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ORIGINAL PAPER

Simulating Mediterranean landscape pattern and vegetation dynamics under different fire regimes

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Abstract In the Mediterranean Basin, landscape patterns are strongly human-modified. In recent decades, because of industrialisation and rural exodus, many fields have been abandoned, generating changes in the landscape pattern. In this framework, I aim to study the effect of landscape pattern on landscape dynamic processes in the Mediterranean Basin using simulation models and considering that fire may interact with landscape pattern. First I generate a gradient of five artificial random landscapes. In each landscape I include four species types growing in the Mediterranean Basin, each type with different plant traits (Quercus, Pinus, Erica and Cistus types). In each landscape scenario, each species covers 30% of the landscape but with a different spatial distribution, from the coarsest-grained (L1) to the finest-grained (L5). Then, the dynamics of each of these five landscapes were simulated for 100 years using the FATELAND simulation model. Simulations were run with six fire regime scenarios in each landscape scenario (no fire, mean fire interval of 80, 40, 20, 10 and 5 years). Landscape attributes were computed for the initial and the final landscapes. As expected, the results suggest that, as expected, some species increase and others decrease depending on the fire regime. However, the results also show that different landscape structures produce different dynamics and thus that there is a clear interaction between landscape pattern and fire regime. For instance, coarse-grained spatial patterns generate slower dynamics than fine-grained patterns, and fire-sensitive species are maintained longer under coarse-grained patterns (i.e., fragmentation accelerates extinction of fire-sensitive species).

Keywords Landscape dynamics · Spatially explicit modelling · Spatial pattern · Spatial autocorrelation · Landscape grain · Mediterranean-type ecosystems

Introduction

It is widely assumed that there is a strong link between ecological patterns and ecological functions and processes (Turner 1989; Levin 1992), and that there may be a two-way dynamic interaction between pattern and process. Historical land uses have produced a range of landscape patterns, and the implications of these patterns on ecological processes may

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persist for long periods (Peterson 2002). Similarly, fire also produces long-lasting landscape patterns (Johnson 1992); furthermore, fire may filter out (Zedler et al. 1983) or favour invasion (D′Antonio and Vitousek 1992; Lloret et al. 2003) of different species and thus produce changes in landscape and ecosystem processes. A clear example of strong landscape changes can be found in the Mediterranean Basin with its millenary history of intensive and extensive land use (Naveh 1990). In the Mediterranean, palaeolithic people used fire to facilitate hunting and food gathering (Oakley 1955; Perlès 1977; Trabaud 1998; Stapert and Johanse 1999) and, since then, millennia of severe pressure resulting in burning, cutting and grazing non-arable lands, and clearing, terracing, and cultivating arable areas, have created a vast array of strongly human-modified landscapes (Farina 1998). In recent decades and especially in the northern (European) rim of the Mediterranean, with the industrialisation and the rural exodus, many fields have been abandoned, increasing the cover of early-succession species (many of which are very flammable), and changing the landscape pattern (Moreira et al. 2001; Pausas 2004). It is assumed that this is the main driver of the increasing number of wildfires and area burned in recent decades, although the influence of climatic changes cannot be denied (Piñol et al. 1998; Pausas 2004). Before the 1970s, fires were few and small areas were affected; after the 70s, the number of fires and the area affected increased exponentially (Pausas and Vallejo 1999; Pausas 2004).

In this framework, I ask to what extent landscape patterns may determine long-term vegetation dynamics in a fire-prone environment. There is a long history of demonstrating non-random spatial patterns in plant communities (Watt 1947; Greig-Smith 1983), and several experiments (van Andel and Dueck 1982; Thórhallsdóttir 1990; Stoll and Prati 2001) indicate that the spatial arrangement of competing species can affect their performance and thus have implications on ecosystem processes. However, the consequences of the spatial pattern at landscape level have been poorly addressed (de Blois et al. 2002). Silvertown et al. (1992), using a simple spatially explicit simulation model for a grassland community, suggested that the process of plant dynamics may be different depending on the initial spatial pattern. To what extent spatial patterns may interact with disturbance remains to be addressed.

