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The effect of landscape pattern on Mediterranean vegetation dynamics: A modelling approach using functional types

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Abstract. In the framework of land use changes in the Mediterranean area, I asked to what extent different landscape structures might determine long-term dynamics in Mediterranean ecosystems. To answer this question, a spatially explicit model was developed (the MELCA model), incorporating two functional types of woody species dominant in Mediterranean ecosystems: a resprouter (R) and a non-resprouter fire-recruiter (seeders, S). The model was used as a tool for generating hypotheses on the possible consequences of different landscape scenarios. Thus, five different hierarchically structured random landscapes were generated, all having the same cover for the two functional types but different landscape structure (ranging from highly heterogeneous to homogeneous landscapes). After a 100-yr simulation, plant cover and spatial pattern had changed and the changes were different for the different initial spatial configurations, suggesting that long-term vegetation dynamics is spatially dependent (the resultant dynamics are sensitive to the initial spatial structure). In the landscapes where R-type species had a low number of large patches and S-species had a large number of small patches, the number of R-patches increased and their size decreased, while the number of S-patches decreased. In these cases, the final cover of the two types changed little from the initial cover. Landscapes with a large number of small R-patches interspersed with S-patches had a decrease in the number of R-patches, an increase in the number of S-patches and a decrease in the size of S-patches. In these landscapes, final cover was significantly changed, increasing in R-type and decreasing in S-type species. These results suggest that low spatial autocorrelation (low aggregation) favours R-type species. Implications for land management are also discussed.

Keywords: Autocorrelation; Cellular automata; Resprouter; Seeder; Spatial dynamics; Spatial model.

Introduction

Current land use changes in the northern Mediterranean basin are having a large impact on the landscapes, changing their spatial structure and heterogeneity. There is a clear change from highly heterogeneous landscapes (maintained by different land uses) to more homogeneous landscapes after land abandonment (Baudry & Bunce 1991). This change is due to a reduction of human pressures on the landscape, i.e. depopulation processes in rural areas, decrease in grazing pressure and reductions in the use of the forest (Anon. 1989; Paniagua 1992; Pausas in press). Currently in the Mediterranean area there is a variety of landscape structures with different degrees of spatial heterogeneity but with similar plant composition. In the present paper I ask to what extent these different landscape structures might determine the long-term dynamics.

The effect of spatial heterogeneity on ecological processes at broad spatial scales has generated increasing interest in ecological research in recent decades (e.g. Turner 1989; Turner et al. 1989; Wiens et al. 1993; Dunning et al. 1995; Kareiva & Wennergren 1995; Lavorel & Chesson 1995; Hanski 1999; Gardner 1998; Vos et al. 2001). Several experiments (van Andel & Dueck 1982; Thórhallsdóttir 1990) indicate that the spatial arrangement of competing species can affect their performance. However, the consequences of this at community level have not been fully addressed (de Blois et al. 2002), and a general theory to predict the effects of spatial heterogeneity on vegetation dynamics has not yet emerged.

This paper presents a study of the effects of spatial heterogeneity on vegetation dynamics in Mediterranean fire prone ecosystems. I used a simulation model to test the possible long-term consequences of both landscape pattern and disturbance processes. The model was used as a tool for generating hypotheses on the possible consequences of different landscape scenarios in a fire prone system, and for suggesting management options. The modelling framework employed includes several components: (1) a landscape generator; (2) a disturbance generator (fire); (3) a spatially explicit dynamic model and (4) a set of quantitative landscape indices.

Landscape generator

This was used for creating non-random landscapes where the spatial arrangement of the vegetation types could be varied independently of the amount of each vegetation type. I applied the percolation theory, as used by Lavorel et al. (1993, 1994), to generate different hierarchically structured landscapes with the same proportion of cover for each type, but with different spatial structures (i.e. different landscape scenarios). This method allowed generation of landscapes with different degrees of patchiness.

Disturbance generator (fire)

Mediterranean landscapes cannot be understood without considering fire. Fire is a disturbance process that propagates *within* the same cover type as well as *between* different cover types (Turner et al. 1989). The rate of fire spread depends on the fuel characteristics of the cover types. Fire may also play an important role in changing landscape heterogeneity and connectivity (Miller & Urban 2000). In the present work, I used two different cover types with contrasting fuel characteristics. Consequently, the disturbance rate depends on the connectivity of these cover types (i.e. on the vegetation spatial pattern). For simulating fire spread, instead of a fine-scale thermodynamic approach (e.g. Rothermel-based fire behaviour models, Rothermel 1972), I used a probability approach because it is often suggested as a simple and appropriate way to simulate fire effects at broad spatial scales (Gardner et al. 1999; Hargrove et al. 2000).

