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The dynamics of mediterranean shrubs species over 12 years following perturbations

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Abstract

The response of woody species to experimental burning, cutting and ploughing was studied for a period of twelve years in a shrub community in NW Spain. The treatments represent the perturbations most frequently imposed by man on these shrub communities throughout history. The response to burning is much faster than the response to cutting. The response to ploughing is slower due to the regeneration mechanism that species use: germination. In general, the dominant species, *Erica australis*, influences the regeneration patterns of the rest of the species, which make up the community. There is a significant increase in the cover of woody species until the fourth year, and of herbaceous species until the third year. Subsequently, *Erica australis* attains dominance, returning to its original spatial occupancy and cover values, removing the herbaceous species and negatively influencing the growth of woody ones like *Halimium umbellatum, Halimium alyssoides* and *Quercus pyrenaica*. Both *Erica australis* and *Chamaespartium tridentatum* regenerated by sprouting in the burnt and cut plots, and by germination in the ploughed plot. *Arctostaphylos uva-ursi* only recovers after burning and ploughing. *Halimium alyssoides, Halimium umbellatum, Erica umbellata* and *Calluna vulgaris* regenerate by germination in the three plots. Differences in cover values and spatial occupancy during the first years of succession tend to be eliminated twelve years after treatment and most of the species tend to recover their initial cover values. These shrubland communities have a high degree of resilience due to the strong sprouting potential of the component species.

Introduction

The Mediterranean ecosystems of Europe have been subject to a long history of human use (Grove 1996; Margaris et al. 1996). For hundreds, and even thousands, of years they have suffered from intense anthropogenic perturbations. Amongst the most important are forest fires (Trabaud 1980, 1991; Casal 1985, 1987; Luis et al. 1989a; Clement and Touffet 1990; Calvo 1993; Le Houerou 1993; Moreno and Oechel 1994; Calvo et al. 1998a; Naveh 1999) and cutting (Casal 1985; Cody 1986). These long-term perturbations have led to the extensive destruction of tree-dominated vegetation in large areas of the Mediterranean basin (Naveh and Dan 1973; Barbero et al. 1990), transforming it into shrubland. In the Province of Leon, in the NW of the Iberian Peninsula, these shrub communities cover 33% of the total area, according to the Ministerio de Agricultura (1984), of which heathland is the dominant shrub formation (Luis et al. 1989a).

These shrub communities have also been affected by human activity since ancient times, although they are currently considered marginal lands because of their low productivity. To improve productivity, they are frequently burnt to open up areas for grazing or for cultivation. They are also cut to provide material for different purposes, including domestic fuel and fertilisers (Casal 1985; Calvo et al. 1992). Finally, these shrub communities are also ploughed in order to grown cereal crops; this was a common practice in the Province of León during the 1960s.

The study area has been affected by all of these alterations, especially burning, due to the fact it was traditionally used as a grazing area for sheep. Shepherds frequently burnt the shrub during the spring in order to obtain pasture of a high nutritional quality, palatability and protein content. Shrub areas close to villages were commonly eliminated in order to create arable fields. Heath was also often cut for firewood. However, the very marked social changes which these areas have undergone, the ageing population and rural depopulation, the desertions of arable land and a decrease in the number of flocks have meant that traditional land-uses have declined or disappeared. Abandonment has caused secondary succession, identified as autosuccession in these formations (Calvo 1993; Calvo et al. 1998b).

After burning or cutting, most of the woody species that make up this type of community are capable of regenerating either by vegetative resprouting or from seed (Keeley and Zedler 1978; Gill 1981; Lloret and Vilá 1997). However, germination from the seed bank is the only possible after ploughing. This can limit those species with a low germination capacity (González Rabanal 1992; Valbuena et al. 2001).

The aim of this study is to analyse the development of plant cover and changes in spatial patterns of the woody species of this type of Mediterranean shrub after burning, cutting and ploughing. We analyse the possible effects of competition among woody species and determine the type of regeneration mechanism. We also try to answer the question: Would the vegetation in all these treatments eventually converge and be indistinguishable? If so, what is the time needed by these species to attain a similar state to the original conditions as regards both spatial occupancy and cover values?

Materials and methods

A study area was selected close to the highlands of the Province of Leon. This area is situated on level ground at UTM co-ordinates 30TUN2429, with an approximate altitude of 1050 m. The heathland community present in this area is classified as a variant of the *Genistelo tridentatae-Ericetum aragonensis-Cytisetosum laurifolii* community in which *Erica australis* L. subsp. *aragonensis* (Willk) P. Cout is the dominant species (Rívas Martínez et al. 1987). Apart from this species, other woody species were also widely represented: *Arctostaphylos uva-ursi* (L.) Sprengel, *Erica umbellata* L., *Calluna vulgaris* (L.), Hull; *Chamaespartium tridentatum* (L.) P. Gibbs, *Halimium alyssoides* (Lam) C. Koch, *Halimium umbellatum* (L.) Spach and shrubby *Quercus pyrenaica* Willd. *Quercus pyrenaica* is the characteristic species of climax communities in these areas. Plant nomenclature follows Tutin et al. (1964–1980).

Mean annual precipitation for this area is 839.8 mm; mean annual temperature is 10.9 °C; mean minimum in the coldest month is − 1.1 °C and mean maximum in the warmest month is 26.9 °C (Ministerio de Agricultura 1980). A period of summer drought occurs between July and August, and consequently the climate is classed as Mediterranean. The soil is classified as a humic cambisol (Junta de Castilla y León 1987). According to granulometric analysis, the soils of this area are very sandy and acidic (pH = 5.5) (Calvo et al. 1998a).

Three 10 m × 10 m plots were randomly selected within an area with homogeneous shrub cover. A 5-m corridor was left between plots. Before the treatments were applied, a vegetation inventory was carried out in 100 units of 1 m^2, covering the whole plot surface. The percentage covers of each woody species were estimated visually in each sampling unit, whereas the herbaceous species were considered as a whole because they represented a very low percentage of the total cover.

In the first plot, all the woody aboveground biomass was cut to ground level manually. All the cut biomass was dried and weighed to estimate the percentage of woody species in dry weight (Luis et al. 1989a). The second plot was burned. No aboveground biomass survived the burning. The third plot was mechanically ploughed (with a tractor; ploughing depth was 50 cm). All the vegetation stumps were removed by this treatment in order to prevent vegetative resprouting. The three treatments were carried out in July 1985. 100 samplings units of 1 m^2 in each plot were studied 1, 3, 4, 5, 9 and 12 years after the treatments. The cover values were estimated in the same way as before the treatment. From the fourth year, when the communities began to show visible differences in the height of the woody species, the height of the tallest plant of each species was recorded in each sampling unit. The area surrounding these experimental plots was burned by a wildfire two months after the treatments, but this did not burn the experimental plots.

In order to analyse temporal changes in each woody species in each plot, the cover values were grouped in six classes of abundance.

We compared the changes in the percentage cover of each species through time and in each plot using a two-way (plots and time, repeated measure) analysis of variance (ANOVA). To normalise errors percentage cover was arc sin transformed (Sokal and Rohlf 1979). The significance of the results was tested using the Scheffe test (Scheffe 1959).

In order to analyse changes in the spatial distribution patterns of each species connectivity analyses were carried out for each species over time (Baudry 1985). The 100 one square metre units in each plot and the possibility of finding the species connected to itself in the consecutive units in relation to the total possible connections (180) were considered. This analysis was carried out using qualitative values (presence/absence), which allows changes in the distribution of each species after being subjected to different perturbations to be interpreted. The connectivity analyses were carried out using the programmes IDRISI 2.0 and CHLOE 1.0 (Baudry et al. 1998) to define the connections between species.

$$C\{i\} = p(i,i)$$

P(i,i) = Number of connections of the species to itself divided by the total number of possible connections

Likewise, in order to define the structural changes in each plot an analysis of heterogeneity was carried out, based on the species richness of each sampling unit (Whittaker 1960).

$$\beta_w = \frac{S}{\alpha} - 1$$

Where: S = Total number of species in the plot and sampling periods α = Mean number of species in the 100 sampling units.