Because landscape–fire interactions are complex, dynamic and non-linear, addressing these issues at large spatial and temporal scales requires the use of simulation models (Kareiva and Wennergren 1995). Many fire-landscape studies/models consider the fuel loads and other important physical fuel characteristics (e.g., fuel continuity, moisture, bulk density) (Finney 1999; Lops et al. 2002; Piñol et al. 2005), but they do not consider the process of plant regeneration. Thus the consequences of the different composition and structure of the landscape (in the sense of the different fire response strategies) have been poorly addressed. One of the main models used for landscape dynamics, the LANDIS model (Mladenoff and He 1999; He and Mladenoff 1999; Sturtevant et al. 2004), which was elaborated for boreal ecosystems, is difficult to use in Mediterranean conditions because it cannot handle short fire frequencies, short-lived species, seed pool dynamics and fire-stimulated recruitment, processes of great importance in the Mediterranean Basin (but see Franklin et al. 2001 and Syphard and Franklin 2004 for LANDIS applications to California Mediterranean landscapes and for future improvements of LANDIS). Spatial versions of gap models have been used for testing fire management strategies and fuel connectivity thresholds in coniferous forests (Miller and Urban 2000a, b).

In this paper I use the FATELAND model (Pausas and Ramos 2006), a spatially explicit version of the FATE model (Functional Attributes in Terrestrial Ecosystems, Moore and Noble 1990) elaborated for fire-prone Australian communities and later tested for fire-prone Mediterranean ecosystems (Pausas 1999b; Lloret et al. 2003). FATELAND allows different species to coexist and compete in each single cell, which is an improvement over some of the previous models testing spatial patterns in which each spatial cell can only be occupied by a single species (e.g., Green 1989; Silvertown et al. 1992; Lavorel and Chesson 1995; Pausas 2003). The aim is to understand how the spatial arrangement of different species types may interact with the fire frequency in vegetated landscape (artificial fuelbreaks such as roads and urban areas are not considered). I hypothesise that landscape with different spatial pattern would have different dynamics, and species with different regeneration strategies should have different responses to the landscape × fire interaction. Thus, a range of artificial random landscape scenarios (Gardner et al. 1987) are generated and their dynamics simulated under different fire regimes (including the absence of fire).

Methods

Modelling vegetation dynamics

To explore the relationships between landscape pattern, fire regime and vegetation dynamics, I use the FATELAND model, which is a (grid-cell) raster-based version of the FATE model (Moore and Noble 1990). This spatial version of FATE is included in the LASS modelling environment (Pausas and Ramos 2006; available at http://www.ceam.es/pausas). Another spatial implementation of FATE has recently been used for studying the effect of different grazing regimes on plant persistence in Swedish grasslands (Cousins et al. 2003). FATE is a general model of vegetation dynamics that is based on the life history traits of individual plants in a stand. It predicts vegetation dynamics at a qualitative level and from simple parameters derived from the Vital Attributes approach (Noble and Slatyer 1980). FATE can be considered a good compromise for capturing the essential processes of community dynamics while remaining relatively simple, easy to parameterise and providing an adequate representation of disturbance dynamics (Pausas 1999b, Cousin et al. 2003). FATE runs at annual time steps and simulates cohorts of plants that pass through a series of four discrete stages: propagules, seedlings, immature, and mature plants. The abundance of each stage is simulated in a qualitative manner (absent, low, medium and high abundance). FATE include three levels of light availability (low, medium, and high) determined by the vertical structure of the vegetation (stratum). Germination and survival are determined on the basis of these light availability levels, and changes in light availability are due to species overtopping each other (for further details see Moore and Noble 1990, Pausas 1999b, Cousins et al. 2003).

FATE is not a spatially explicit model, while FATELAND is a two-dimensional array of cells with a FATE in each cell. Different species may co-occur in each cell. FATELAND also includes a spatially explicit dispersal module and a disturbance module. The FATE model is deterministic, but in FATELAND stochasticity is included in both the dispersal and the fire modules. Dispersal is simulated by computing the probability of dispersal (p) according to the negative exponential equation (Ellison and Parker 2002): $p = A \times \mathrm{Exp}(k \times \mathrm{Distance}/\mathrm{MaxDistance})$, where *Distance* is a random number between 0 and *MaxDistance*, and k and A are the species-specific input parameters for modelling dispersal (Table 1); k provides the shape of the curve and A the magnitude of the dispersal (set to 0.3, 0.5 and 0.9 for low, medium and high, respectively).