Spatially explicit vegetation model

This model is based on the traits of two contrasting fire based plant functional types, i.e. functional types based on different regeneration strategies after fire (and their associated traits; Keeley 1998; Pausas 1999a, 2001): a resprouter and a fire recruiter (seeder). The functional type approach is considered an appropriate and effective way to simulate vegetation dynamics in disturbed ecosystems (Noble & Slatyer 1980; Moore & Noble 1990; Noble & Gitay 1996; Pausas 1999b). Models for Mediterranean fire-prone ecosystems are just starting to be developed. Rego et al. (1993) developed a non-spatial transition matrix model for garrigue ecosystems. Their model assumed constant transition probabilities. Pausas (1999b) developed a non-spatial gap type (individual based) model for Mediterranean ecosystems (BROLLA); the main difference between this and other gap models was that resprouting and fire stimulation of germination were considered. Recently, two models with more emphasis on plant physiology (and less on population dynamics) have been developed for Mediterranean ecosystems. The Osborne et al. (2000) model is very detailed in the physiology and phenology of the species, but does not consider disturbance. Mouillot et al. (2001) developed another model that considers both plant physiology and disturbance. The model used in this paper (MELCA) does not consider physiological processes but has a strong emphasis on landscape pattern and fire interactions. This model requires very few parameters and was not built to be very precise, but rather to be useful for developing alternative hypotheses.

Quantitative landscape indices

Finally, a set of quantitative indices (O'Neill et al. 1988; Gustafson 1998) were needed to compare landscapes. These indices consider both the abundance of plants (e.g. cover) and their spatial distribution (e.g. number and size of the patches, autocorrelation).

The approach used in the present work aims to study to what extent vegetation dynamics is spatially dependent, and to develop a hypothesis on the effect of spatial patterns on the long-term dynamics of Mediterranean landscapes. Spatial pattern here means the distribution and arrangement of plant patches in the landscape. Implications for land managers are also discussed.

Methods

Model description

To explore the relationships between landscape pattern and vegetation dynamics I have built a model called MELCA (available upon request), which is a (grid-cell) raster based stochastic model, designed to simulate the spatio-temporal dynamics in fire prone ecosystems.

In MELCA, each cell has five possible states: Empty, Seedbank (cells with seeds of different species), Immature, Mature and Burnt (just after fire). Each cell may contain one established plant (or group of plants that behave in the same way and are of the same functional type and cohort) or one or more seeds in the seedbank (of the same or different species). That is, seeds of several species may be in a cell (seedbank), but only one species survives within one cell. In this case, survival depends on the competitive hierarchy, which is based on the species shade tolerance.

For each functional type, a set of specific parameters (life traits) are needed (see below; Tables 1 and 2) for simulating the different dynamic processes (germination, growth, resprouting, mortality, dispersal). Parameters are chosen to be simple, often qualitative, to be able to simulate poorly known ecosystems.

MELCA enables different spatial configurations to be created by using a landscape generator. With this module a variety of artificial landscapes can be generated; such as random, single and multiple-scale checkerboard patterns and hierarchical multi-scale patterns (curdled); (Meisel & Turner 1998; Lavorel et al. 1993, 1994). All MELCA processes assume the 8-cell Moore neighbourhood (Hogeweg 1988). Thus, for spreading algorithms and spatial pattern indices, diagonal cells are considered

to be connected.
Mortality. In Melca, there are three mortality causes: age dependent mortality (Table 1, Eq. 1), fire mortality (non-resprouting species after fire) and resprouting failure (for weak resprouters after fire; Table 1, Eq. 5). Seeds in the seed bank may also die (e.g. due to loss of germination capacity) when approaching their maximum seed life span (age dependent seed mortality; see germination below).

Growth. After germination, plants are immature and the annual probability to mature is a function of the species maturity age (Table 1, Eq. 2). Species with rhizomes may also have lateral growth; in these cases I assume that plants that are at ca. 80% (default) of their maximum age will invade one of the adjacent (randomly chosen) empty cells.