Results

Changes in plant cover and spatial patterns of the woody species

The dominant species in the León Province heathlands, *Erica australis*, has a very good regeneration response (Figure 1) as regards the three types of perturbation (burning, cutting and ploughing). In all three, the increase in cover values is pronounced until the fourth year, with marked significant differences between disturbance types. However, there are few subsequent changes, with no significant differences between disturbance mechanisms (Table 1). Spatial analysis shows that rapid regeneration by vegetative resprouting occurs after one year in the burnt and cut plots. There is also full occupancy from the fourth year, after which cover is significantly greater than the pre-perturbation levels. However, the response is slower in the ploughed plot. The connectivity values (Table 2) show that this species has greater spatial connectivity four years after any perturbation than in the original situation. As regards height, the increase is similar in all three plots. From the ninth year, the heights reached in the three plots are very close to the original values (100 cm) (Calvo et al. 1998a).

Erica umbellata (Figure 2) is negatively affected by the perturbations during the first years. This species recovers by germination. During the first year it appears only in the burnt plot. In the cut and ploughed plots germination is visible from the third year. In the three plots, both spatial occupancy (Table 2) and cover increase from the third-fourth year. However, original cover levels are only reached after twelve years in the case of ploughing. Once recovery begins 12 years post-treatment, connectivity has the same value as in the original situation. As regards height, the patterns of change are similar to those for cover: the highest plants appear in the cut plot and the smallest in the ploughed plot. There are significant differences between the treatments throughout the study period (Table 1).

Calluna vulgaris regenerates by germination, probably from the seed bank because the surrounding area was burned. This is the main regeneration mechanism and this does not start until the second year in any of the plots (Figure 3). In spite of this initial delay and low cover, spatial occupancy is extensive in the three plots and, from the fourth year is, very similar to that present originally. This is evident from the connectivity values (Table 2), which indicates that spatial occupation is important from the fourth year, reaching values similar to the original conditions 12 years after starting the study. The increase in cover values is more pronounced in the ploughed plot than in the burned and cut areas, with significant differences between plots (Table 1). The response in these last two plots is very similar, with no significant differences between them throughout the study period. The variations in maximum height follow the same patterns as the cover values, showing significant differences between the ploughed plot and the other two treatments.

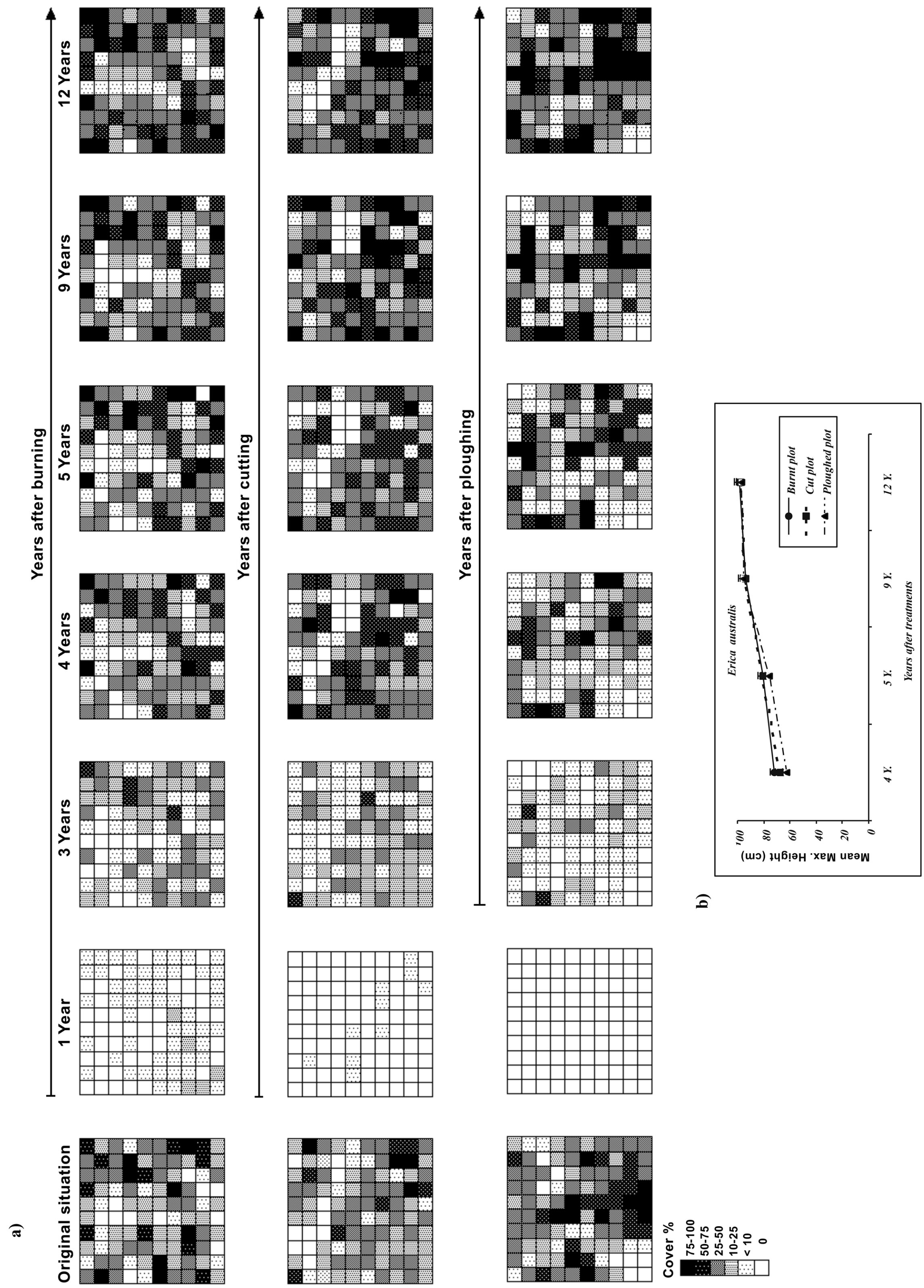

Figure 1. a) Spatial and temporal dynamics of *Erica australis* cover, originally and after the experimental treatments. b) Mean (and standard error) of maximum heights after burning, cutting and ploughing. 0 = original situation; 1,3,4,5,9,12 = years after treatments.

Table 1. ANOVA tables on two-way (treatment and time, repeated measure) analysis of variance among cover values (after arc-sin transformation) comparing different plots and sampling periods for each shrub species.