Table 1 Plant functional traits used for the FATELAND modelling

Traits	Quercus	Erica	Pinus	Cistus
Lifespan	200	40	120	15
Age at maturation	20	7	15	3
Innate dormancy (years)	0	0	0	15
Stratum (adult/juvenile)	3/1	2/1	3/1	2/1
Germination rate *	L, M, H	L, M, M	N, L, M	N, L, H
Seedling survival*	N, Y, Y	N, N, Y	N, N, Y	N, N, Y
Immature survival*	Y, Y, Y	N, N, Y	N, N, Y	N, N, Y
Mature survival*	Y, Y, Y	N, Y, Y	N, N, Y	N, Y, Y
Dispersal capacity (A)	Low	Medium	High	Medium
Max. dispersal distance (m)	500	20	100	20
Dispersal shape (k)	−5	−3	−42.5	−2
Resprouting	All	All	None	None
Propagule fire survival	None	Few	All	All
Flammability	Low	High	Moderate	High

*Abbreviations used: L: low, M: medium and H: high (germination rate); Y: yes and N: no (survival). The three values for each species refer to low, medium and high resource levels (respectively). See Methods section and Moore and Noble (1990) and Cousin et al. (2003) for details)

Fire is also probabilistic in time and space. The fire year is chosen by following the given probabilities (see the fire scenarios below); fire starts in a randomly chosen cell and spreads depending on the fuel in the surrounding cells. The fuel in the cell is computed on the basis of the species abundance in the cell and their flammability (defined as low, moderate or high). The higher the fuel and/or the flammability, the higher the probability of the cell being burned. Thus, the fire module is very simple and does not intend to be very realistic in the sense of predicting fire size or area burnt, as do most mechanistic fire simulation models (e.g., Finney 1999; Lops et al. 2002). In contrast, the objective of this module was to be able to impact in the landscape, produce plant mortality and generate opportunities for post-fire regeneration, and thus generate dynamics processes.

Simulation scenarios

I simulate the dynamics of four groups of species (functional types) found in the eastern Iberian Peninsula (Table 1): two resprouters (R + P − *sensus* Pausas et al. 2004a; Pausas and Verdú 2005), one tree and one shrub: Quercus (broadleaved evergreen resprouter); Erica (heath, ericoid-leaved resprouter); and two seeders (R−P+), also one tree and one shrub: Pinus (needle-leaved non-resprouter with serotinous cones) and Cistus (non-resprouter with germination stimulated by fire). Quercus is the most shade-tolerant species and Pinus and Cistus the most intolerant. These species types are representative of species typically growing along the Mediterranean coast of the Iberian Peninsula, where fire is a very important factor (Pausas 2004). Species attributes (Table 1) are obtained from field experience and from the literature (Lloret 1998; Pausas 1999a, b; Pausas et al. 1999, 2004c; Lloret et al. 2003; Pausas and Verdú 2005).

All simulations began with a square artificial landscape containing 10,000 square cells (100 × 100 grid cell), each side of which is 10 m in length (i.e., 100 ha). FATELAND cannot handle much larger landscapes (e.g., two orders of magnitude larger) due to computational limitations of the current LASS version (Pausas and Ramos 2006); and further implementations in other operate systems may overcome this limitation. Five different landscape structures were selected by generating five hierarchically structured random landscapes for each species. I designed five landscape scenarios (L1 to L5), each of the same size, and in each landscape I included the four species types above. In all landscapes, each species covers approximately 30% of the landscape, but the spatial distribution (the degree of patchiness) of the species varies in each landscape (Fig. 1). L1 was the most aggregated (coarse-grained) pattern and was generated by including each species in a single patch at each corner of the landscape. For L2 to L5, species were located by using different parameters (Table 2) for the generation of hierarchically structured random landscapes (see details in O′Neill et al. 1992; Lavorel et al. 1993). L5 corresponds to a pure random pattern without any spatial structure. All species in all landscapes were included in the corresponding cells as a single cohort and with an intermediate abundance. By including the four species types in the landscape for the simulations, in all five scenarios most of the landscape is vegetated (and thus burnable, although the burnability of each cell depends on the species composition and abundance).