Seed dispersal. To provide a flexible way to characterize dispersal by different dispersal strategies, this parameter is classified in three categories: short distance dispersal (dispersal to the eight neighbouring cells), medium distance dispersal (< 100 m; Table 1, Eq. 3) and long distance dispersal (> 100 m; anywhere in the landscape). Short dispersal may reflect the dispersal of large seeds not dispersed by vertebrates (barochory), while long dispersal may represent wind dispersal of very small seeds (anemochory) or endozoochory. Both long and short distance dispersal are computed as uniform random dispersal. Medium distance dispersal is computed using a decay function (Table 1) and may represent wind or animal dispersal. For all the simulations considered in this paper dispersal is equally likely to occur in all directions (i.e. factors such as wind are not considered). Seeds may fall in an empty cell or a cell with other seeds (independent of the species). Seeds landing in a cell with immature or mature plants or beyond the limits of the grid are lost (i.e. the boundary of the map is assumed to be absorbing and all processes stop at the boundary, Green 1989), increasing the probability of local extinction on very small landscapes.

Table 1. Probability functions (rules) to estimate different plant processes in the Melca model. Variables are: *Dist* = distance from the source plant to the cell (chosen randomly between the cell size and 100 m); *nBurnt*s = number of times that the cell has burnt; *SeedAge* = age of the seed. Variables with the subscript *s* refer to specific parameters of functional types (see Table 2): k_1, k_2, k_3, k_4, k_5 are constant shape parameters with default values set equal to 0.01, 0.01, 2, 2.3, 0.1, respectively.

Process	Equation	No.
Age dependent mortality	$P_{am} = 1 - \exp(\ln(k_1) / MaxAge_s)$	1
Maturation	$P_m = 1 - \exp(\ln(k_2) / MatureAge_s)$	2
Dispersal		3
short distance	$P_{sd} = SDC_s$	
medium distance	$P_{md} = MDC_s * \exp(-k_3 * Dist / 100)$	
long distance	$P_{ld} = LDC_s$	
Germination	$P_g = \exp(SeedAge * (-k_4 / SeedLong_s))$	4
Resprouting	$P_r = P_{ir} * \exp(-k_5 * nBurnts)$	5

Germination. For fire recruiter species ($FireEst_s$ = yes) after fire, all burnt cells which had mature fire recruiter plants germinate. In the case that a cell contains seeds of several fire recruiter species, one species is randomly chosen. For non fire recruiters ($FireEst_s$ = no), or in non-fire years, the probability of germination is a function of species-specific parameters (shade tolerance and seed longevity) and seed age (time in the seed bank, *SeedAge*; Table 1, Eq. 4). In these cases, if seeds of two species are in the same cell, germination is decided by considering the shade-tolerance hierarchy to mimic within-cell competition.

Resprouting. Functional types able to resprout can have a weak, medium, high or very high resprouting capacity. The initial probability of resprouting (P_{ir}) in weak, moderate, high and very high resprouters is set at 0.25, 0.50, 0.75 and 1.00 respectively. However, fire recurrence reduces these initial probabilities by mimicking resprouting depletion (Canadell & López-Soria 1998) (Table 1, Eq. 5).

Fire. Fire modelling is divided into two components, ignition and spread; ignition is also subdivided in time and space. Melca allows several options for each component, depending on the objective of the simulation. For the current work, fires start randomly in space and time, and only one fire is lit in each fire year. Fire only spreads if it ignites on cells containing fuel (i.e. burnability is a function of plant fuel). Burnable cells are those with mature or immature plants. Fire may propagate to the next cell by chance, and on the basis of the combustibility index of the plant, the probability of burning can be estimated (Hargrove et al. 2000). Fire spread is driven by the fuel in each cell, and fire is restricted to a contiguous cluster of burnable cells. Each species has a given combustibility index for a population of mature individuals ($Comb_s$), which ranges from 1 (very low) to 9 (very high). The model assumes that the combustibility index for mature plants is equal to the species combustibility, but is one unit lower for immature plants (lower biomass). Climatic conditions are not considered. The effect of the combustibility index is that lower values produce more unburned patches than higher values. This fire module is not intended to be realistic, but rather to facilitate creating differences in post-fire heterogeneity depending on the vegetation fuel type.

There is no explicit fire extinction (burn-out) procedure. Fire may be extinguished if fuel values are low, if fuel bed (vegetation) is discontinuous or when all the landscape is burnt. Patches of unburned vegetation are possible due to fuel bed heterogeneity and to the stochasticity of the process.