Erica australis				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	22.20	1.50	0.2251
Subjects w. groups	297	2199.35		
Repeated Measure (B)	6	300.21	681.79	0.0001
AB	12	151.02	17.16	0.0001
Bx subjects w. groups	1782	1306.95		
Erica umbellata				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	1342.52	209.30	0.0001
Subjects w. groups	297	952.54		
Repeated Measure (B)	6	2123.16	322.24	0.0001
AB	12	609.85	46.28	0.0001
Bx subjects w. groups	1782	1956.87		
Calluna vulgaris				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	164.08	26.26	0.0001
Subjects w. groups	297	927.83		
Repeated Measure (B)	6	2835.21	698.38	0.0001
AB	12	82.61	10.18	0.0001
Bx subjects w. groups	1782	1205.72		
Arctostaphylos uva-ursi				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	1644.69	92.71	0.0001
Subjects w. groups	297	2634.53		
Repeated Measure (B)	6	939.71	125.81	0.0001
AB	12	253.68	16.98	0.0001
Bx subjects w. groups	1782	2218.44		
Halimium alyssoides				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	193.41	27.74	0.0001
Subjects w. groups	297	1035.54		
Repeated Measure (B)	6	2098.13	498.19	0.0001
AB	12	109.70	13.02	0.0001
Bx subjects w. groups	1782	1250.82		
Halimium umbellatum				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	27.60	8.20	0.0003
Subjects w. groups	297	499.66		
Repeated Measure (B)	6	300.95	117.47	0.0001
AB	12	49.04	9.57	0.0001
Bx subjects w. groups	1782	760.90		
Chamaespartium tridentatum				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	31.40	3.59	0.0289
Subjects w. groups	297	1299.90		
Repeated Measure (B)	6	231.70	67.13	0.0001
AB	12	9.84	1.43	0.1470
Bx subjects w. groups	1782	1025.07		
Quercus pyrenaica				
Source	df	Sum of Squares	F-test	P values
Plots (A)	2	197.06	32.10	0.0001
Subjects w. groups	297	911.71		
Repeated Measure (B)	5	16.93	7.24	0.0001
AB	10	20.42	4.37	0.0001
Bx subjects w. groups	1485	694.52		

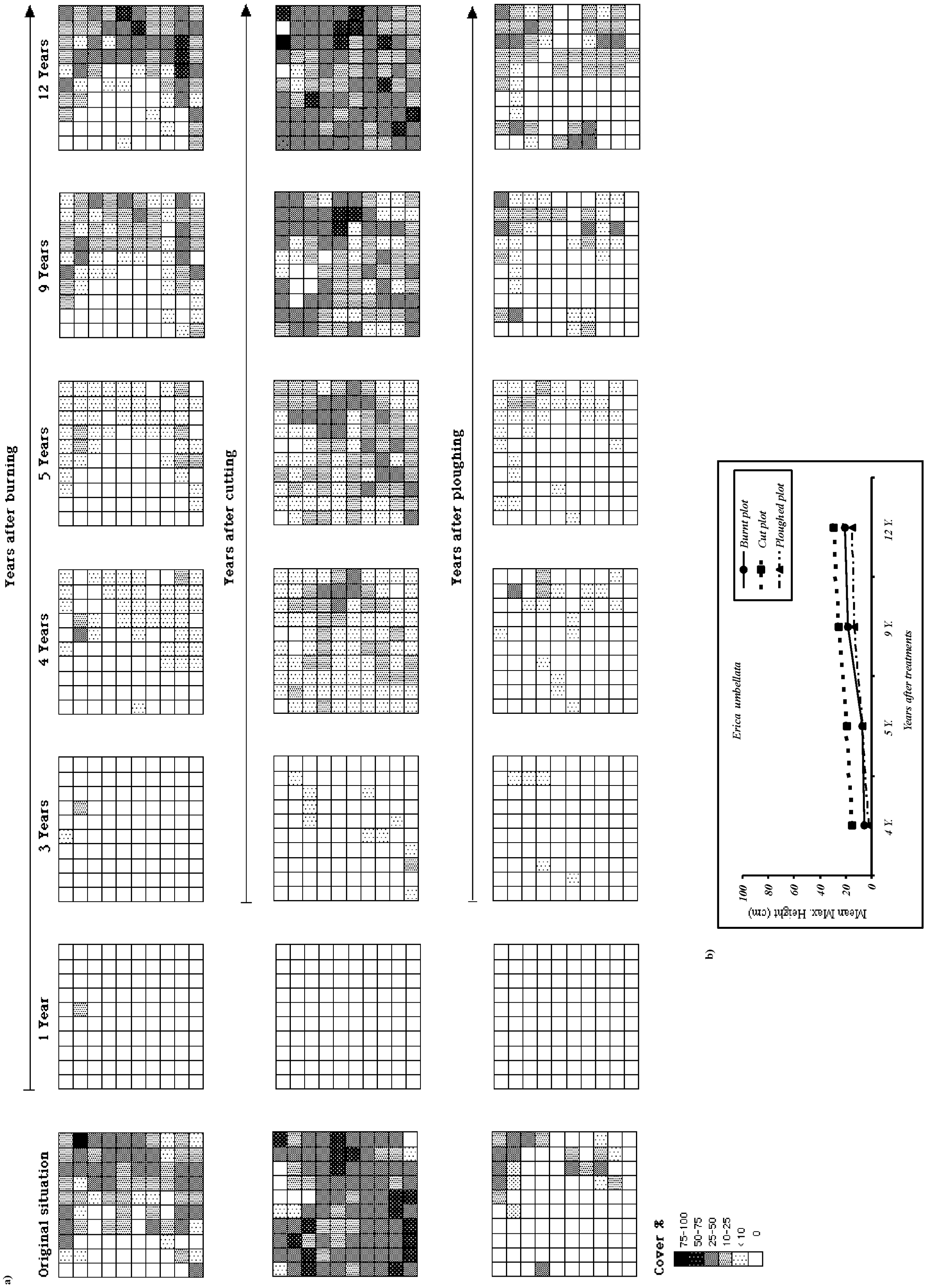

Figure 2. a) Spatial and temporal dynamic of *Erica umbellata* cover originally and after the experimental treatments. b) Mean (and standard error) of maximum heights after treatments. 0 = original situation; 1,3,4,5,9,12 = years after treatments.

Table 2. Connectivity value changes in each woody species in the original situation. 1, 3, 4, 5, 9, 12 = years after treatments.

	Erica australis	*Erica umbellata*	*Calluna vulgaris*	*Arctostaphylos uva-ursi*	*Halimium alyssoides*
Burning plot					
Original situation	0.80	0.56	0.76	0.61	0.36
1 year	0.37	0.00	0.00	0.48	0.06
3 years	0.76	0.00	0.06	0.46	0.74
4 years	0.87	0.05	0.38	0.50	0.82
5 years	0.82	0.17	0.50	0.53	0.76
9 years	0.86	0.54	0.63	0.49	0.71
12 years	0.94	0.56	0.89	0.53	0.77
Cutting plot					
Original situation	0.82	0.97	0.83	0.32	0.57
1 year	0.00	0.00	0.00	0.00	0.00
3 years	0.90	0.02	0.16	0.00	0.95
4 years	0.77	0.00	0.64	0.00	0.96
5 years	0.82	0.00	0.73	0.00	0.97
9 years	0.91	0.89	0.62	0.00	0.93
12 years	0.89	0.97	0.79	0.00	0.93
Ploughing plot					
Original situation	0.87	0.36	0.87	0.76	0.37
1 year	0.00	0.00	0.00	0.00	0.00
3 years	0.68	0.01	0.16	0.09	0.89
4 years	0.94	0.00	0.81	0.11	0.96
5 years	0.97	0.00	0.86	0.11	1.00
9 years	0.97	0.24	0.75	0.11	0.96
12 years	0.97	0.36	0.83	0.10	0.93

Another Ericaceae of great importance in the original state is *Arctostaphylos uva-ursi* (Figure 4). The high water content of this species allows it to resist burning easily (Luis et al. 1989b). This aspect, together with the ability to sprout from subterranean organs, allows recovering very quickly. Thus, after burning, spatial occupancy (Table 2) during the first year is close to that in the original state. By the 12th year, values are identical to the original state. In the cut plot this species does not reappear during the study period (Figure 4, Table 2). However, in the ploughed plot, recovery begins from the third year, although with a very small increase over time. The connectivity values are relatively low throughout the study period (Table 2).