In each landscape scenario I applied six fire scenarios (called f0, f80, f40, f20, f10 and f5) representing a gradient of fire frequency (at the landscape level) from no fire (f0), to different mean interfire periods (80, 40, 20, 10 and 5 years). These fire frequency values are input values at landscape level and not at cell level, because cells may burn depending on plant abundance and flammability. Each fire × landscape scenario was run for 100 years, which is a reasonable time window to see landscape changes. Because the model does not consider climatic changes, longer time windows would probably be too speculative. Species abundance (cover) at landscape scale was computed as the proportion of cells in the landscape occupied by the species (including mature or immature individuals). Landscape analysis was performed for both initial and final landscapes, using the tools available in LASS. For each species, I compute spatial autocorrelation by the joint-count statistics (Cliff and Ord 1981) and the number of patches, edge length and mean patch size following the equation in FRAGSTAT (McGarigal and Marks 1994). Spatial autocorrelation for species richness is computed using the Moran index (Cliff and Ord 1981). Given the strong correlations between some of these landscape attributes, I will focus mainly on edge length because it may be a good indicator of species spatial interactions. Both the generation of landscape scenarios and the simulations with different

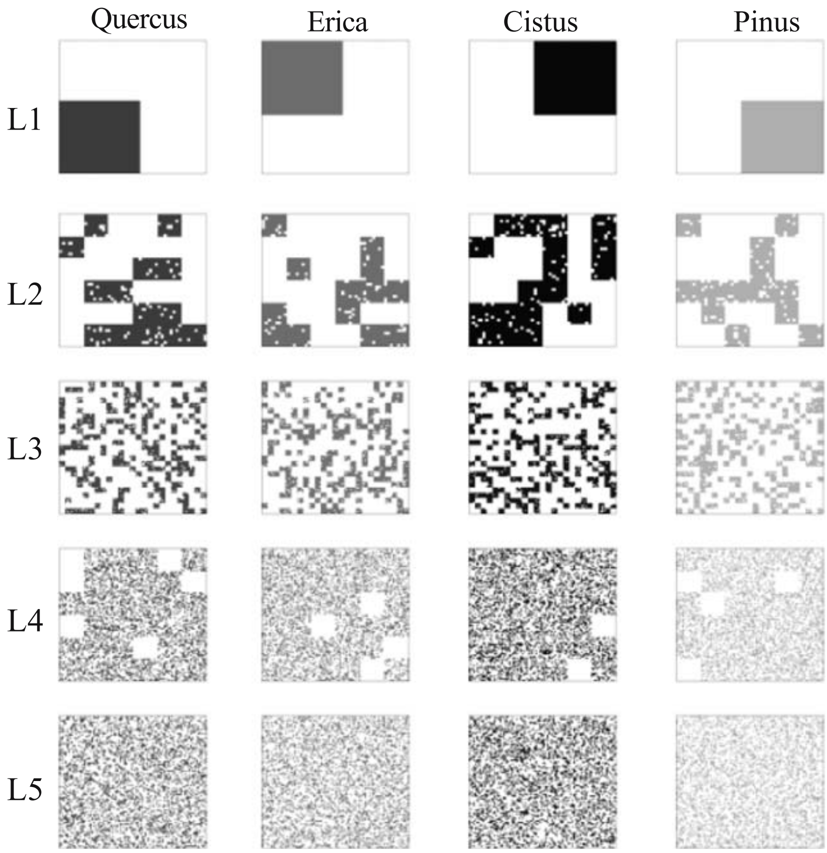


Fig. 1 Initial spatial configuration of the four species groups (termed Quercus, Erica, Cistus and Pinus) in the five landscape scenarios (L1 to L5)

fire regimes were replicated 10 times (starting with different seed for the random generator); mean values and the variability between runs are shown in the results section.

Results

The five landscapes generated represent a gradient of landscape patterns (Fig. 2), from landscapes with a low number of large patches, low edge length and high spatial autocorrelation (coarse-grained pattern) to landscapes with the opposite characteristics (high number of small patches, long edge and low autocorrelation; fine-grained pattern). The results show the strong correlation between the four landscape attributes. Species richness also shows a trend from high to low spatial autocorrelation (Fig. 3).

After 100 years of simulation, the species abundance differs from the initial abundance (30%) and the differences depend on both the fire regime (Fig. 4) and the initial spatial pattern (Fig. 5). Trees (especially Pinus) tend to decrease with fire frequency, while shrubs tend to increase (Fig. 4). Quercus species increase in abundance from the initial 30%, but the increase is lower with high fire frequency (Fig. 4) and in fine-grained landscapes (Fig. 5). Pinus species increase with low fire frequency and decrease with high fire frequency (Fig. 4), but this increase or decrease also depends on the spatial pattern (Fig. 5). Erica decreases in abundance from its initial situation in