Plant functional types

Two sets of traits are used for defining two different fire functional types of woody plants (R and S; Table 2), i.e. functional types with contrasted fire response (Pausas 1999a, b, 2001). R represents long-lived evergreen resprouting species. S corresponds to species that are not able to resprout after fire but produce seed banks with seeds that not only survive fire but whose germination is stimulated by fire (often called fire recruiters, seeders or propagule persisters). Seeds of S are small, refractory and long-slasting in the soil, while seeds of R are fire sensitive, vertebrate dispersed and short-lived. Combustibility is higher in S than in R. These two functional types are common in vegetation of the Mediterranean basin (Trabaud 1987, 1991; Pausas 1999a; Pausas et al. 1999) and in California (Keeley 1991, 1998). Examples of R-type species growing in the Mediterranean basin are *Quercus* spp. (shrub and trees species), *Rhamnus* spp., *Phyllerea* spp. and *Pistacea* spp. S-type species include pines (e.g. *Pinus halepensis*), but also many shrub such as many *Cistus* spp. or *Ulex parviflorus*.

Simulation experiments

All simulations begin with a square artificial landscape containing 10 000 square cells (100 × 100 grid cell), each side of which is 10 m long. Five different landscape structures were selected by generating five hierarchically structured random landscapes, following Lavorel et al. (1993). In brief, three-level hierarchical landscapes were recursively generated by creating a matrix of ($m_1 \times m_1$) elements and randomly setting the elements to 1 with a probability of p_1. If the element was set to 1 then this element was subdivided into a ($m_2 \times m_2$) matrix and elements at this finer scale were randomly set to 1 with a probability of p_2. The process was repeated a third time by subdividing those elements equal to 1 into an ($m_3 \times m_3$) matrix and randomly labelling elements at this finest resolution with a probability of p_3 (see Lavorel et al. 1993 for more details). The elements set to 1 at the finest scale (cells) were assigned to be filled by R plants and the others by S plants. Different combinations of m_i and p_i values were chosen to provide five different landscape structures with different degrees of patchiness (L1 to L5, Table 3) but with the same number of cells (cover values) for each functional type (R, S) in all landscapes. The chosen patchiness (Table 3) may resemble the patchiness of land abandonment in eastern Spain because most (85%) agricultural patches are smaller than 5 ha (Anon. 1991). Because of the stochastic nature of the landscape generation process, five initial maps (replicates) were created with every combination of the landscape generator parameters (m_i, p_i) but with different seeds for the random generator.

Simulations of vegetation dynamics were performed starting from the initial landscapes (L1i – L5i) and simulating 100 years. Fire was simulated as a background disturbance for all landscapes with an annual probability of 0.025, which may be a reasonable fire regime for landscapes in the Mediterranean basin.

Spatial analysis

The spatial indices used, at class (functional type) level, were: number of patches, mean patch size (in number of cells), coefficient of variation for patch size (%) and mean shape index (≥ 1). At landscape level, the

Table 2. Plant traits used in the simulations for the two functional types (R and S).

Plant traits	Notation	Unit	Type R	Type S
Maximum age	$MaxAge_s$	yr	200	30
Mature age	$MatureAge_s$	yr	10	5
Seed longevity	$SeedLong_s$	yr	2	20
Dispersal capacity				
short-distance dispersal	SDC_s	0-3[1]	low	high
medium-distance dispersal	MDC_s	0-3	low	med
long-distance dispersal	LDC_s	0-3	none	low
Shade tolerance	$ShTol_s$	1-3	high	low
Resprouting capacity	$Resp_s$	0-3	high	no
Establishment stimulated	$FireEst_s$	y/n	no	yes
Rhizome	$Rhizome_s$	y/n	yes	no
Combustibility index (mature plants)	$Comb_s$	0-9	3	6

[1] Dispersal capacity corresponds to probability values of 0, 0.25, 0.50, 0.75 for none (0), low (1), medium (2) and high (3) in SDC_s and MDC_s, and 0, 0.03, 0.06, 0.10 for LDC_s (see Table 1).