Among the Cistaceae, *Halimium alyssoides* was the most important in the original state, and its recovery is favoured during the first few years of succession after the alterations (Figure 5). This species uses germination as a regeneration mechanism. It starts during the first year after burning and cutting and from the second year after ploughing. Cover values increase significantly during the first four years. Subsequently, coinciding with the quantitative increase and the wide spatial occupancy of *Erica australis*, growth is no longer significant. Spatial analysis shows that, despite more rapid germination in the burnt and cut plots, in all three cases, spatial occupancy is practically complete in the third year. This is also evident in the connectivity values (Table 2). From the fourth year, there are no important variations in connectivity. The increase in cover from that year is significantly greater in the ploughed plot than in the burnt and cut areas. This is because spatial occupancy of *Erica australis* is delayed after ploughing and possible competition effects thus appear later. A comparison of the cover values attained by *H. alyssoides* after the perturbations with those in the original state indicates that cover and space occupancy are significantly favoured by disturbance (Table 1). The maximum heights reached show significant differences between the three treatments, with the tallest plants appearing after ploughing and the shortest after burning. There is no significant increase through time following each treatment.

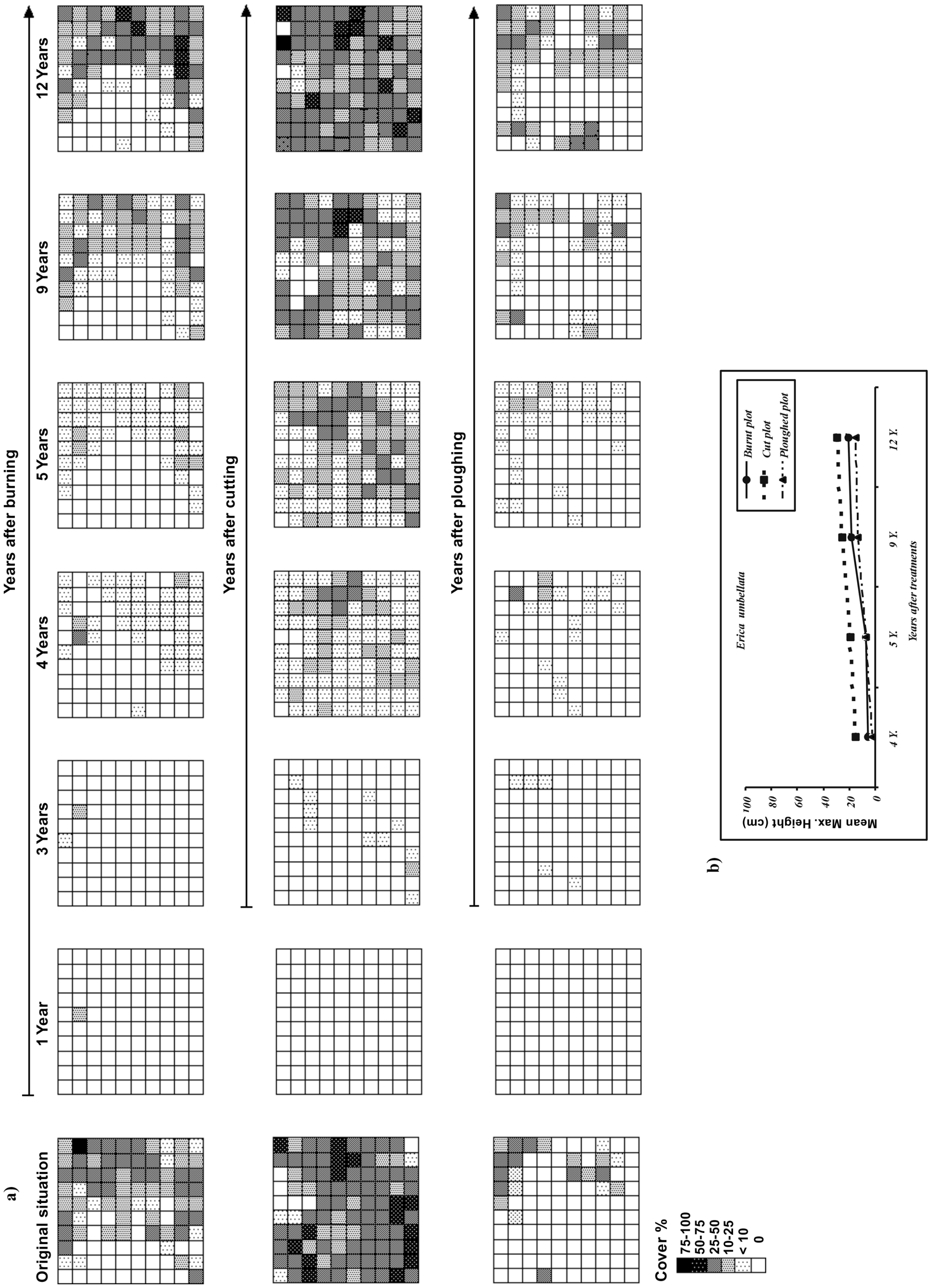

Figure 3. a) Spatial and temporal dynamic of *Calluna vulgaris* cover originally and after the experimental treatments. b) Mean (and standard error) of maximum heights after treatments. 0 = original situation; 1, 3, 4, 5, 9, 12 = years after treatments.