Table 2 Input values for the hierarchically structured landscape generator to set the initial distribution of the species in each landscape scenario (L2 to L5)

	m_1	m_2	P_1	P_2
L2	6	8	0.33	0.90
L3	25	8	0.33	0.90
L4	6	20	0.90	0.33
L5	10	10	1	0.30

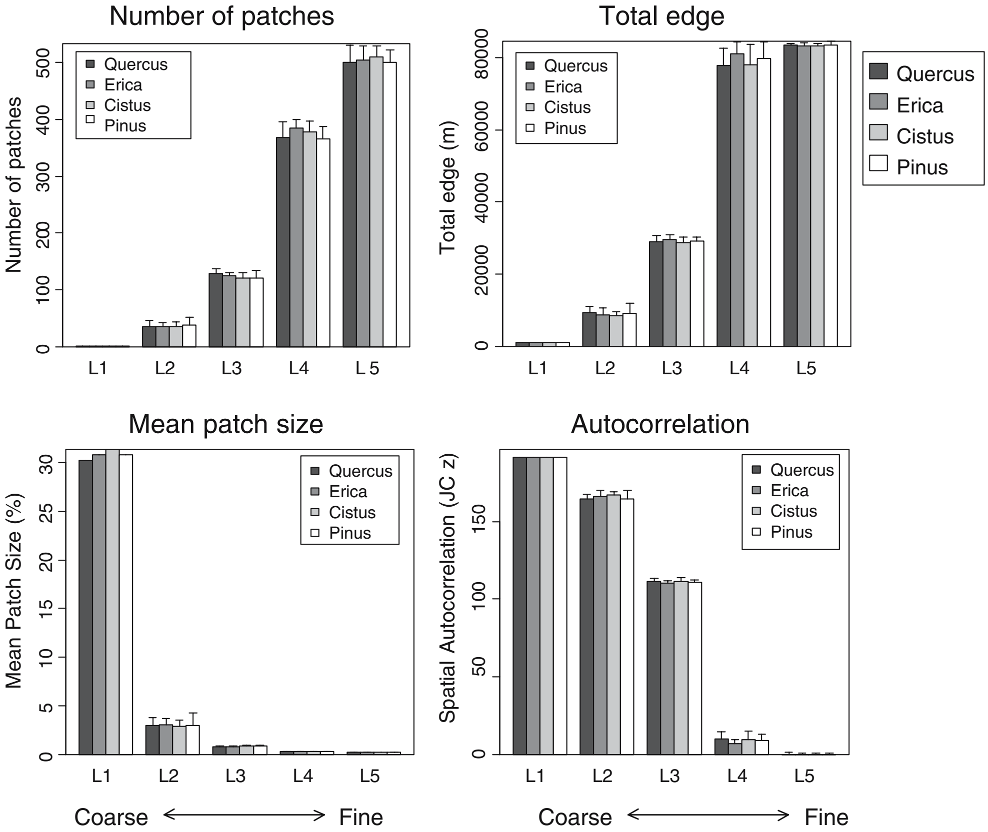


Fig. 2 Landscape statistics of the four species groups (Quercus, Erica, Cistus and Pinus) in the five initial landscape scenarios (L1 to L5): Number of patches, total amount of edge (in m), mean patch size (as proportion of the landscape, %), and spatial autocorrelation (join-counts statistic)

most fire × landscape scenarios except under the highest fire frequency. Cistus also decreases in low fire frequency, remains about the same at intermediate fire frequency, and increases under high fire frequency. Both the increase and the decrease (i.e., the changes) are stronger in fine-grained landscapes (Fig. 5). Variability between simulation runs (mean coefficient of variation) is low for resprouting species (mean CV = 4 and 19% in Quercus and Erica), but relatively important in non-resprouters (mean CV = 45 and 36% for Pinus and Cistus). Inspection of single runs (Pausas and Ramos 2004) suggests similar trends to those produced by averaging runs (Figs. 4, 5).

Landscape structure also changes from the initial pattern. For instance, the amount of edge shows a clear change with both fire frequency and spatial pattern (Fig. 6). For the low fire frequency, the edge decreases or shows low variation from the coarse to the fine-grained landscape pattern, while for high fire frequency there is a clear increase in edge. In these situations of no-fire or low fire frequency, edge length increases from the initial conditions in coarse-grained patterns and decreases for fine-grained ones. However, this tendency to decrease in fine-grained patterns is very sensitive to fire regime; a high fire frequency reduces the decrease from initial conditions (low change from initial conditions). Variability between simulation runs is also lower for resprouting (mean CV = 21 and 18% in Quercus and Erica) than for non-resprouting species (mean CV = 37 and 30% for Pinus and Cistus). Inspection of single runs suggests that the general trend shown above (Fig. 6) does not change (Pausas and Ramos 2004). The remaining landscape metrics (number of patches, edge length and spatial autocorrelation) also change from the initial to the final landscapes; the change depends on the initial landscape configuration and the fire regime (not shown).