Table 3. Input values for the landscape generator to set the initial distributions of the R species (hierarchical structure random landscapes). m_i values indicate the subdivisions of the landscape in the three hierarchical levels, and p_i values the probability of occupying a site within the cell at hierarchical level *i*.

	m_1	m_2	m_3	p_1	p_2	p_3
L1	2	2	25	1.0	0.50	0.90
L2	2	5	10	1.0	0.50	0.90
L3	10	5	2	1.0	0.50	0.90
L4	2	10	5	1.0	0.90	0.50
L5	10	10	1	1.0	1.00	0.45

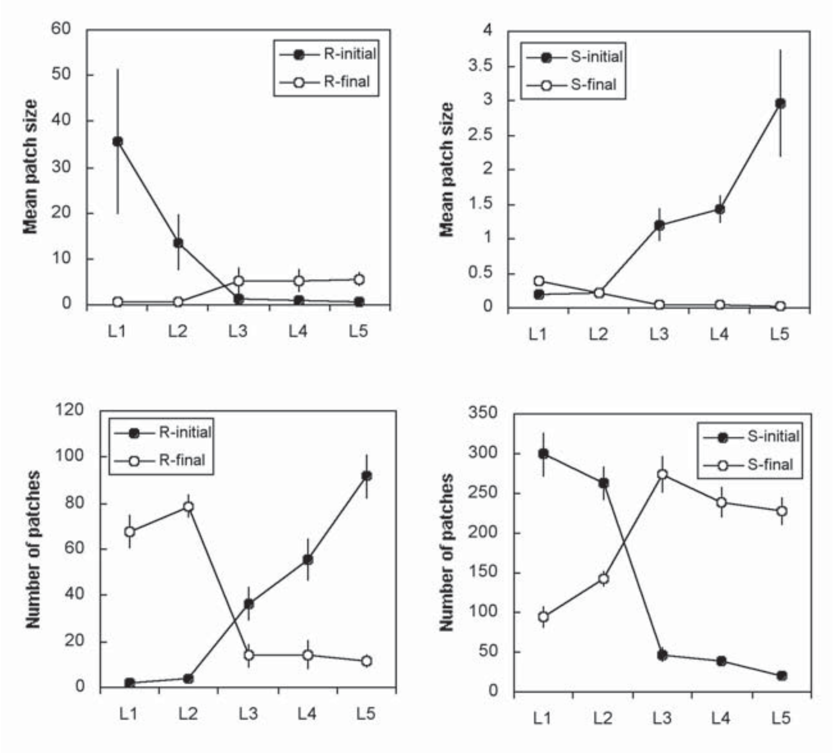

Fig. 1. Mean patch size (number of cells) and number of patches for R- and S-type species, in the initial (●) and final (○) conditions for the five landscape scenarios (L1 to L5).

spatial indices considered were: number of patches, size of the largest patch (%), edge length (number of cells), contagion (%, O'Neill et al. 1988; Li & Reynolds 1993), autocorrelation (Moran) index, and landscape shape index (≥ 1). Both contagion and autocorrelation refer to the tendency of patch types to be spatially aggregated (i.e. to occur in large, aggregated distributions), although the computation methods are very different and may not always be correlated (O'Neill et al. 1988). Spatial analysis of both initial (L1i – L5i) and final (L1f – L5f) landscapes was performed with the FragStats software, and detailed formulation is given in McGarigal & Marks (1994). Comparisons of mean spatial indices for the five replicated landscapes were performed by ANOVA.

Results

Analyses of the initial landscapes (L1i to L5i, Table 4, Fig. 1) showed that although the cover was similar in all of them, for R-type species the number of patches and the coefficient of variation for patch size increased from L1i to L5i while the mean patch size and shape index decreased. The opposite trend was observed for S-type species. The largest patch size did not change significantly from L1i to L5i for either of the two functional types (ca. 40-50%). These trends produced, at landscape level (Table 5, Fig. 2), a gradient from L1i to L5i of decreasing autocorrelation, increasing contagion index and increasing edge length between R and S. These trends indicate that the landscape structure ranges from a few large, continuous patches (L1i) to many small, interspersed patches (L5i). The input values of the landscape generator reproduced a gradient of different landscape structures that keep the cover values constant.

Table 4. Spatial indices for the two functional types (class indices) in the initial landscapes (L1i – L5i). Values are means of five replicates. ANOVA results are significant ($p < 0.001$) for all variables in the two functional types, except for Cover.

	L1i	L2i	L3i	L4i	L5i
Cover (%)					
R	46.1	44.7	45.2	45.4	45.2
S	53.9	55.3	54.8	54.6	54.8
N patches					
R	1.6	3.6	36.4	55.6	91.6
S	299.4	263.8	47.0	39.0	19.6
Mean Patch Size (cells)					
R	35.62	13.61	12.94	0.83	0.49
S	0.18	0.21	1.20	1.42	2.95
Patch Size CV (%)					
R	24.39	135.7	516.7	702.4	853.1
S	1360.3	1324.8	650.7	604.3	424.0
Mean Shape Index					
R	7.29	4.40	1.95	1.82	1.71
S	1.12	1.10	1.49	1.94	2.92