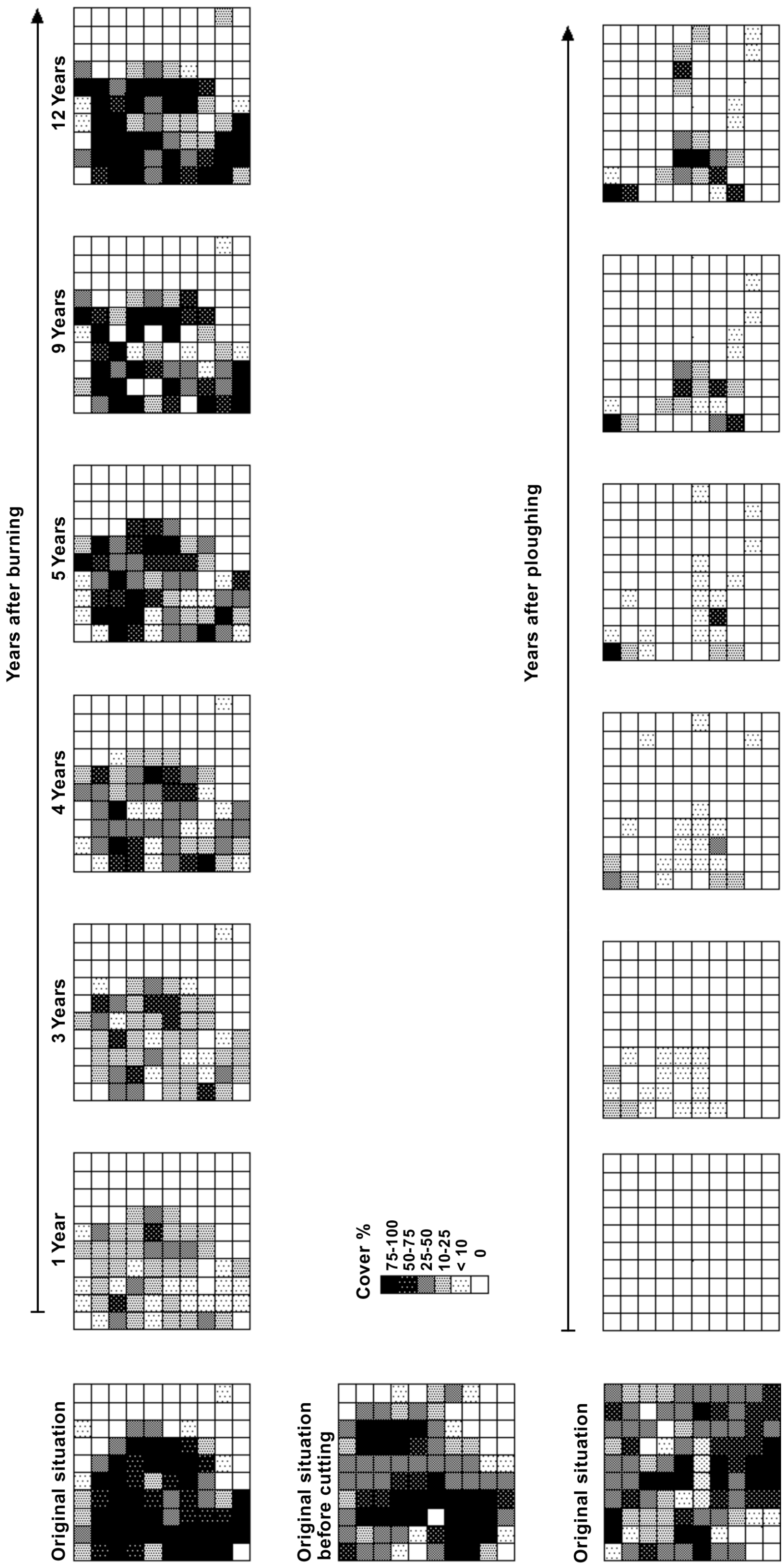

Figure 4. Spatial and temporal dynamic of *Arctostaphylos uva-ursi* cover originally and after the experimental treatments.

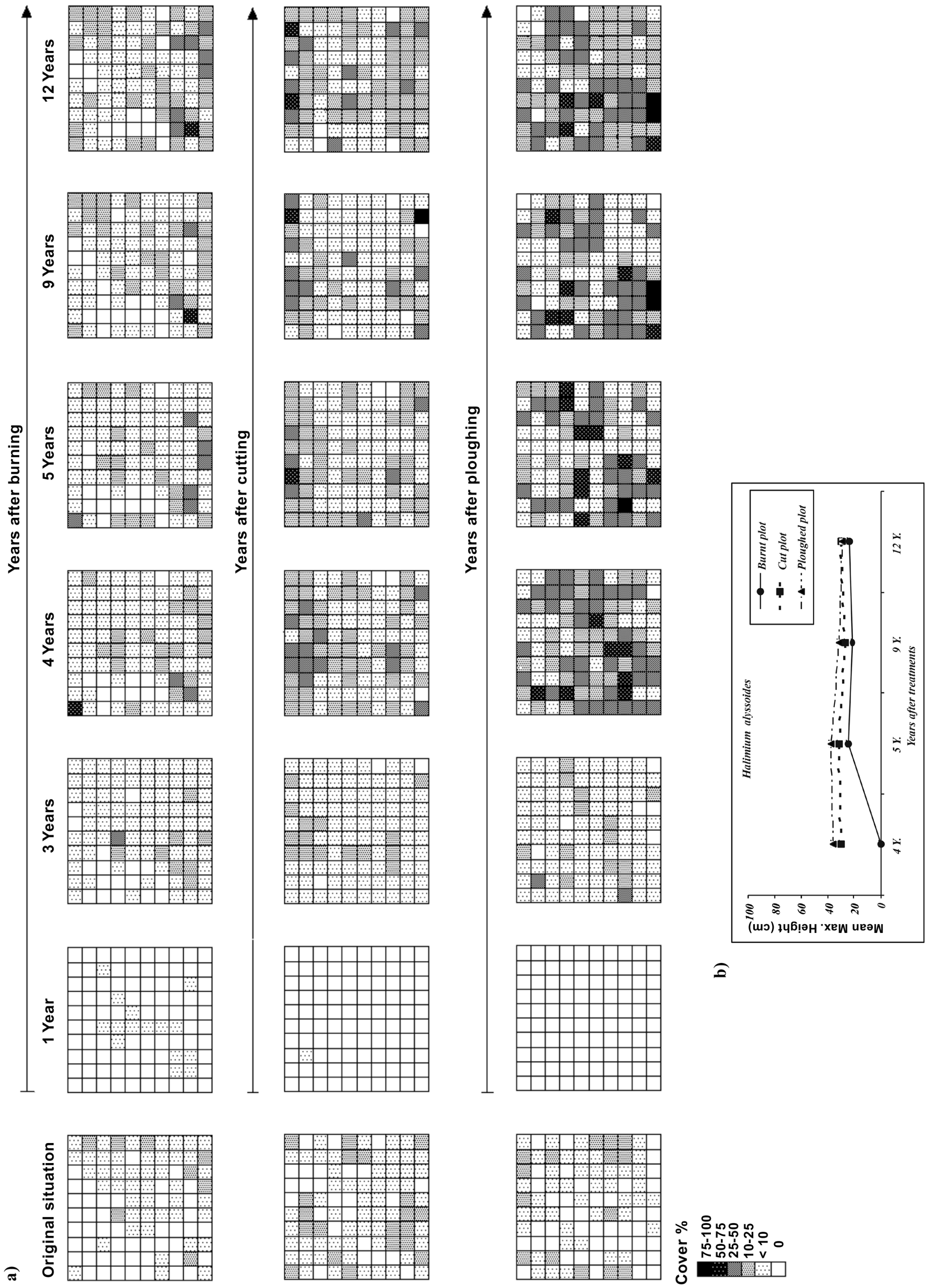

Figure 5. a) Spatial and temporal dynamic of *Halimium alyssoides* cover originally and after the experimental treatments. b) Mean (and standard error) of maximum heights after treatments); 0 = original situation; 1, 3, 4, 5, 9, 12 = years after treatments.

The other species of Cistaceae, *Halimium umbellatum*, had low abundance in the original state (0.2% cover) (Figure 6). This species uses germination as a regeneration mechanism. The perturbations appear to have eliminated competition from species of greater size and this is reflected by higher values for both spatial occupancy and cover compared with the original state. This favourable effect can be seen until the fourth year, when species of greater size and cover begin to dominate, providing strong competition, resulting in a decrease in *H. umbellatum*.

Chamaespartium tridentatum is another of the woody species that had very low cover (< 1%) values in the original state (Figure 6). Both spatial occupancy and cover are favoured after the three perturbations, which eliminate competition with *E. australis*. It recovers very slowly by resprouting after burning and cutting, and by germination after ploughing. The increase in cover does not show any significant differences between plots (Table 1). The favourable effect of burning is shown by the presence of the species in this plot from the first year.

Quercus pyrenaica is considered to be the dominant species in the climax arboreal communities of this area. Recovery after burning is relatively fast because its capacity to resprout increased its cover values from the fourth year. The effect of competition with *E. australis* is evident from the ninth year. There are no significant differences between the cut and ploughed plots due to the very low representation throughout the period.

Behaviour of the herbaceous species

After all the treatments, changes in the cover of the herbaceous species, considered as a whole, show an inverse relationship with woody species (Figure 7), such that values increase until the third year and then begin to decrease. After ploughing, herbaceous recovery is much greater than after the other two treatments and the effects of competition become evident one year later than in the cut or burnt plots. Cutting produces fewer variations in herbaceous cover values in time.