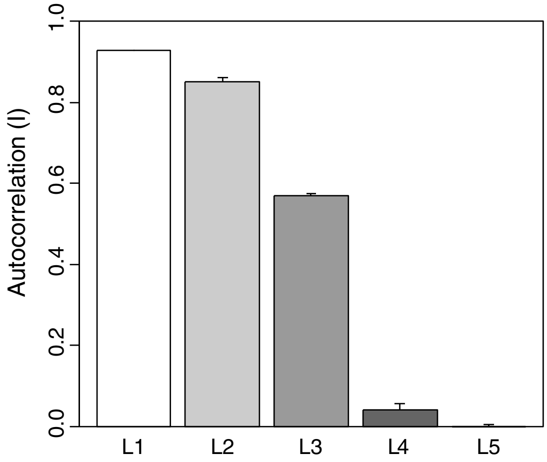


Fig. 3 Spatial autocorrelation (Moran index) of species richness in the five initial landscape scenarios (L1 to L5)

Discussion

The landscape generator parameters (Table 1) produced the desired gradient from coarse to fine-grained landscapes (Fig. 1), which is associated with a gradient of landscape attributes such as number of patches, amount of edge, mean patch size or spatial autocorrelation (Fig. 2). Consequently, the species richness also showed a clear spatial structure gradient (Fig. 3). If we define fragmentation as the degree the cells of the same species are separated in the landscape, low fragmented species are associated to low number of patches, low patch edge length, high mean patch size and high autocorrelation. The opposite attributes would define the high fragmented landscapes.

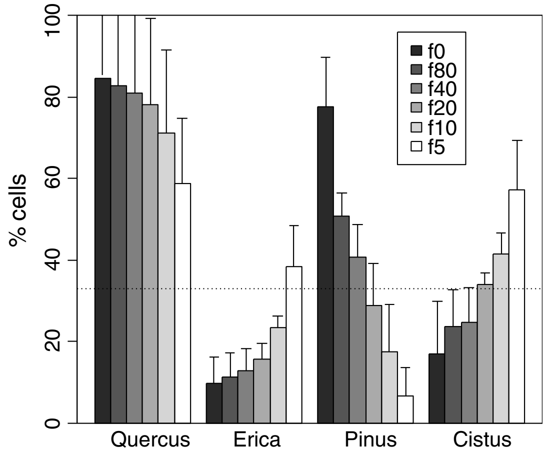


Fig. 4 Changes in species abundance (expressed as % of the landscape occupied by each species) due to different fire frequencies. Horizontal dotted line indicates the initial abundance of each species. Values are means and standard deviations of the five landscape scenarios

After 100 yr simulations, changes in species abundance are observed. These changes refer to the proportion of the landscape covered by the species (i.e., occupied cells), and not to the number of individuals. The area occupied by the two trees, Quercus and Pinus, decreased with increasing fire frequency (Fig. 4); Quercus decreased very little while Pinus showed a strong decrease and could even be eliminated under high fire frequency (low mean and high standard deviation, Fig. 4). Cistus and Erica showed a tendency to increase with fire frequency, suggesting a change in structure from forest to shrublands when fire frequency increases. These general trends are consistent with previous studies reported for the Mediterranean ecosystem using both field and simulation approaches (Pausas 1999b; Mouillot et al. 2001; Lloret et al. 2003; Rodrigo et al. 2004). However, the results provide a new dimension, i.e., the spatial dimension, and suggest that the changes in the different fire regimes also depend on the spatial structure of the different species types (lines are not parallel in Fig. 5). In general, coarse-grained patterns produce fewer changes from the initial conditions (slow dynamics) while the changes are much more important and more fire-sensitive in fine-grained patterns (Fig. 5). The importance of spatial arrangement in plant dynamics was already detected for undisturbed grasslands (Silvertown et al. 1992), but the interaction with disturbance has seldom been studied. The effect of spatial pattern is shown in the four species groups considered, but the most clear examples are for the non-resprouting (fire-sensitive) species (Pinus and Cistus). For instance, at high fire frequency (f5), Pinus disappears in fine-grained (low autocorrelated) landscapes, but aggregated coarse-grained landscape patterns permit its persistence at high fire frequency, that is, aggregation provides refuge for poor competitors (Shimda and Ellner 1984) and thus permits coexistence (Lavorel and Chesson 1995). Similar results have been observed in field experiments (Stoll and Prati 2001). A similar persistence pattern is observed with Cistus (poor competitor non-resprouter), but this species also shows an optimum at high fire frequency with intermediate to fire-grained patterns (L3 to L5), probably as a

