. and Allen A. 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. J. Veg. Sci. 10: 903–920.
- Osty P.L. 1978. Le Causse Méjan. Elevages et éleveurs en 1975. INRA-ESR, Paris, France.
- Perevolotsky A. and Seligman N.G. 1998. Role of grazing in Mediterranean rangeland ecosystems. Inversion of a paradigm. Bioscience 48(12): 1007–1017.
- Petit F. 1978. Le Causse Mejean. Exode rural et utilisation du territoire (de 1850 à nos jours). INRA-ESR, Paris, France.

- PNC 1999. Plan de gestion Antennes Causses et Gorges 2000– 2006. Management plan report of the French Cévennes National Park.
- Prévosto B., Hill D.R.C. and Coquillard P. 2003. Individualbased modelling of *Pinus sylvestris* invasion after grazing abandonment in the French Massif Central. Plant Ecol. 168: 123–137.
- Quétier F., Marty P. and Lepart J. 2005. Farmers management strategies and land use in an agropastoral landscape: Roquefort cheese production rules as a driver of change. Agric. Syst. 84: 171–193.
- Quilès D., Rohr V., Joly K., Lhuillier S., Ogereau P., Martin A., Bazile F. and Vernet J.-L. 2002. Les feux préhistoriques holocènes en montagne sub-méditerranéenne: premiers résultats sur le Causse Mejean (Lozère, France). C. R. Palevol 1: 59–65.
- Rousset O. and Lepart J. 2002. Neighbourood effects on the risk of an upalatable plant being grazed. Plant Ecol. 165: 197–206.
- Segerström U. and Emanuelsson M. 2002. Extensive forest grazing and hay-making on mires – vegetation changes in south-central Sweden due to land use since Medieval times. Veg. Hist. Archaeobot. 11: 181–190.
- Thiault M. 1968. Reconnaissance phyto-écologique des hautes terres des Grands Causses lozériens, Vol 37. CNRS-CEPE, Montpellier, France.
- Thirgood J.V. 1981. Man and the Mediterranean Forest. Academic Press, New York.
- Toupal R.S. 2003. Cultural landscapes as a methodology for understanding natural resource management impacts in the Western United States. Conserv. Ecol. 7(1): [online]
- Vernet J.-L. 1972. Nouvelle contribution à l'histoire de la végétation holocène des grands causses d'après les charbons de bois. Bull. Soc. Bot. Fr. 119: 169–184.
- Von Droste B., Plachter H. and Rössler M. (eds) 1995. Cultural Landscapes of Universal Value. Components of a Global Strategy. Gustav Fisher Verlag, Stuttgart, New York.
- Zamora R., Gomez J.M., Hodar J.A., Castro J. and Garcia D. 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. Forest Ecol. Manage. 144(1–3): 33–42.