Changes in woody species cover in each plot

In the burned plot (Figure 8), *Erica australis* and *Arctostaphylos uva-ursi* recover most rapidly, reaching or exceeding the original cover values. *Halimium alyssoides* increases its cover values until it attains its original status (4th year after burning). Two of the typical germinating species, *Calluna vulgaris* and *Erica umbellata*, also begin to increase their cover values in the fourth year after burning. The rest of the woody species are of very little importance in the overall changes in the burnt plot. Similar changes occur in the cut plot (Figure 8), except that *A. uva-ursi* does not resprout and *E. umbellata* is more important. In the ploughed plot (Figure 8), recovery starts more slowly but the situation is similar to the original state from the fifth year in the case of the dominant species, *Erica australis*. The cover values of the typical germinating species, *Halimium alyssoides* and *Calluna vulgaris*, are higher in this plot than after burning and cutting.

Structural analysis in each plot

Temporal changes in spatial heterogeneity (Figure 9) show that the three plots have relatively high values immediately after the perturbations, due to only some woody species recover, and those with very different cover values. Heterogeneity values are highest in the ploughed plot. However, from the fourth year heterogeneity decreases considerably in all cases, since changes in cover and species appearance stabilise. In the last year of the study, the heterogeneity values are slightly lower the original state in each of the three plots.

Discussion

Mediterranean shrubs are mainly associated with nutrient-poor, acidic soils and with relatively mild climatic conditions (Ojeda 2001) are widespread in the northwest of the Iberian Peninsula (Rivas Martínez 1979; Luis-Calabuig et al. 2000). These communities occur in areas, which are frequently subjected to perturbations, especially fires associated with human activity (Vazquez and Moreno 1998). Disturbance by clearing and ploughing are also frequent (Calvo et al. 1998a). As a result, most woody species present in these communities are capable of regenerating easily and are highly resilient to disturbance, as in the case of the Californian chaparral after fires (Keeley 1992).

In these shrub communities resprouting and germinating species clearly coexist and it is common to find species, which can use both mechanisms. The use of one mechanism or another determines the speed at which they are capable of returning to the pre-distur-

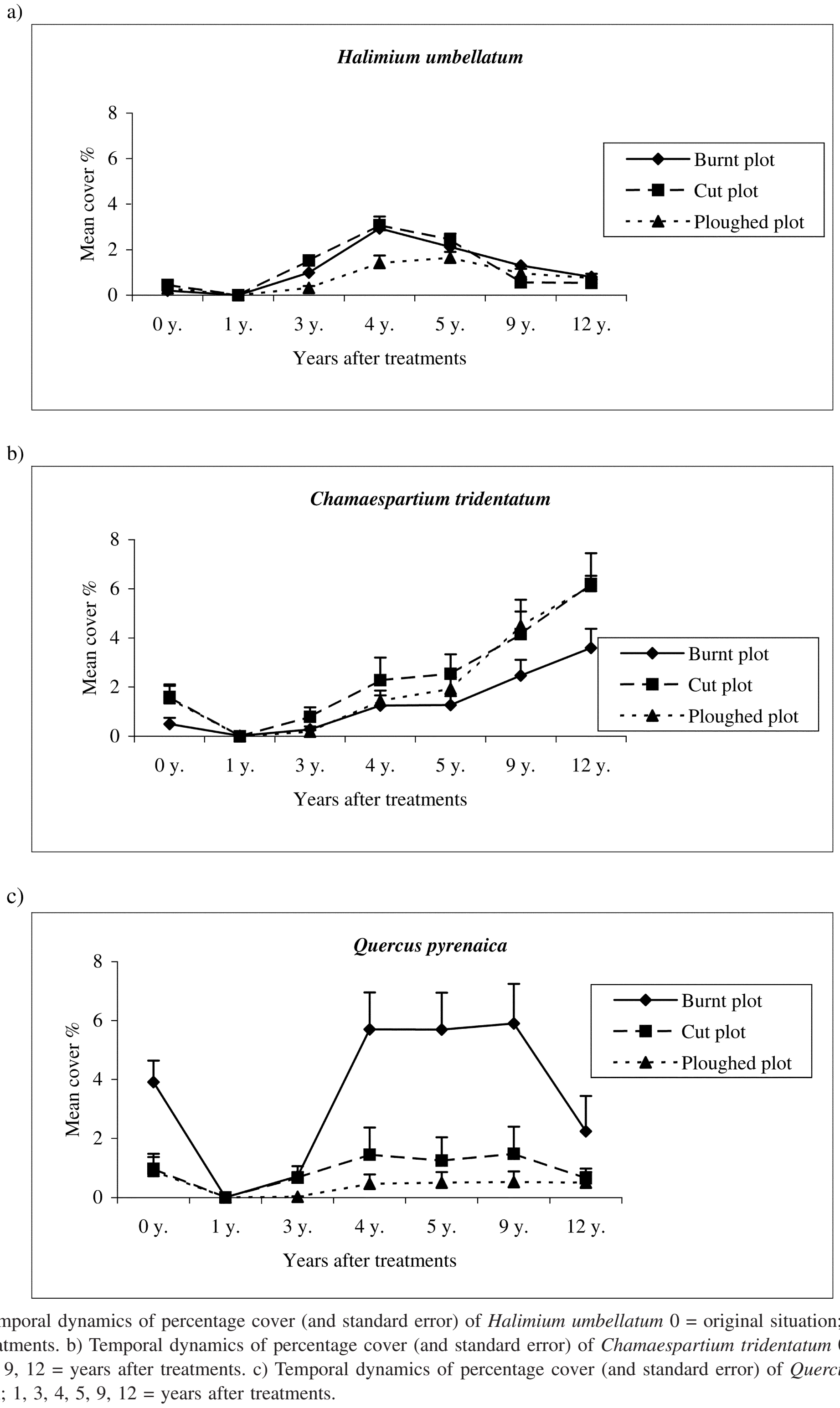

Figure 6. a) Temporal dynamics of percentage cover (and standard error) of *Halimium umbellatum* 0 = original situation; 1, 3, 4, 5, 9, 12 = years after treatments. b) Temporal dynamics of percentage cover (and standard error) of *Chamaespartium tridentatum* 0 = original situation; 1, 3, 4, 5, 9, 12 = years after treatments. c) Temporal dynamics of percentage cover (and standard error) of *Quercus pyrenaica* 0 = original situation; 1, 3, 4, 5, 9, 12 = years after treatments.

bance state. When seeds are the main source, the process is often slower than when vegetative regeneration takes place (Forgeard 1990). It is also obvious that vegetation structure in autosuccession processes

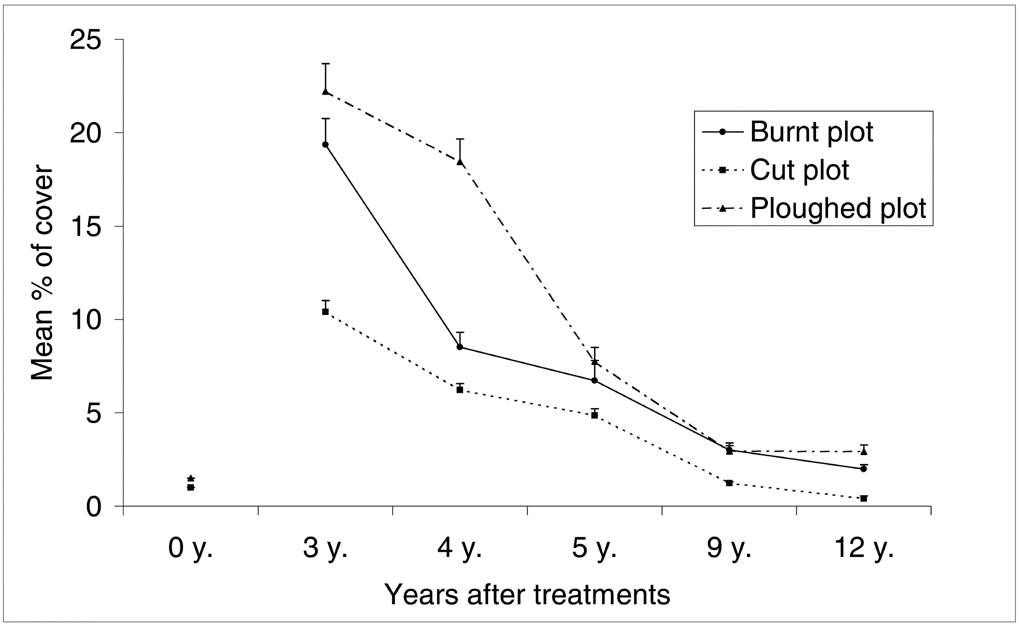

Figure 7. Percentage cover (and standard error) of herbaceous species originally and after the experimental treatments.