Fig. 5 Abundance of each of the four species types (Quercus, Erica, Cistus and Pinus) after 100 years of simulation in the five landscape scenarios (L1 to L5) and under the six fire scenarios (f0 to f5). The initial abundance of all species in all landscape scenarios was 30% (dotted lines). Lines represent mean values of 10 simulations. Mean coefficients of variation between runs were 4, 19, 45 and 36% for Quercus, Erica, Pinus and Cistus, respectively

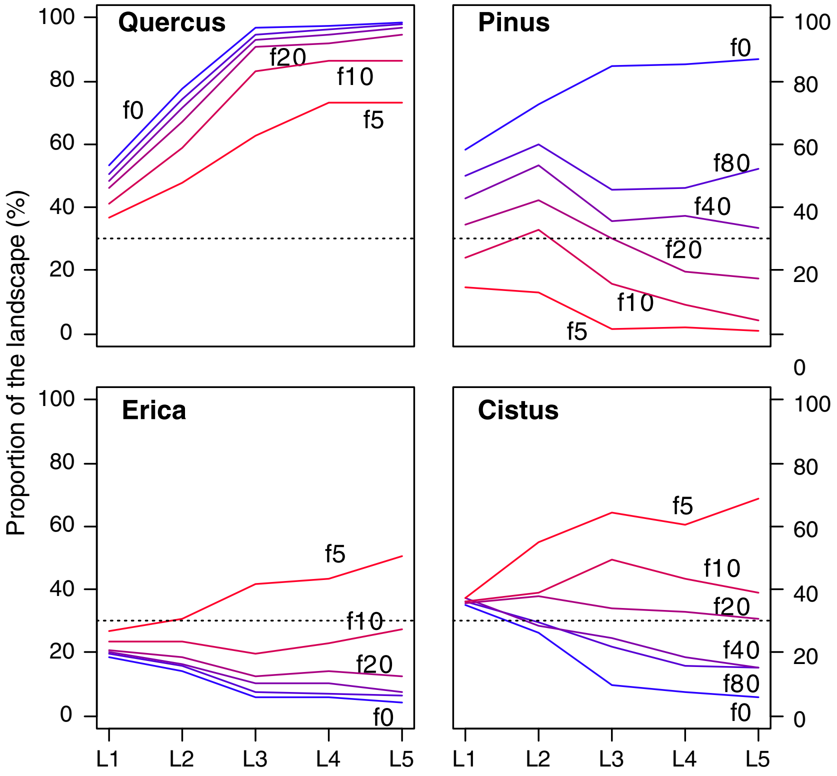
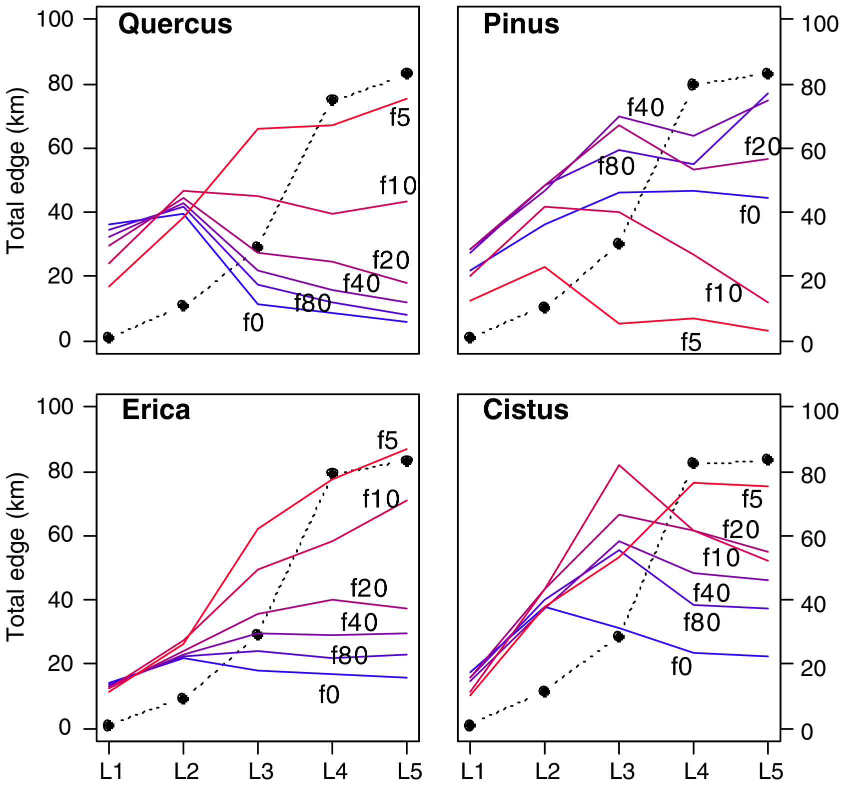