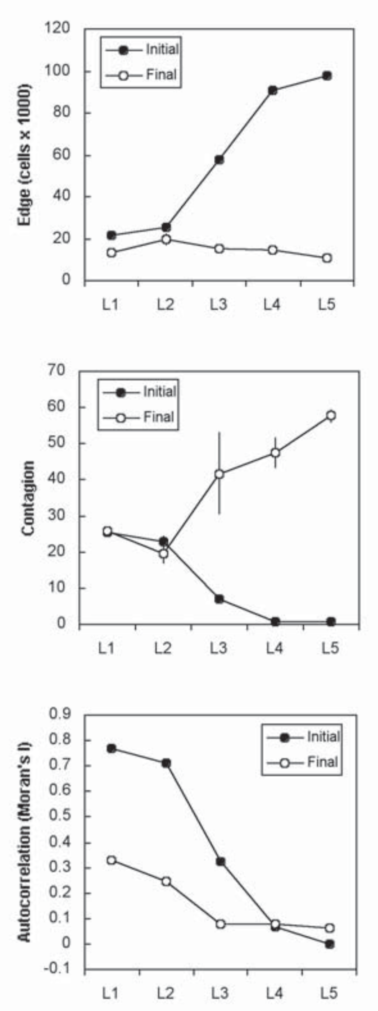

Fig. 2. Edge length, contagion index and spatial autocorrelation for the five landscape scenarios in the initial and final conditions. Values are means and s.d. (some very small) of the five replicates.

During the simulations all landscapes were burned several times, and the area burned in each landscape was similar, with the exception of L1 which had a lower cumulative proportion of burnt area (Table 6). After 100 yr simulations (Table 7, 8), plant cover and spatial patterns had both changed, the changes differ between the different initial landscape patterns. Although the initial cover of each functional type was the same for all landscapes, the final cover of R-type species was similar (for L1 and L2), and higher (for L3, L4 and L5) than the initial cover. The final cover of S-type species was lower than the initial cover in all landscape scenarios (Fig. 3). The final cover of R-type species was always greater than the cover of S-type species, this difference increased from L1 to L5 (Fig. 3).

In the landscapes where R-type species had a low number of large patches and S species had a large number of small patches (L1i, L2i), the number of R-patches increased and their size decreased, while the number of S-patches decreased (Fig. 1). In these conditions, edge length and contagion did not change, but autocorrelation decreased (Fig. 2). Landscapes with a large number of small R-patches and few large S-patches (L3i – L5i) showed a decrease in the number of R-patches, an increase in the number of S-patches and an decrease in the size of S-patches. For these conditions, the largest patch index increased for R and decreased for S (not shown); the edge length decreased and the contagion increased (Fig. 2).

Table 5. Spatial indices for the whole landscape (landscape indices) in the initial configurations. Values are means of five replicates. ANOVA are significant ($p < 0.001$) for all variables.

	L1i	L2i	L3i	L4i	L5i
N patches	301.0	267.4	83.4	94.6	111.2
Largest patch (%)	47.2	45.3	52.9	53.7	54.3
Edge (cells)	2148.8	2538.6	5776.4	9108.4	9807.2
Contagion (%)	25.57	22.92	6.94	0.82	0.66
Landscape shape index	6.37	7.35	15.44	23.77	25.52
Autocorrelation (Moran)	0.771	0.712	0.326	0.067	0.000

Table 6. Simple fire statistics of the simulations. Values are mean for each landscape structure (L1 to L5). Variables are the number of fires, the proportion of the landscape burned in each fire (%), and the cumulative proportion of area burned (%).

	No. fires	Burned %	Cumulative%
L1	2.0	18.6	37.1
L2	3.0	32.2	96.6
L3	3.4	22.7	77.1
L4	2.8	26.6	74.9
L5	4.1	22.5	103.4

Table 7. Spatial indices for the two functional types (class indices) for the final landscapes (L1f to L5f). Values are means of five replicates. ANOVA are significant (p<0.001) for all variables in the two functional types.