will be more similar to the original when the recovery mechanism is vegetative resprouting. According to Keeley and Zedler (1978); Trabaud (1980, 1991); Malanson (1985) germination is favoured by perturbations with a long return interval, i.e. intervals of 40 years in shrubs on the Californian coast after fires, whilst vegetative resprouting is favoured by shorter intervals of 20 years. Mixed communities with both strategies coexisting appear at intermediate perturbation intervals. The return times that favour one strategy or another may differ in other types of shrubland (Menges and Kohfeldt 1995). In the shrubland studied, the disturbance frequency is relatively high, recurring approximately every 15 years, and this can influence the relative abundance of species with both regeneration mechanisms.

Resprouters survive perturbations such as fire and cutting, since, although their photosynthetic biomass is destroyed, they are still able to resprout from latent buds using stored reserves, which feed the shoot or growth of the buds after perturbations (Pate et al. 1990; Iwasa and Kubo 1997; Canadell and López-Soria 1998).

The buds of *Erica australis*, a resprouting species typical of these communities, are found in the lignotuber (Canadell and López-Soria 1998). The presence of a lignotuber gives these ecosystems a great advantage in their response to burning and cutting (Moreno et al. 1999). The presence of this type of storage mechanism is probably associated with recurring perturbations that eliminate all the aboveground biomass. The potential capacity for storing starch is much greater in *Erica* genus species than in other resprouters (Bell and Ojeda 1999). This starch is degraded and freed to supply the sprout (Canadell and López-Soria 1998). However, in addition to resprouting vigorously, it is also capable of germinating from the seeds stored in the soil seed bank. Recovery in the ploughed plot occurs only via this mechanism. Several authors have studied the germination capacity of various Ericaceae after perturbations such as fire (Calvo 1993; Ojeda et al. 1996; Obeso and Vera 1996; Calvo et al. 1998a, 1998b). This results in open areas with unusually high light levels and adds nutrients to the soil. In the ploughed plot, in addition to the existence of open spaces, the possible scarifying effect of ploughing favours germination. The main difference in the use of germination in comparison with resprouting in these plots is that the first mechanism requires a minimum of two years before it begins to appear. It is possible that the great modification in the structural characteristics of the soil, caused by the ploughing treatment, also influences this delay. The species' ability to resprout and germinate in these areas may be due to the frequent recurrence of perturbations. Twelve years after recovery, independent of the perturbation to which it was subjected, *Erica australis* shows symptoms of ageing and new shoots begin to

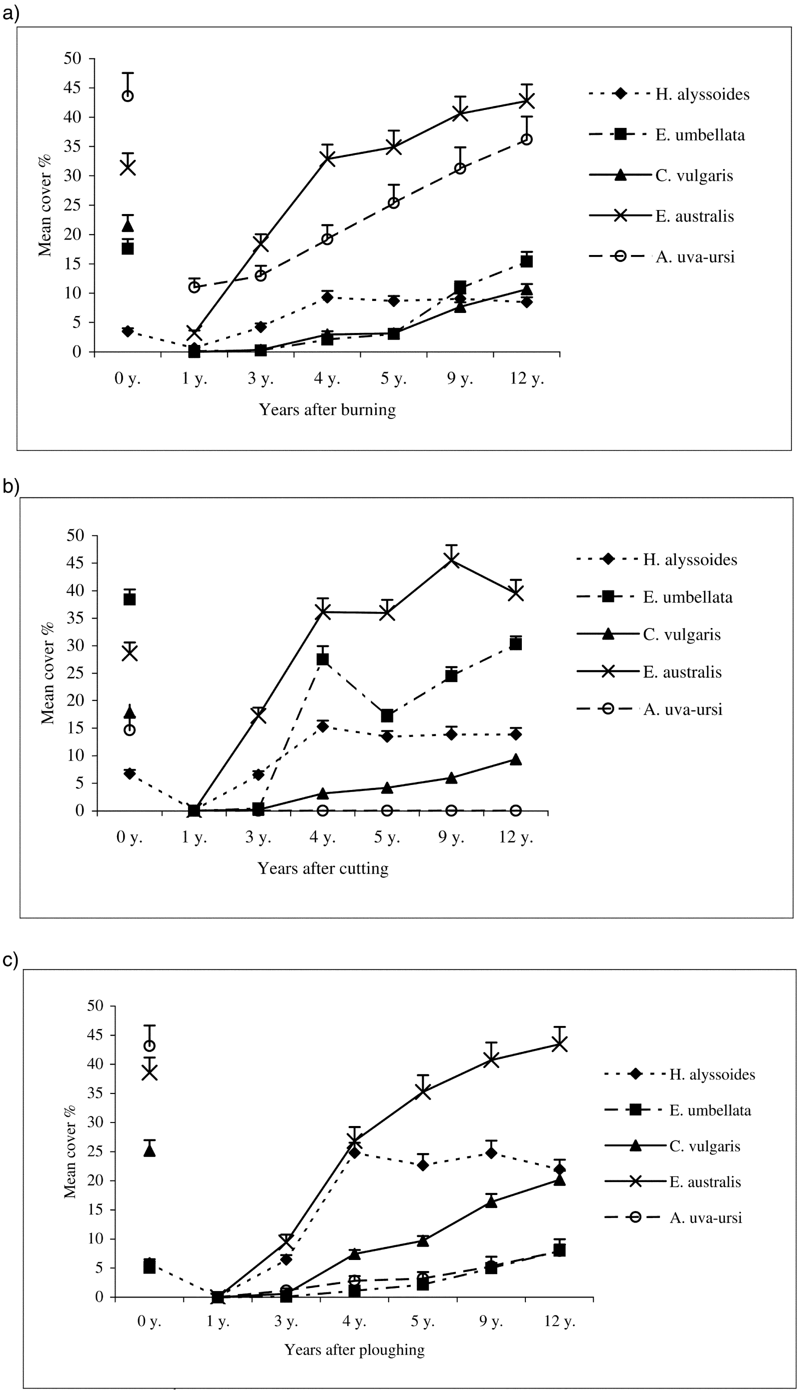

Figure 8. a) Percentage cover (and standard error) of most important woody species originally and after the experimental burning; b) Percentage cover (and standard error) of most important woody species originally and after the experimental cutting, c) Percentage cover (and standard error) of most important woody species originally and after the experimental ploughing.

appear in the central part of the lignotuber (Personal observation).