Fig. 6 Changes in edge length (in km) in each of the four species types (Quercus, Erica, Cistus and Pinus) after 100 years of simulation in the five landscape scenarios (L1 to L5) and under the six fire scenarios (f0 to f5). Lines represent mean values of 10 simulations. Mean coefficients of variation between runs were 21, 18, 37 and 30% for Quercus, Erica, Pinus and Cistus, respectively



consequence of the fire-cue germination (Table 1; e.g., Roy and Sonié 1992; Ferrandis et al. 1999). The finding of higher extinction rates in random landscapes compared with aggregated landscapes was already proposed using simpler cellular automaton models (Silvertown et al. 1992; Pausas 2003).

Landscape attributes for each species also change as a consequence of both the fire regime and the landscape pattern (Fig. 6). Without fire, there is a tendency for convergence towards intermediate or low edge length in both coarse and fine-grained patterns. However, high fire frequency maintains the high edge length in fine-grained patterns but does not produce important spatial changes in coarse-grained patterns. There is a clear trend towards increasing variability (produced by the different fire regimes) in spatial pattern from coarse-grained to fine-grained landscapes, for the four species types (Fig. 6).

The simulation results emphasise the importance of the landscape–fire interactions and allow us to generate some hypotheses (sensus Carley 1999) on the effect of landscape patterns on landscape processes. (A) Coarse-grained spatial patterns generate slower dynamics than fine-grained patterns. If dynamics is driven by the interaction between species, then aggregate coarse patterns with low edge (low interaction with other species) may produce slower dynamics. (B) Fine-grained landscapes are more sensitive to changes in fire regime than coarse-grained landscapes. (C) Fire-sensitive (non-resprouting) species may be maintained under high fire recurrence in coarse-grained landscapes (i.e., fragmentation may accelerates extinction in fire-sensitive species). This may be interpreted as a consequence of A, that is, fire-sensitive species (non-resprouting) may be poor competitors with fire-persistent species (resprouters with well stablished root system that allows quick recolonisation and that outcompetes the seedlings from non-resprouters). There are some experimental evidences on changes in plant dynamics due to spatial aggregation although at smaller temporal and spatial scales (e.g., Stoll and Prati 2001).

These results have implications for the conservation and restoration of Mediterranean landscapes. The amount of habitat is important for ecological restoration but the spatial arrangement may also be important. For instance, highly fragmented fine-grained pine-type forests are more vulnerable (to be eliminated by fire) than unfragmented forests, and this is where restoration efforts should be reinforced. Consequently, new pine plantations will do better when planted in an aggregated design. Forests dominated by Quercus-type species are highly resilient to fire (Malanson and Trabaud 1988; Pausas 1997), but fine-grained landscapes are even more resilient and regenerate faster, thus restoration with this species should follow disaggregated designs. In the eastern Iberian Peninsula, traditional forest restoration techniques were based on planting Pinus species; current techniques are pointing towards increasing late-successional high resilience plant communities, such as those dominated by Quercus-type species (Pausas et al. 2004b). Our results suggest some differences for the conservation and restoration of the two types of trees at landscape level (different spatially explicit solutions). For a cost-effective planning, these differences together with other physiological differences between the two types of species (Vilagrosa et al. 2003; Pausas et al. 2004b) should be considered. The importance of the different spatial arrangement of plants and amount of edge between plant species may also have implications for the conservation and restoration of fauna and thus for the corresponding ecosystem functions and processes (Hobbs 2002).

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