	L1f	L2f	L3f	L4f	L5f
Cover (%)					
R	42.28	46.25	60.90	61.37	62.09
S	35.63	29.95	9.64	8.30	6.16
N patches					
R	67.6	78.8	13.8	14.2	11.6
S	95.2	142	274.2	239	227.6
Mean Patch Size (cells)					
R	0.63	0.59	5.208	5.14	5.592
S	0.384	0.21	0.036	0.032	0.028
Patch Size CV (%)					
R	720.18	790.23	348.44	352.91	322.47
S	525.12	455.10	135.94	169.79	102.93
Mean Shape Index					
R	1.51	1.54	3.41	3.33	3.52
S	1.36	1.44	1.28	1.27	1.22

Table 8. Spatial indices for the whole landscape (landscape indices) in the final configurations. Values are means of five replicates. ANOVA results are significant ($p < 0.001$) for all variables.

	L1f	L2f	L3f	L4f	L5f
N patches	157.5	209.0	273.8	271.6	236.3
Largest patch (%)	45.7	53.8	80.3	86.5	90.6
Edge (cells)	13032.5	19534	15536	14798	11078.3
Contagion (%)	25.79	19.51	41.78	47.41	57.82
Landscape shape index	22.77	25.43	28.61	28.84	29.15
Autocorrelation (Moran)	0.328	0.246	0.079	0.08	0.061

Discussion

The initial spatial patterns generated by MELCA (L1i-L5i) created a gradient from strongly structured (high autocorrelation and contagion, i.e. coarse patchiness) landscapes (e.g. L1i) to homogeneous (low autocorrelation and contagion, fine patchiness) landscapes (e.g. L5i). Consequently, the R-S edge increased from L1i to L5i. The main threshold of change from aggregated to homogeneous landscapes was observed between L2i and L3i (Fig. 1 and 2). These two landscape scenarios were generated by the same probability values (p_i, Table 3) but different subdivision sizes (m_1, m_3); these coefficients determined the aggregation pattern (patchiness).

After 100 yr simulations, autocorrelation tended to decrease (Fig. 2) in all landscape scenarios except in those with already very low values (homogeneous landscapes) where autocorrelation either did not change (L4) or increased very slightly (L5). However, the change in structure, from higher autocorrelation to lower autocorrelation, was still apparent (L1f-L5f; Fig. 2). Moreover, the contagion index changed from decreasing (L1i-L5i) to increasing (L1f-L5f), suggesting that the increase in R cover (Fig. 3) increased dominance and consequently created large continuous patches (high contagion). The contagion index seems to be sensitive to cover (class abundance), and it is not directly correlated to autocorrelation (O'Neill et al. 1988).

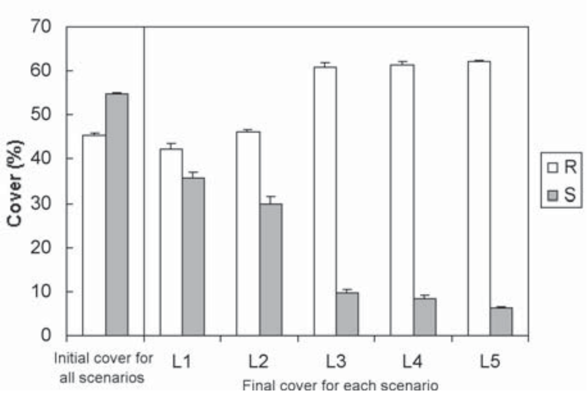

Fig. 3. Initial cover (%) for all landscape scenarios and final cover for each landscape scenario (L1 to L5).

This tendency towards decreasing aggregation and increasing homogenization with time (e.g. succession), as measured by the autocorrelation index (Fig. 2; bottom), is similar to what is currently occurring in many Mediterranean landscapes with the reduction in the use of agricultural land (e.g. land abandonment and reduction in grazing pressure; Pausas & Vallejo 1999; Pausas in press). Highly structured (aggregated) landscapes (e.g. L1, L2) are mainly the result of (and are maintained by) different land uses; reducing human pressure increases landscape homogeneity.

After the simulations, the differences in plant cover between R and S plants of the final landscapes in relation to the initial ones were larger as the autocorrelation decreased (from 7% in L1f to 56% in L5f; Fig. 3), suggesting that homogeneous landscapes with low spatial autocorrelation (e.g. L5i) favour R-type species (Fig. 3). This is probably due to the large edge length, i.e. to the large interaction between the two functional types. A large edge length implies that when a plant dies there is a high chance that the cell will be filled by seeds of both types, and the established plant will be the most competitive. R-type species are competitively superior to S-species because of their higher shade tolerance (late successional) and their strong resprouting capacity. Thus, despite the fact that S-type species have a much better dispersal system, in the long-term, large edge length favours R-type species. In highly structured landscapes, with a small R-S edge, there are fewer R-S interactions than in low structured (well interspersed) landscapes. In other words, the increase in late successional (R-type) species was faster when plants were not aggregated, i.e. aggregation provided refuge for poor competitors (i.e. spatial dependent co-existence). The fact that aggregation could reduce the rate at which stronger competitors are able to exclude weaker ones has been suggested in different analytical models (Shmida & Ellner 1984; Ives 1988).