Quercus pyrenaica also typically resprouts from the shoots on the rhizome or the stem of the subterranean roots (Calvo et al. 1991; Luis-Calabuig et al. 2000). The resprouting capacity of this species is shared by others of the genus *Quercus*, distributed over the Mediterranean area, including *Quercus coc-*

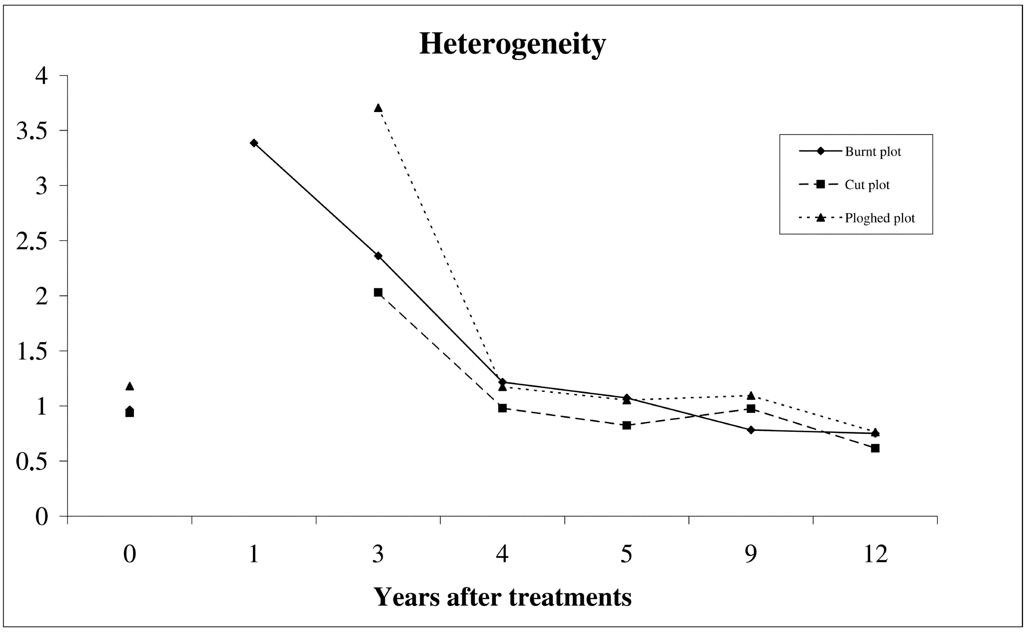

Figure 9. Temporal dynamics of heterogeneity, originally and after the experimental treatments.

cifera (Trabaud 1980; Lloret and Vilá 1997), *Quercus ilex* (Pausas and Vallejo 1999), *Quercus calliprinos* (Alon and Kadmon 1996; Kadmon and Harari-Kremer 1999). However, germination capacity in the field is low. Field observations indicate that recovery is very good, where this species was originally present around the plots: seedlings from germination appear 5–9 years after cutting and ploughing. In other areas, where the oaks are not nearby, they require 15 years to colonise the shrub area. In contrast recovery by vegetative resprouting is more rapid.

In many woody species, resprouting typically occurs from the bank of shoots situated in the root (Casal 1987; Tárrega et al. 1992), as is the case for *Chamaespartium tridentatum*. This species undergoes similar changes to those described by many authors for other resprouting species (Le Maitre and Midgley 1992): in a process of progressive ageing of the aerial biomass only the outer edge of each branch remaining green. Therefore recurring perturbations favour rejuvenation. Herbivores in many areas consume small buds from the regenerating plant. In addition to resprouting, successful germination also occurs after burning and ploughing.

Arctostaphylos uva-ursi has evergreen coriaceous leaves, which protect it from fire, and it thus sprouts easily from the first year, regaining its original cover. However, in this experiment, once all its aboveground biomass was removed by cutting, it could not recover. This does not agree with Del Barrio et al. (1999), who found good recovery after cutting. This is probably due to the fact that, on creating a 2-m wide safety margin around this area, entry from outside is difficult. However, it recovered rapidly from burning. After ploughing there is low cover, indicating that it is able to germinate, like other species of *Arctostaphylos* in the Californian chaparral (Keeley and Parker 1990)

Erica umbellata and *Calluna vulgaris* are also typical of Mediterranean shrubs. According to several authors, they are capable of resprouting (Naveh 1975; Berdowski 1993) but in this study they only reappear by germination. In the case of *Calluna vulgaris*, this has previously been described as the only recovery method after experimental fires in the north of Portugal (Rego et al. 1991), and in communities in SW Spain (García Novo 1977). One possible explanation for the exclusive use of germination is that given by Gimingham (1960) in studies of *Calluna* communities in Scotland: *Calluna vulgaris* only resprouts when in mature stages and not when it has reached senescent ones. A similar process has been observed in *Calluna* communities in high areas of the Cantabrian mountain range, where populations more than 30 years old do not resprout after cutting (Personal observation). Resprouting capacity also declines with plant age in other species of Californian chaparral shrub (Hobbs and Mooney 1985). It therefore seems that the different mechanisms used by this species are not related to fire intensity, as questioned by Pausas (1999), since it uses germination in this area after any perturbation; it is possibly related to aspects of plant age. In general the recovery of both species is slower than in resprouters during the first few years of succession, but after the 4th or 5th year post-perturbation both show very considerable increases in cover. This means that they are not pioneering species as far as colonisation is concerned but they will not be replaced by competition with the dominant species, since *Erica australis* dominates the community from the moment its cover increases.

Two species that can be considered as colonisers are *Halimium alyssoides* and *Halimium umbellatum*. Changes in cover values over time show that both species take advantage of the empty spaces to germinate and increase cover as well as the space they occupy. However, when the dominant species (mainly *Erica australis*) reaches cover values similar to the original (4th year), that is, close to 60%, *H. alyssoides* stops spreading and *H. umbellatum* cover starts to decrease. In the ploughed plot, where the dominant species needs longer to attain high cover, *H. alyssoides* retains higher cover values for longer. The beneficial effects of thermal shock on the seeds of these species have been widely studied (Thanos et al. 1992). However, in this study, cutting and ploughing also had a significant positive effect on the germination of these species. Therefore perturbations that create open spaces favour both species.

It seems clear that the dominant species in these communities, as measured by cover, is *E. australis* and, because of its regeneration speed and method, it influences regeneration patterns in the other woody species and in the whole community in general. Interspecies competition occurs between all species (Fuentes and Gutiérrez 1981) during the first regeneration stages. Therefore, there is a big increase in the opportunist woody and herbaceous species, *H. umbellatum* and *H. alyssoides*, during the first three years. From the fourth year after cutting and burning, and from the fifth year after ploughing, the community stops showing significant changes in the cover values and the importance of some species, like *H. umbellatum*, *Q. pyrenaica* and herbaceous taxa, decreases.

Analysis of the changes in heterogeneity values shows that the small differences between plots of these shrub communities tend to decrease 12 years after the perturbations and that heterogeneity is lower than the original situation; that is, the shrub community tends to become more homogeneous.

These types of communities, subjected to very frequent burning, cutting and ploughing, the possibility of replacement by a different vegetation type is very low. The strong sprouting capacity of the component species confers a high degree of resilience in the spatial structure of shrub communities (dominated by Ericaceous) during recovering from perturbations in the short term (Clemente et al. 1996; Calvo et al. 1998a). This is also supported by long term studies carried out by Kadmon and Harari-Kremer (1999) in maquis communities. This high resilience, in the sense of recovery capacity, is not only attributed to the strong resprouting potential of these species but also to their germination capacity, as can be seen in the ploughed plot. In other types of Mediterranean community, such as those dominated by *Cistus ladanifer* and *Cistus laurifolius*, which are obligate seeders, germination also confers high resilience, as shown in the studies of Tárrega et al. (1995, 1997).

Differences in cover values and spatial occupancy during the first years of succession tend to be eliminated after twelve years of perturbations and most of the species tend to recover their initial cover values. The vegetation in all these treatments probably converges after fifteen- sixteen years and becomes indistinguishable. The fast recovery of dominant species, *Erica australis*, after burning, cutting and ploughing decreases structural differences between treatments by increasing spatial homogeneity.

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