The most aggregated landscapes (with the highest autocorrelation) (L1) had the least fires and the lowest cumulative proportion of area burned; the most homogeneous (least aggregated, lowest autocorrelation) landscapes (L5) had the most fires and cumulative area burned (Table 6). However, this tendency was unclear when analysing the intermediate degrees of aggregation (L2, L3, L4). This tendency is in agreement with the idea that changing vegetation patterns, via abiotic, biotic or anthropogenic processes (e.g. land use changes), have the potential to alter a fire regime, even if the drivers of that disturbance regime (e.g. climate, fire ignitions) remain constant (Peterson 2002). However, the degree to which a fire regime changes in response to landscape modifications or to interactions with changes in other drivers (e.g. climate change, plant invasions; e.g. D'Antonio & Vitousek 1992) needs further research using a more detailed vegetation model than the one used in the present work.

From the results, we can hypothesize that long-term vegetation dynamics in Mediterranean ecosystems are spatially dependent, i.e. the resultant dynamic process is sensitive to the initial spatial structure, and that low autocorrelation (fine patchiness) favours R-type species and high autocorrelation (coarse patchiness) permits the maintenance of S-type species. Although long-term field data are needed to validate this hypothesis, these results provide evidence of the relationship between patterns (e.g. patchiness) and population processes (Kareiva & Wennergren 1995; Turner et al. 2001) and are supported by different theoretical studies (e.g. Shmida & Ellner 1984; Ives 1988). The results also highlight the shortcomings of non-spatial models (e.g. Rupp et al. 2000), i.e. given a set of species and their abundance, a spatial model would predict different results depending on the initial spatial pattern of the plants, while a non-spatial model would produce one outcome only. For example, in the context of habitat destruction, the non-spatial model by Nee & May (1992) predicts that co-existence is dependent on the proportion of sites that are inhabitable, while spatial models predict that the spatial arrangement of the patches is an important factor influencing colonization, persistence and co-existence (Dytham 1995; Huxel & Hastings 1998). Some studies with non-spatial models have already showed the different results obtained when considering different values of spatial dependent parameters (e.g. dispersal in Pausas 1999b).

The model results also emphasize that differences in basic traits are very important and have long-term consequences. Midgley (1996) asked why the world's vegetation is not totally dominated by resprouting plants. He suggested that this is because resprouters are shorter and so are less competitive (and so overshadowed) in low disturbance forest ecosystems (Kruger et al. 1997). The analysis presented here for Mediterranean basin functional types suggests that the spatial pattern should also be considered, and that seeders may be maintained by spatial heterogeneity. That is, in heterogeneous landscapes where R-type species are clumped (high autocorrelation), S-type species are maintained because of their better dispersal system and high recruitment in open spaces, especially after fire. In homogeneous landscapes where R- and S-species types are well interspersed, the R-type tends to dominate.

Application to land management

In the Mediterranean basin, the recent increase in fire frequency and size (Pausas & Vallejo 1999) has led to a re-thinking of reforestation and restoration techniques (Vallejo et al. in press). In Spain, traditional forestry recommended reforesting large burnt areas with *Pinus* species (S-type species), because they grow much faster and regenerate (re-green) the landscape more quickly than the corresponding R-type tree species of the area (*Quercus*). Modern forestry is suggesting that despite the slow growth rate, R-type species should also be considered because of their high capacity to regenerate after recurrent fires (Trabaud 1991; Canadell et al. 1991; Pausas 1997). In this sense, a mix of both R- and S-type plants would benefit from both strategies, i.e. the fast growth of S-species and the high resilience of R species. In using this modelling approach, I have been able to hypothesize that landscape structure has an important role in vegetation dynamics. If the ultimate target is to achieve late successional high resilience plant communities, the simulation results presented here suggest that the most efficient way to reach that target is to plant a given amount of R- and S-type plants in a well interspersed design. Including R-type species in reforestation actions would increase the diversity and resilience of the system although the consequences of the different reforestation design in the long-term fire regime need further research.

The analysis provided here suggests the importance of incorporating landscape pattern not only for fauna conservation (e.g. Arnold 1995) but also for plant conservation and restoration programs.

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